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Geoecohydrological mechanisms in semiarid tropical forests: spatial and temporal use of water of two coexisting forest tree species

Tesis que presenta

Ulises Rodríguez Robles

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Dedicatorias

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Resumen

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Las regiones semiáridas ya enfrentan un fuerte estrés hídrico y es probable que aumente, ya que los cambios en los patrones de lluvia, asociados al cambio climático, son cada vez más variables. El Centro-Norte de México representa una de las regiones más expuestas a sequía para los bosques semiáridos, a lo largo del gradiente de precipitación estacional que va de Norte-Sur, siendo un excelente sistema para estudiar las interacciones ecohidrológicas, incluyendo; las relaciones hídricas de la planta, la dinámica de la humedad del suelo y los patrones de distribución de raíces. Llevamos a cabo un estudio para identificar los mecanismos y estrategias que permiten la coexistencia de las especies de bosques semiáridos mixtos en temporada de sequía. Este estudio se realizó en tres diferentes tipos de rodales, que incluyen: rodales monoespecíficos de pino, rodales moespecíficos de encino y rodales mixtos de pino-encino. Con la utilización de herramientas geofísicas, identificamos que el bosque se encuentra establecido sobre un suelo rocoso poco profundo de material volcánico impermeable, con un alto grado de fracturamiento y fisuras, y una muy delgada capa de suelo (15 – 30 cm). Con los valores de ^{18}O y ^{2}H de las lluvias provenientes de las cuencas oceánicas del Pacífico y Atlántico, y manantiales, trazamos nuestra Línea Meteórica Local de Agua, la cual se comparó con las 2,800 muestras de abundancias naturales de agua en el xilema. Confirmamos que las especies utilizan diferentes fuentes de agua durante todo el año, lo que nos ha permitido identificar nichos y rasgos funcionales de las especies. *Quercus potosina* utiliza el agua de la roca volcánica fracturada, particularmente durante la estación seca, moviéndola a través del perfil del sustrato, cuando está en asociación con *Pinus cembroides*, evitando así la exclusión competitiva. En contraste, *P. cembroides*, no muestra adaptaciones para adquirir agua de la roca, sin embargo, utiliza el agua levantada por los encinos (levantamiento hidráulico). Durante la estación seca, *Q. potosina*, puede depender únicamente del agua almacenada en su tronco proveniente de eventos pasados, dejando cierta proporción de humedad del suelo disponible a los pinos. Hemos demostrado que los suelos rocosos también generan un alto grado de variabilidad en el contenido de agua y grandes desplazamientos en el estado fisiológico de los árboles. La interacción positiva observada entre el encino y pino, arroja dudas sobre la capacidad a largo plazo para tener éxito bajo condiciones geohidrometeorológicas cada vez más limitadas, y proporcionamos evidencia de la importancia de Q. potosina en el mantenimiento de la estructura y funcionamiento del ecosistema en este bioma con deficiencias de agua. Estos resultados modifican significativamente el paradigma actual del uso de agua por las plantas, donde el agua que ocurre en las rocas no se considera un recurso potencial.

Palabras clave: *Pinus cembroides*, *Quercus potosina*, rasgos funcionales, estrategias de coexistencia, nicho, redistribución hidráulica, pulsos de agua, roca fracturada, suelo poco profundos, isotopos estables, oxigeno-18, deuterio, radar de penetración terrestre, tomografías de resistividad eléctrica.

Abstract

Geoecohydrological mechanisms in semiarid tropical forests: spatial and temporal use of water of two coexisting forest tree species

Semiarid regions already facing strong water stress are likely to be exposed to higher levels as rainfall patterns change and are becoming more variable under climate change. Central North Mexico represents one of the most drought prone regions for semiarid forest along the north–south seasonal precipitation gradient, making it an excellent location to study ecohydrological interactions, including; plant–water relations, soil moisture dynamics and root distribution patterns. We conducted a study to identify the type of mechanisms and strategies permitting species coexistence in a mixed forest during the drought season. This study was carried in three different stand types including: monospecific *P. cembroides* stands; monospecific *Q. potosina* stands and mixed oak-pine stands. Using geophysical tools, we identified that the forest is colonizing shallow rocky soils over impermeable volcanic material with high fracturing and fissuring and an extremely thin layer of soil (15 - 30 cm). With the ^{18}O and ^{2}H values of all recorded rainfall events either coming from the Pacific or Atlantic ocean and of water from springs, we generated our Local Meteoric Water Line and analyzing the natural abundance of water isotopes of 2,800 samples of water in pine and oak xylem confirmed that trees used different water sources throughout the year. This confirmed that trees used different water sources throughout the year, permitting us to identify temporal and spatial niches and functional traits of species. *Quercus potosina* used fractured volcanic rock water, particularly during drought, moving through the substrate profile when in association with *Pinus cembroides*, thus avoiding competitive exclusion. In contrast *P. cembroides* showed no adaptations to acquire water rock however it took advantage of water uplifted by oak (hydraulic lift). During the dry season, *Q. potosina* rely only on water stored in their trunks from past rain events leaving available the soil moisture for pines. Here we demonstrated that rocky soils also generate a high degree of variability in water content and large offsets in the physiological status of trees. The observed positive interaction between oak and pine shed doubts on the long-term capacity of *P. cembroides* to succeed in monocultures under increasingly limiting geohydrometeorological conditions, and provided evidence of the importance of *Q. potosina* to maintain ecosystem structure and function in this water-limited biome. These results significantly modify the current paradigm of water use by trees, where water held in the rocks is not regarded as a potential water source.

Key words: *Pinus cembroides*, *Quercus potosina*, functional traits, coexistence strategies, niche, hydraulic redistribution, water pulse, fractured rocky, shallow soil, stable isotope, oxygen-18, deuterium, ground penetrating radar, electrical resistivity tomography.

GENERAL INTRODUCTION

Plants are able to survive and function under extremely variable environmental conditions, including dramatic changes in soil water availability, high atmospheric evaporative demand and the rocky shallow soils in which they are supported. This could not be achieved without powerful regulatory mechanisms allowing plants to modulate water transport in response to these conditions (Schwinning et al. 2005). Water use strategies of plants and water transport in the soil–plant–atmosphere continuum are critical to understand ecosystem functioning in arid and semiarid habitats where plant productivity is often limited by soil moisture (Abrams 1990; Burgess &Bleby 2006). They are intrinsically related to precipitation variability. Indeed, because precipitation in drylands is highly dependent on forest evapotranspiration, deforestation and land cover changes will likely reduce precipitation, and thus, increase the risk of regional droughts (McDowell et al. 2008). With global climate change, drought occurrences may become more common in the future (Sardans&Penuelas 2007; Klein et al. 2011).

For semiarid climate regions with warm springs, rain regime distributed mainly in summer but with slight winter rains, are forecasted by the Intergovernmental Panel on Climate Change (IPCC), to display substantial warming in winter and a longer dry period. Thus, under the assumption that a climate scenario with increased the length of the dry season (winter/spring), would exacerbate water deficits and subsequently plant mortality. In spite that winter rains are proportionately small (around 5% of total rain), this rain provides water pulses allowing vegetation to withstand the prolonged dry season (Schwinning& Sala 2004; Schwinning et al. 2005). Variability in water availability, directly affects the characteristics of several processes; gas exchange, xylem hydraulic conductivity, productivity, interaction between species and community structural characteristics (Duff et al. 1997; Wayne & Van Auken 2002). Consequently, semiarid woody species do not necessarily rely on water uptake from a single soil water deposit, optimizing the use of water sources, developing different strategies for their acquisition and regulation of traits directly related to the form and extent of the root system (Schenk 2008) as well those associated to the leaves (Parent et al. 2010), and mycorrhizal (Querejeta et al. 2003), specialized storage tissues (Gottwald 1972), deep root systems (Dawson & Pate 1996), hydraulic redistribution (hydraulic lift, Prieto et el.2012).

Hydraulic redistribution has been described in a wide variety of ecosystems, from Mediterranean and semiarid savannahs (Nadezhdina et al. 2009) to tropical forests (Meinzer et al. 2004), and involves a wide range of life forms, from woody trees and shrubs (Prieto et al. 2010) to herbaceous species and crops with shallow roots (Espeleta et al. 2004). Deep roots may connect deep soil layers storing moisture, acting as conduits, allowing the passive movement of water following vertical water potential gradients in the soil. This passive movement of water usually takes place between deep, wet soil layers and upper, dry soil layers (hydraulic lift, HL). At the ecosystem scale, HL can modify seasonal microclimate by increasing transpiration during dry periods (Pinto et al. 2014). At the community scale, hydraulic redistribution may have positive effects for both the plant lifting water and its neighbors (Smith et al. 1999)

It is recognized that forest species with deep root system are able of exploiting groundwater sources during drought periods. This adaptation also enables the extraction of water from a large soil volume facilitating spatio-temporal niche partitioning among species (Silvertown et al. 2015). In semiarid environments, tree rooting depth and distribution can differ substantially depending on site characteristics (Schwinning 2010). For instance, during wet spring months, it is the shallow superficial roots that uptake water, while during dry summers, it is the deep roots, penetrating cracks of relatively unweathered bedrock, that are in charge of tree water supply. It is generally assumed that shallow soils over solid bedrock restrict vertical root growth beyond the soil matrix, as it impedes downward soil water and root penetration (Jackson et al. 1996; Nadezhdina et al. 2008; Poot et al. 2012). On the other hand, water stored in or under rock layers is relatively safe from evaporative loss, thus can await slow extraction rates by root systems (Brunet et al. 2010).

What adaptations are needed so that roots can dispose of water stored in rocks? Several lines of evidence suggest that plants require specific adaptations to grow well in shallow soils over bedrock (Nadezhdina et al. 2006). Thin and deformable fine roots may be required to effectively extract water from narrow fissures (Zwieniecki& Newton 1995). The ability to form mycorrhizal associations may be critical as well (Bornyasz et al., 2005). Successful establishment on a thin soil may also require a comparatively high investment into deep root growth to search the soil–rock interface to penetrate the bedrock (Poot&Lambers 2008) Rooting space within rocks is limited by the frequency of fissures that are wide enough to permit root growth. Wide fissures are usually filled with a mixture of coarse grains and organic materials with hydraulic properties similar to soil, supporting high root densities (Poot et al. 2012; Ogretmen&Seren 2014). However, the possibility that plants could use water from fractures in impermeable rock remains unexplored.

Under circumstances where roots of a single plant experience steep water potential gradients between deep and shallow soil layers, water may be passively lifted by roots and thus temporarily increase soil water availability in the soil surface during dry periods (Querejeta et al. 2007). This mechanism may reduce the decoupling of plant and soil water potential until this alternative water source becomes depleted (Burgess &Bleby 2006). In the 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 with water from deep sources to 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.

Hence, I pose the following research questions: What short- and long-term adaptation mechanisms have two key forest tree species developed to survive and coexist in this semiarid forest ecosystem? 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. Empirical evidences in support of several theories related to plant coexistence (see Silvertown 2004), are ambiguous, since current techniques and methodologies have limited capacity to differentiate belowground niches and potential belowground foraging responses.

We studied mechanisms of coexistence between two species from the tropical semiarid forest in central México. Our study contributes to the understanding of plant coexistence in shallow soils on top of fractured rock. By applying multidisciplinary concepts, techniques and tools, including; ecophysiology, anatomy, stable isotope ecology, hydrogeology and geophysical exploration images (Ground Penetrating Radar, GPR and Electric Resistivity Tomography, ERT). We provide experimental evidences of niche segregation as well as root foraging and plant water adaptations allowing the survival and coexistence of these two forest species. Our approach permitted us to distinguish explicitly among distinct spatial and temporal niches. With the GPR we were able to characterize trait adaptations such as in root growth, diameter and distribution for each forest species growing in mixed stands. In addition, by using ERT techniques, we could examine the distribution of soil and rock water as well as its dynamics. By combining all these techniques and methods we gained invaluable information, which clearly demonstrates, how niches are spatially partitioned and how forest species are adapted to access water in particular niches and physiological adaptations to stand long-lasting droughts.

These questions were addressed in the four chapters of this thesis. **Chapter I** details a unique geoecohydrological mechanism that allows maintaining a tightly coupled hydrology between the shallow rocky soil and trees. The mechanism permits species coexistence in this mixed forest, where oak facilitates water access to pine in extreme dry periods. **Chapter II** addresses the geophysical image application, as tools for ecohydrological research in forest. Showing the potential to estimate root diameters and water reservoirs using GPR non-invasive mapping and ERT to characterize the weathered soil/rock interface, also reveals scale-field spatial information, these variables traditionally have been explored using coring and excavations methods. **Chapter III** exhibits how a niche is spatially partitioned and how forest species are adapted to access water in their particular niche. **Chapter IV** addresses the multidimensional niche and life-history strategies in species coexistence.

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CHAPTER

GEOECOHYDROLOGICAL MECHANISMS COUPLE SOIL AND LEAF WATER DYNAMICS AND FACILITATE SPECIES COEXISTENCE IN SHALLOW SOILS OF A TROPICAL SEMIARID MIXED FOREST

Abstract

- Trees growing on shallow rocky soils must have exceptional adaptations if 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 get dry due to 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 ca. 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.

Keywords: shallow soils, geoecohydrological mechanisms, weathered rocks, tropical semiarid forest, plant coexistence

1.1. Introduction

Semiarid forests in North America extend from Mediterranean California and South-Western United States (Linton et al., 1998) to central México, 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 in the transition from Northern to Southern latitudes (West et al., 2008). Mediterranean and Northern subtropical regions have wet winters and springs 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 (Gsw) in response to reductions in soil water potential (Ψ_s), while maintaining midday leaf water potential (Ψ_l) relatively constant. In Anisohydric plants, midday Ψ_l decreases in response to declining Ψs, however they maintain generally higher G_{sw} for a given Ψ_s than Isohydric plants (Barnes, 1986). These alternative mechanisms of controlling plant water relations have evolved in distinct habitat types, with Anisohydric species occupying the ecologically driest sites (McDowell et al., 2008). These mechanisms seem to have evolved 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).

Another characteristic of semiarid forest ecosystems relates 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 indicates that trees tend to be deeply rooted with average rooting depths of 7.9 m (± 1.7 m) compared to 2.2 m (± 0.1 m) observed in trees growing on deep soils (Schenk & Jackson, 2002; Schenk, 2008). Shallow soils hydrology depends on rain periods to get recharge providing water to the plants, while it remains decoupled from plant hydrology during dry periods (Schwinning, 2013). However, under circumstances of steep water potential gradients between deep and shallow soils experienced by roots of a single plant, 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). Thus, this may temporarily reduce the decoupling of plant and soil water potential until this alternative water source becomes depleted as well (Bleby et al., 2010). In the specific case, where the rocky substrate is of volcanic origin and deep rock fractures have been sealed by previous volcanic events (Orozco et al., 2002; Tristán et al., 2009), it appears unlikely that shallow soils (15 to 30 cm) could be resupplied with 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 does not seem conditioned for hydraulic lift mechanisms. We postulate that two fundamental ecohydrological processes are still unclear in plant-water relations on shallow soils; 1) 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 2) 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 dry season thereby reducing water demand and allowing evergreen trees temporal access to water (Tang & Ohsawa, 2002). Alternatively, spatial partitioning of soil resource 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 geo-hydro-meteorological conditions in tropical semiarid latitudes in Central-North Mexico limit the development of forest ecosystems seen elsewhere in semiarid regions around the world (Grunzweig et al., 2003). These limiting conditions include extremely shallow soils (<20 cm) on top of a shallow weathered fractured rock matrix (~70 cm below the surface) with impermeable bedrock underneath (Orozco et al., 2002; Tristán et al., 2009). Furthermore, low annual precipitation (~400 mm) with most rainfall (95% of total precipitation) occurring during summer, narrows temporal niches (Pérez et al., 2014), increasing probabilities that coexisting tree species compete very strongly for water. These forest ecosystems provide few spatio-temporal 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 coexistence and survival.

This study addresses two principal questions: 1) how will extreme geo-hydro-meteorological 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 2) Considering an extremely low spatial and temporal water availability what short and long-term adaptation mechanisms have two key forest species developed to survive and coexist?. Shallow rocky substrate (< 0.70 m, below the surface) together with negligible winter rains (< 5%) seem insufficient to contribute to large water storage; therefore, limiting potential advantages for Anisohydric strategies (Ryan, 2011). Also, long lasting droughts (6 to 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 (H_1) that both deciduous *Quercus potosina* and evergreen *Pinus cembroides* tree species will not display strict Anisohydric or Isohydric mechanisms, but rather exhibit adaptations allowing them to survive with extremely low Ψ_l during several months of drought. Considering predominantly shallow soils and long intense droughts, we hypothesized (H_2) 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, it is expected (H_3) that Q*. potosina* and *P. cembroides* should display niche overlap and therefore strongly compete for soil water with the better competitor exhibiting higher G_{sw} and Ψ_l and lower *WUE* during periods of soil water depletion.

1.2. Materials and Methods

1.2.1. 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, Fig. S1.1) at the Southern most extent of the Chihuahuan 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 according to site climate records). For the last 40 years, average annual rainfall ranges from 380 to 640 mm (avg. 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 form both 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 mountainous region is abrupt and irregular, thus representing a “complex terrain”. The landscape is characterized by slopes steeper than 30° and elevation ranging between 1900 and 2870 m.a.s.l.. 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). Average depth of the organic soil horizon ranges from 10 to 20cm; it accumulates into crevices and rock pockets (Pérez et al., 2014), on top of a highly fragmented weathered rock matrix that reaches maximum 70 cm deep.

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 twenty experimental plots in mid-slope position on steep North (n=10) and South (n=10) exposed slopes, which allowed us to examine differences in drought intensity. On each plot, we selected one pine and one oak tree with similar size characteristics within and among plots (n=20 per tree species). The two target trees within each plot had a minimum distance of two meters. Monitoring of soil and leaf physiological variables lasted from September 2010 until December 2011. Soil depth was determined by coring from the soil surface to the rock matrix. Coring was carried out twice on each plot in both expositions (n = 20).

1.2.2. Study species

Pinus cembroides is a small tree (avg. 4.2 m) with evergreen needles, while *Quercus potosina* is a short statured (3 m) deciduous broadleaf tree. During the driest months, broadleaf oak usually sheds all its leaves (March to April, Perez et al., 2009), while evergreen pine sheds the oldest (3-4 years old) needle cohort (Zavala & García, 1991). *Quercus potosina* produces more litter with higher quality than pine (2,820 ± 307 vs.1,360 ± 128 kg/ha/yr, 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 reduces lateral runoff seven-fold and increases water-holding capacity by 16% compared to pine stands (Pérez et al., 2014). Forest canopy characteristics also greatly influence rainfall re-distribution through throughfall and stemflow (Pérez et al., 2014). Little is known on root morphology and distribution of these two species, however, in general *Quercus* species exhibit dimorphic roots, while Pinus species spread superficial roots horizontally (Kutschera & Lichtenegger, 2002).

1.2.3. Water potential and gas exchange

At biweekly intervals from October 2010 to December 2011, we measured midday soil and leaf water potential (Ψ_s and Ψ_l, respectively) from 11 to 13 hrs. We used psychrometric techniques and a dewpoint microvoltimeter HR-33 (Wescor Inc. USA) to determine soil (TSP-55, Wescor Inc. USA) and leaf water potential (C-52, Wescor Inc. USA). To determine Ψ_l we harvested 3-4 leaf discs from healthy mature leaves exposed to sunlight, allowing 20 minutes for stabilization within C-52 chambers. For soils, we inserted one soil psychrometer per tree at nearly 12 cm deep within 100 cm from the tree trunk.

Leaf gas exchange was measured at biweekly intervals to obtain G_{sw} (mol H_2O m^{-2} s^{-1}) and *WUE* (µmol CO2 (photosynthetic assimilation; *A*) $mmol^{-1}$ H_2O (transpiration; *E*); A/E) using a portable photosynthesis system LI-6400XT (LI-COR, Inc., 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 air concentration in the chamber was set to nine CO_2 concentrations to build a photosynthesis response curve (800, 0, 100, 200, 300, 400, 500, 600, 700, 900 µmol mol^{-1}, lasting for 3 minutes each level). Leaf temperature and air relative humidity were maintained within 25 ± 2 °C and 30% relative humidity (RH), respectively. For each gas exchange measurement, we introduced about seven mature oak leaves or 20-25 pine needles (Brooks et al., 2002). Measurements occurred between 11:00 AM and 16:00 PM 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 and their leaf areas determined (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 trees within four plots that were rotated each time to include eventually 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 the percentage of canopy cover in trees a digital photograph was monthly taken from the bottom of each plot; subsequently they were analyzed with Gap Light Analyzer software v.2.0 (Frazer et al., 1999).

1.2.4. Data analysis

To compare ecophysiological water relation variables, we used a multifactorial repeated measures analysis of variance (ANOVA). The mixed model included as classification factors, species that included 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 soil water potential (Ψ_s, MPa), leaf water potential (Ψ_l, MPa), instantaneous water use efficiency (WUE, µmol CO2 $mmol^{-1}$ H_2O) and stomatal conductance (G_{sw}, mol H2O 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 Ψ_l and Ψ_s, between WUE and both Gsw and Ψ_l, and between canopy cover and Ψ_s. Prior to statistical analyses, response variables were examined for normality using Shapiro-Wilk's 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 2002-2003) using a mixed model (PROC MIXED) for the repeated measures analysis and a generalized linear model (PROC GLM) for the univariate analysis.

1.3. Results

1.3.1. 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). The study year exhibited an extreme drought starting in October 2010 and lasting until May 2011 (4.6 mm during 9-months) followed by a period of rather low monsoon precipitation from June to September 2011. This is considered the driest period recorded in the last 70 years, when climatological data have been systematically recorded (Fig. S2).

1.3.2. 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 S1.1; Fig. 1.1).

Observed variations in Ψ_s explained changes in Ψ_l, although no differences between slopes (a) were detected when contrasting species or aspect ($P > 0.05$, Fig. 1.1). Depending on aspect, soil and plant Ψ exhibited different ranges; with South exposed forest reaching the most negative Ψ. Soil depth apparently acted as an additional control for soil and plant Ψ and differed significantly between aspects (Fig.1.1 inset, $P < 0.0001$). North facing forest with overall deeper soils exhibited higher leaf and soil water potentials.

Monitoring of leaf and soil Ψ started at the end of the 2010 rainy season (October, Fig. 1.2.). To help interpreting plant responses to soil water availability, Ψ_l and Ψ_s time series were divided into three ecohydrological periods: two dry (depletion and recovery) and one wet (wet season) periods. 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 Ψ (October – December 2010 and 2011). The recovery period started once leaf and soil Ψ reached its lowest 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 Ψ had fully recovered (June – September 2011). Statistical analyses were carried out considering the whole dry period (including both depletion and recovery periods).

Differences in soil and leaf Ψ in the course of the whole dry and wet periods depended on aspect (aspect x date, $P < 0.0001$ for all cases, Table S1.2) and species (species x date, $P<0.0001$ for all cases, Table S1.2). Highly variable soil and leaf Ψ were observed during the whole dry period (including both depletion and recovery periods). Overall, South exposed stands reached the lowest soil and leaf Ψ (Ψ_s for South pine = -5.3 ± 0.089 MPa, Ψ_l for South oak = -6.00 ± 0.090 MPa, Figs. 1.1 and 1.2) in December 2010, with Ψ differences of around 2 MPa ($P < 0.001$) compared to North exposed stands. Beginning in January 2011 (recovery period), Ψ_s began to rise steadily, however at a faster rate for South oak compared to North oak ($P < 0.01$, Fig. 1.2b). At the end of the 2011 rainy season (September 2011), Ψ_s returned to almost initial values of soil field capacity. During the wet season, Ψ_l differed significantly between species only in July in both aspects.

During the second depletion period, in North exposed stands, pine displayed significantly higher Ψ_l than oak (P < 0.01, Fig. 1.2a) in October and December 2011. Soil water potentials associated with trees of both species, started diverging significantly beginning December 2010 with maximum differences observed in February 2011 (recovery period, Fig. 1.2b), with Ψ_s nearly ~1 MPa more negative in pine than in oak in both aspects (P < 0.05). For the depletion period of 2011, the largest difference in Ψ_s was recorded also in December with 0.47 MPa more negative for South exposed oak than for pine.

As leaf senescence progressed between January and April 2011, oak trees adjusted Ψ_l in the remaining leaf area (Fig. 1.2 and 1.3), depending on season and aspect. Thus, from February to April (recovery period), Ψ_l was almost constant in North exposed trees, while an increase in Ψ_l was noted for trees in South aspect (Fig. S1.3a, North a = -0.006 ± 0.002, P < 0.05; South a = -0.02 ± 0.025, P<0.01) as leaves started shedding. Another trend is observed for the second depletion period as we noticed a decline in Ψ_l that concurred with an important loss of canopy cover (Figs. 1.2, 1.3).

1.3.2. Seasonal variation of leaf gas exchange

Tree species, aspect and season influenced G_{sw} differently for the whole dry and wet seasons (aspect x species x date, P < 0.0001 and P < 0.059, respectively; Table S1.3). During the recovery period, G_{sw} increased with increasing drought (Fig. 4a), with average maximum G_{sw} recorded in April (0.28 ± 0.02 mol H_2O m^{-2} s^{-1}). For the recovery period, G_{sw} of pine was on average 14% lower in South (0.16 ± 0.009 mol H_2O m^{-2} s^{-1}) compared to North-exposed slopes (0.19 ± 0.011 mol H_2O m^{-2} s^{-1}), while G_{sw} of oak was 27% lower in South compared to North aspects.

WUE differed in the dry and wet seasons depending on species, aspect and time (aspect x species x date, P < 0.0001 and P < 0.002, respectively, Table S1.3). 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 season (15 vs. 7 µmol CO_2 $mmol^{-1}$ H_2O, Fig. 1.4b).

Average *WUE* in oak increased significantly in the dry season (depletion period) compared to wet season (13 vs. 10 μmol CO_2 $mmol^{-1}$ H_2O). Trees on South aspects behaved differently; *WUE* in pine was constant during the recovery period prior to 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 μmol CO_2 $mmol^{-1}$ H_2O) and it increased and remained constant during the wet and depletion period (10 to 12.5 μmol CO_2 $mmol^{-1}$ H_2O; Fig. 1.4b).

For oak, G_{sw} decreased when Ψ_l dropped in the recovery and depletion periods in North and South aspects (Table S1.4a, c, e; Fig. S1.4a, c, e). For pine, G_{sw} decreased with declines in Ψ_l during the recovery period only in South aspect trees, however in both aspects during the wet and depletion periods (Fig. S1.4a, c, e). A negative relationship indicates that as Ψ_l becomes more negative, Gsw decreases to reduce water vapor loss. Ψ_l also controlled *WUE*; however this response depended on forest species and seasonal period (Table S1.4b, d; Fig. S1.4b, d, f). In the recovery period, only North exposed oak showed a significant positive linear relationship (P < 0.001, Fig. S1.4b) between *WUE* and Ψ_l, with a rate of 1 MPa decline causing a 4.2 μmol CO_2 /$mmol^{-1}$ H_2O increase in *WUE*. For the wet period, only North exposed pine showed a significant rise in *WUE* (2.7 μmol CO_2 $mmol^{-1}$ H_2O) per unit drop in Ψ_l (Fig. S1.4d). In the depletion period, except in North-exposed pine, *WUE* in trees of all other locations were controlled by Ψ_l (Fig. S1.4f). In North oak, *WUE* increased with a drop in Ψ_l, while in South exposed pine, *WUE* decreased with a drop in Ψ_l.

1.4. Discussion

1.4.1. 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.1.1, R^2 = 0.95) by which Ψ_l and Ψ_s maintained a constant offset throughout dry and wet seasons with up to 5 MPa inter-seasonal fluctuations. This constant offset would be expected if both soil humidity and fine root distribution were confined to the upper soil layer 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. 1.5). Thus, once rain ceases and dry season progresses, trees and shallow soils hydrology are expected to rapidly decouple (e.g., Ψ_s declines while Ψ_l remains constant) unless alternative water sources feed the shallow soils. Also, the placement of actively growing fine roots of both tree species may not be restricted to the soil surface but likely 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 showing preferentially superficial lateral roots (Phillips, 1963; Nadezhdina & Cermak, 2003; Veselkin et al., 2010). If this was the case, and humidity was located in the weathered rock, oak should exhibit less negative Ψ_l than pine, since oak might likely access water from rock fractures, however Ψ_l of oak was similar to that of pine during the recovery period and it was even lower at times than that of pine during the wet and depletion periods (Fig 1.2a).

Taking into account the spatial and temporal limitations to store water in these semiarid forest ecosystems as well as the high water vapor deficit at the site, the question arises: how can this tight soil-leaf Ψ coupling 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) in a single volcanic event (Orozco et al., 2002; Tristán 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 sub-hypodermic water fluxes (Ramos et al., 2007). Hence, we postulate that tree roots entering these superficial soil fractures should be able accessing this slowly flowing water during dry periods.

With our experimental setup, similarities between Ψ_l and Ψ_s suggest that the two forest species preferentially acquired water from the shallow soil 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 Ψ_l in the latter case. This observation is not in agreement with previous studies examining 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 withdraw water from deep water sources (e.g., karstic caves, fissures and cracks, deep soils). Thus, hypothesis 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 ground penetrating radar (PGR) 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 (Rodriguez et al., unpublished) most likely to garner water from summer rain pulses. In these latitudes, most precipitation occurs as small events (< 5 mm; Medina-Roldán et al., 2013) during Monsoon season (~58-60%); therefore, rapidly responding roots in shallow soils are an effective adaptation to profit from these pulses. The same trait might also enhance the acquisition of surface water previously deposited via hydraulic redistribution mechanisms. Increasing Ψ_s in shallow soils during the dry period suggest soil moisture increases were supported by water redistribution mechanisms, which rewetted the soil surface between January and May, after Ψ_s had dropped to their lowest values in December in all sites (Fig. 1.2).

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, i.e. steeper water potential gradient between moisture conditions in rock fractures and in above-surface air experienced by the same plant. (Richards & Caldwell, 1987; Espeleta et al., 2004). Alternative mechanisms include horizontal redistribution of water previously stored in 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 (Rodriguez Robles et al., unpublished data) at the site, two potential “geological water sources” were identified: 1) soil pockets and rock fractures in the weathered rock matrix, and 2) slow subsurface water flows (i.e. sub-hypodermic flux, Ramos-Leal et al., 2007) at the interface between weathered bedrock and sealed rock at ~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 did vary up to 28%, as water was likely released from the stem, via lateral roots into the soil surface (Rodriguez Robles, unpublished data). This previous mechanism has been reported for Mediterranean oak forests (Prieto et al., 2012).

1.4.2 Mechanisms of hydraulic control in tropical semiarid forest

Considering the rather extreme geo-hydro-meteorological 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 itself (H_1). Still, it was the Anisohydric mechanism that prevailed in the two contrasting, deciduous and evergreen forest species, both on North and South aspects. Examining environmental conditions and plant responses, this is similar to the mechanism reported for Anisohydric species from Northern semiarid forests, which are able to access stored water in deep soils or deep rock cracks (McDowell et al., 2008; West et al., 2008) and thereby maintain Ψl constant. In our study, Ψ_s and Ψ_l dropped to a minimum in December (Fig. 1.2), followed by an unexpected switch in Ψ trends in absence of rain and synchronously in both North and South aspects. Franks et al. (2007) reported that a mechanism that allowed Anysohydric species to reach very low midday Ψ_l was the unusually constant midday hydrodynamic (transpiration-induced) water potential gradient from roots to shoots, $\Delta\Psi$ plant. This mechanism under stomatal control allowed to maintain transpiration rates under the driest and hottest day times. This could be a mechanism operating also in our case.

Hence, this was a general ecosystem level response, however with a constant 2 MPa difference between aspects. Potential drivers triggering such a synchronic switch in Ψ, include an increasing water vapor pressure deficit (VPD) and thus a steeper Ψ gradient between soil fractures, shallow soil, leaves/needles and near-surface atmosphere (see above). We observed a close linear positive relationship between Ψ_l and *VPD* for both species during the recovery period (Fig. 1.5a) suggesting hydraulic redistribution supplied plant water needs. We observed that the transition from depletion to recovery periods coincided with lowest values of Ψ_l, lowest values of *VPD* and lowest air temperatures (Fig. 1.5b, c). These seemingly “threshold” conditions activated geoecohydrological mechanisms to resupply shallow soils with water. 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 Ψ_l.

For the recovery period (January to May 2011) in North exposed forests, Ψ_l of oak and pine stabilized at values reached in December 2010 and in absence of rain since October 2010. In South exposed trees, however, Ψ_l did not only stabilize but even rise an equivalent of ~1.5 MPa in absence of rain, a phenomenon that has not been described previously. This rise in Ψ_l occurred concomitantly with an increase in G_{sw} from January to May in both species (Fig. S1.4a). For G_{sw} to increase in the recovery period, a concurrent rise in soil water availability must have been occurred. This ecophysiological response is an additional source of evidence that plants used stored water from highly fragmented rocks (Schwinning, 2010) and/or from sub-hypodermic water fluxes. A further mechanism allowing stabilization and recovery of Ψ_l - and corroborated by our data - relates to strictly plant controlled leaf senescence exhibited by oak (Fig. 1.3). Hence, during the recovery period in South exposed forests a decrease in leaf canopy cover reduced plant water uptake and thus allowed Ψ_s to rise by ~1.5 MPa (Fig. S1.3). In oak, leaf senescence and thus a reduction in the overall transpiring leaf area likely stimulated G_{sw} in the remaining active leaves and thus sustained gas exchange activities and even increased *WUE* in South exposed forests (Fig. S1.5b). Leaf shedding by oak seemed to have induced a positive effect in pine as Ψ_l and G_{sw} increased similarly as in oak trees (Fig. S1.5a) likely 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). The other contrasting pattern observed at the early 2011 depletion period (October to December) by which a canopy decrease (Fig. 1.3) did not coincide with Ψ_l recovery but with its decline (Fig. 1.2). This response likely emerged from the combination of conditions by which the loss of soil water observed from October concurred with a drop of air temperatures and therefore a decline of *VPD* (Fig. 1.5). This resulted in a reduction of the gradient triggering hydraulic redistribution and the recovery of Ψ_l.

1.4.3. Pine and oak coexistence under extreme drought

Our results do not support hypothesis 3 stating that given 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 by which oak facilitated water access to pine throughout water redistribution mechanisms (Figs. 1.2 and 1.6). This conclusion is supported by spatial trends in Ψ_s and G_{sw} observed at different distances between neighboring pine and oak trees (Figs 1.6, S1.6). As the distance between trees increased, Ψ_s 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 Ψ_s on transpiration as soil water is reduced (Fig. S1.6). The Ψ_s associated with oak trees, on the other hand, did not change with increasing distance to pine trees (data not presented) and there were no indications that closeness to pine trees negatively or positively affected Ψ_s or G_{sw}. We are not aware of other reports that showed similar interplant distance effects on the behavior of Ψ_s or G_{sw} in mixed forest ecosystems.

Tightly coupled geoecohydrological feedback mechanisms ultimately control 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 doubts on the long-term capacity of *P. cembroides* to succeed in monocultures under increasingly limiting geohydrometeorological conditions, and provided evidence of the importance of *Q. potosina to* in maintaining ecosystem structure and functioning in this water-limited biome.

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1.6. Tables and Figures

Table 1.1. 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, México.

Exposition / species	***n***	**DBH (cm)**	**Age (years)**	**Tree height (m)**
North Pine	10	20.9 (11.6 – 32.6)	81 (77 – 87)	5.7 (3.8 – 7.5)
North Oak	10	18.3 (14.8 – 30.7)	97 (87 – 111)	4.3 (3.1 – 5.5)
South Pine	10	17.7 (10.2 – 24.2)	89 (49 – 135)	4.3 (2.6 – 6.8)
South Oak	10	18.1 (13.4 – 23.7)	93 (78 – 107)	3.9 (1.9 – 6.5)

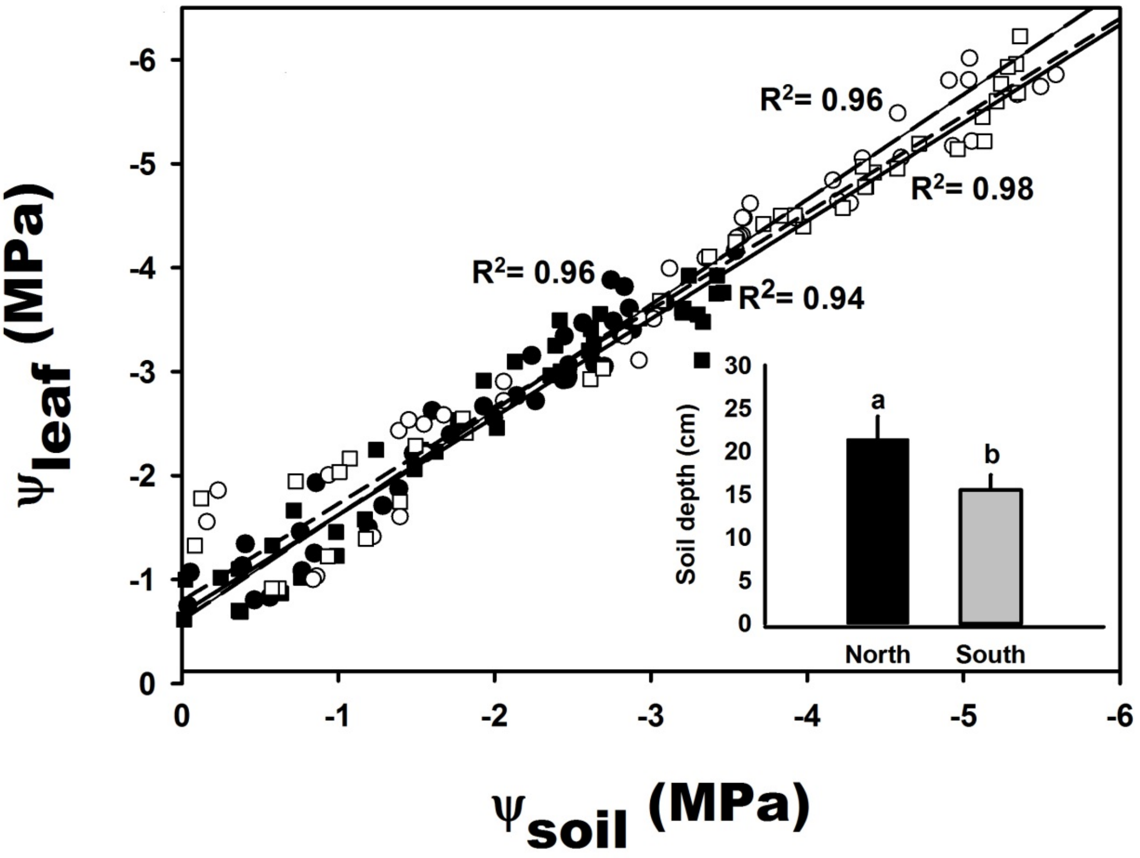
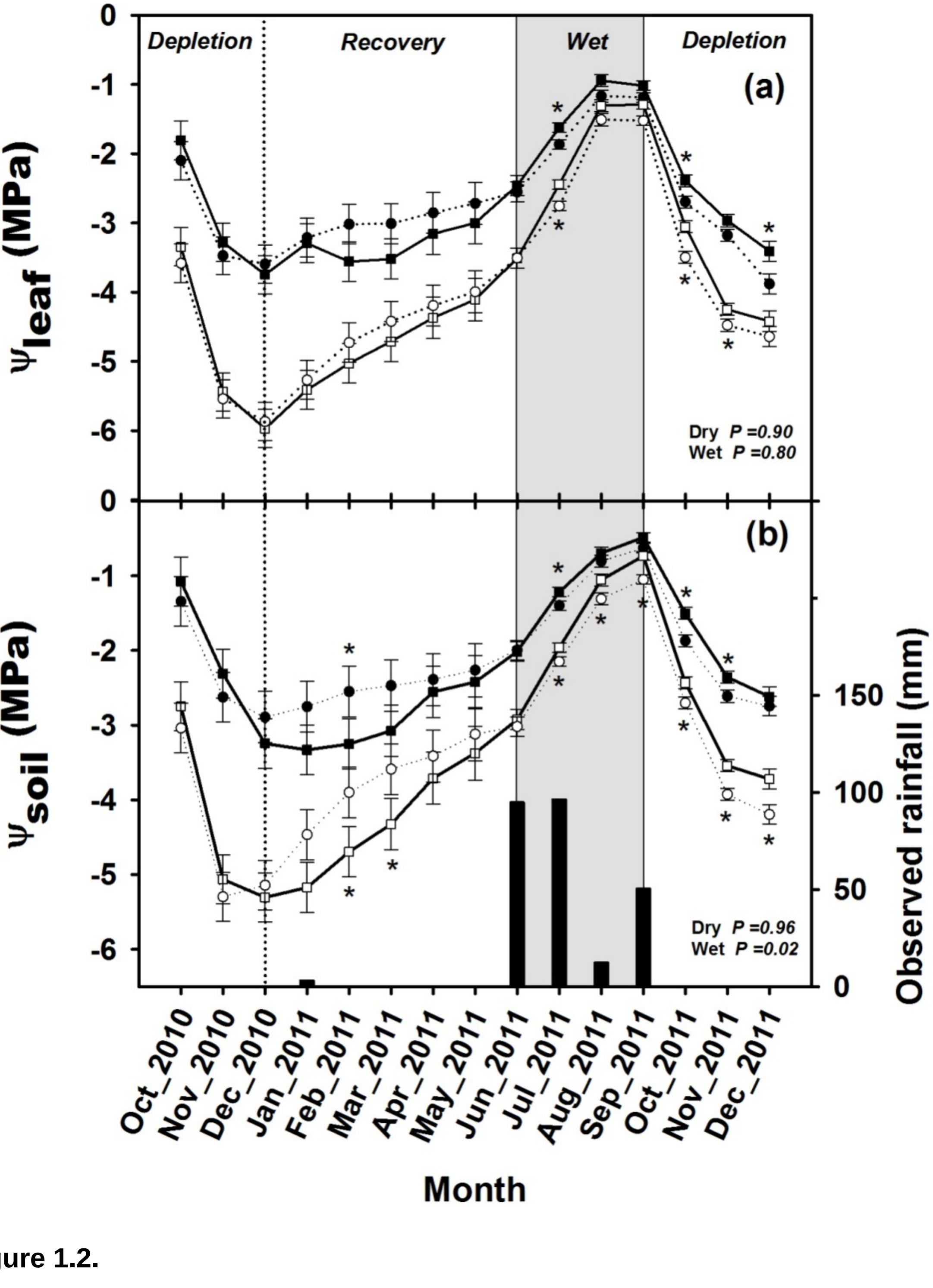

R2= 0.96
R2= 0.98
R2= 0.96
R2= 0.94
ψleaf (MPa)
ψsoil (MPa)
-6
-5
-4
-3
-2
-1
0
-1
-2
-3
-4
-5
-6
Soil depth (cm)
30
25
20
15
10
5
0
a
b
North
South

Figure 1.1.



Depletion
Recovery
Wet
Depletion
(a)
Dry P =0.90
Wet P =0.80
(b)
Dry P =0.96
Wet P =0.02
Ψ_{leaf} (MPa)
Ψ_{soil} (MPa)
Observed rainfall (mm)
0
-1
-2
-3
-4
-5
-6
0
50
100
150
Oct_2010
Nov_2010
Dec_2010
Jan_2011
Feb_2011
Mar_2011
Apr_2011
May_2011
Jun_2011
Jul_2011
Aug_2011
Sep_2011
Oct_2011
Nov_2011
Dec_2011
Month

Figure 1.2.

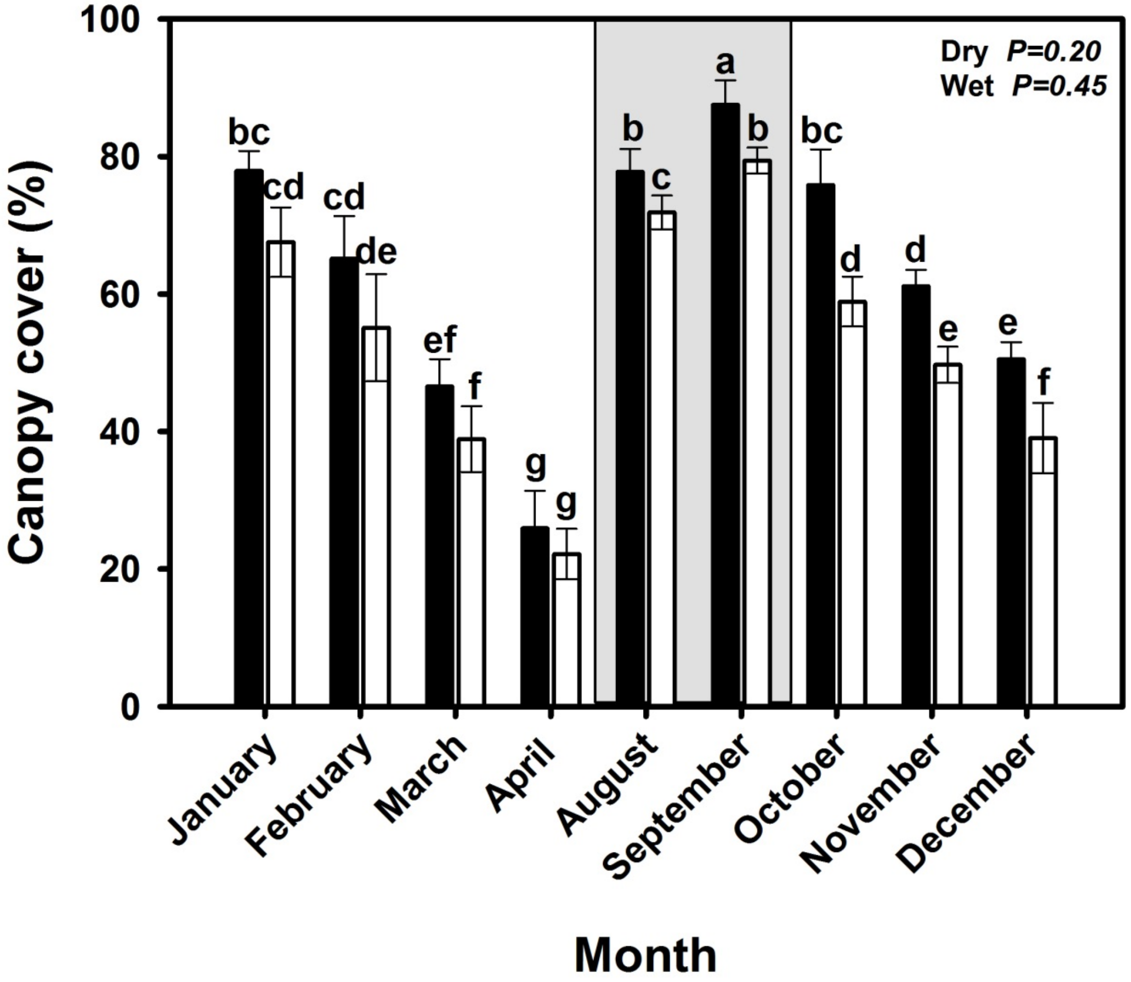

Canopy cover (%)
100
80
60
40
20
0
Dry P=0.20
Wet P=0.45
bc
cd
cd
de
ef
f
g
g
b
c
a
b
bc
d
d
e
e
f
January
February
March
April
August
September
October
November
December
Month

Figure 1.3.

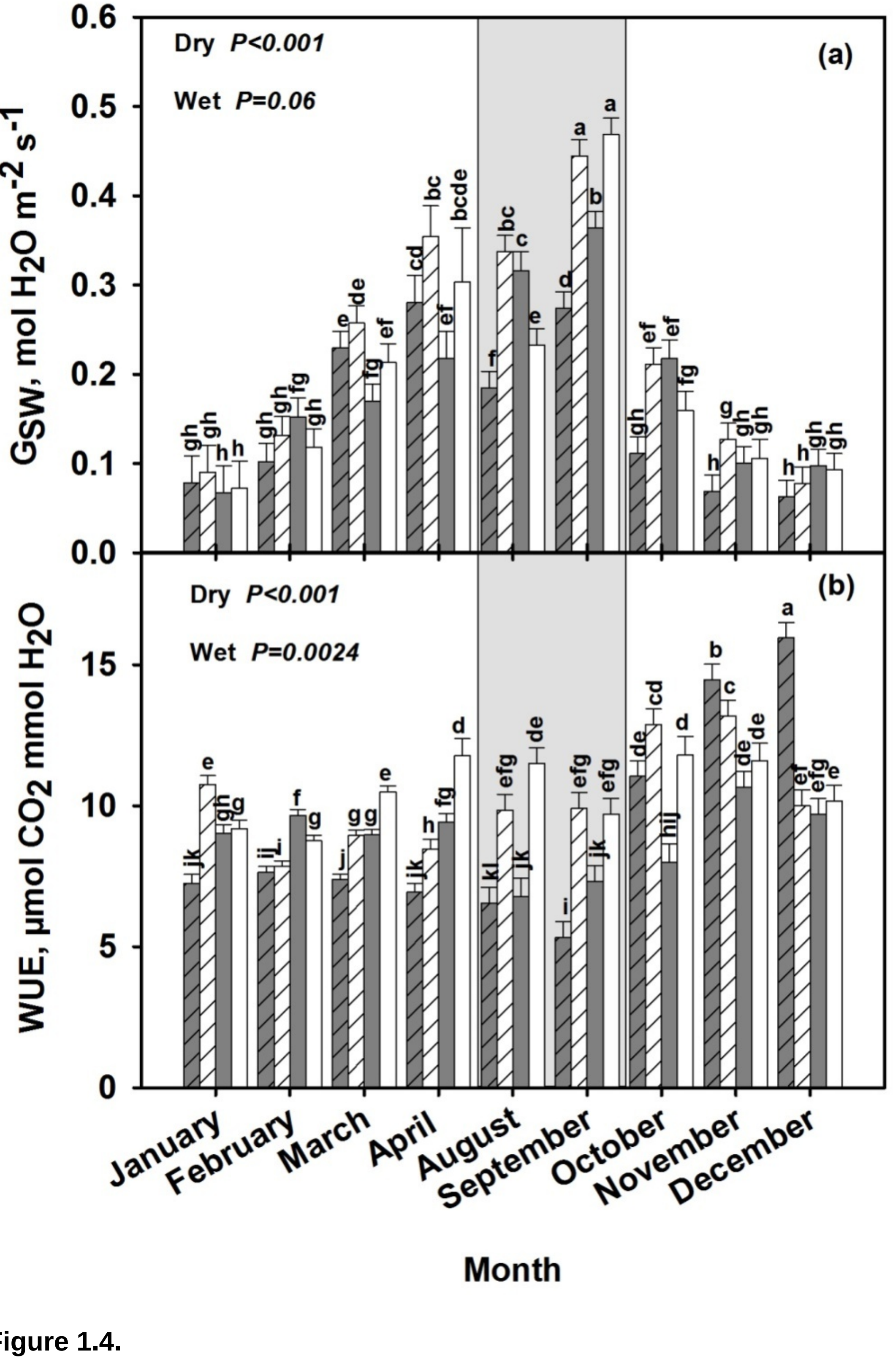

(a)
Dry P<0.001
Wet P=0.06
GSW, mol H_2O m^{-2} s^{-1}
0.0
0.1
0.2
0.3
0.4
0.5
0.6
gh gh h h
gh gh fg gh
e de fg ef
cd bc ef bcde
f bc c e
d a b a
gh ef ef fg
h g gh gh
h h gh gh
(b)
Dry P<0.001
Wet P=0.0024
WUE, µmol CO_2 mmol H_2O
0
5
10
15
jk e gh g
ij L f g
j g g e
jk h fg d
kl efg jk de
i efg jk efg
de cd hij d
b c de de
a ef efg e
January
February
March
April
August
September
October
November
December
Month

Figure 1.4.

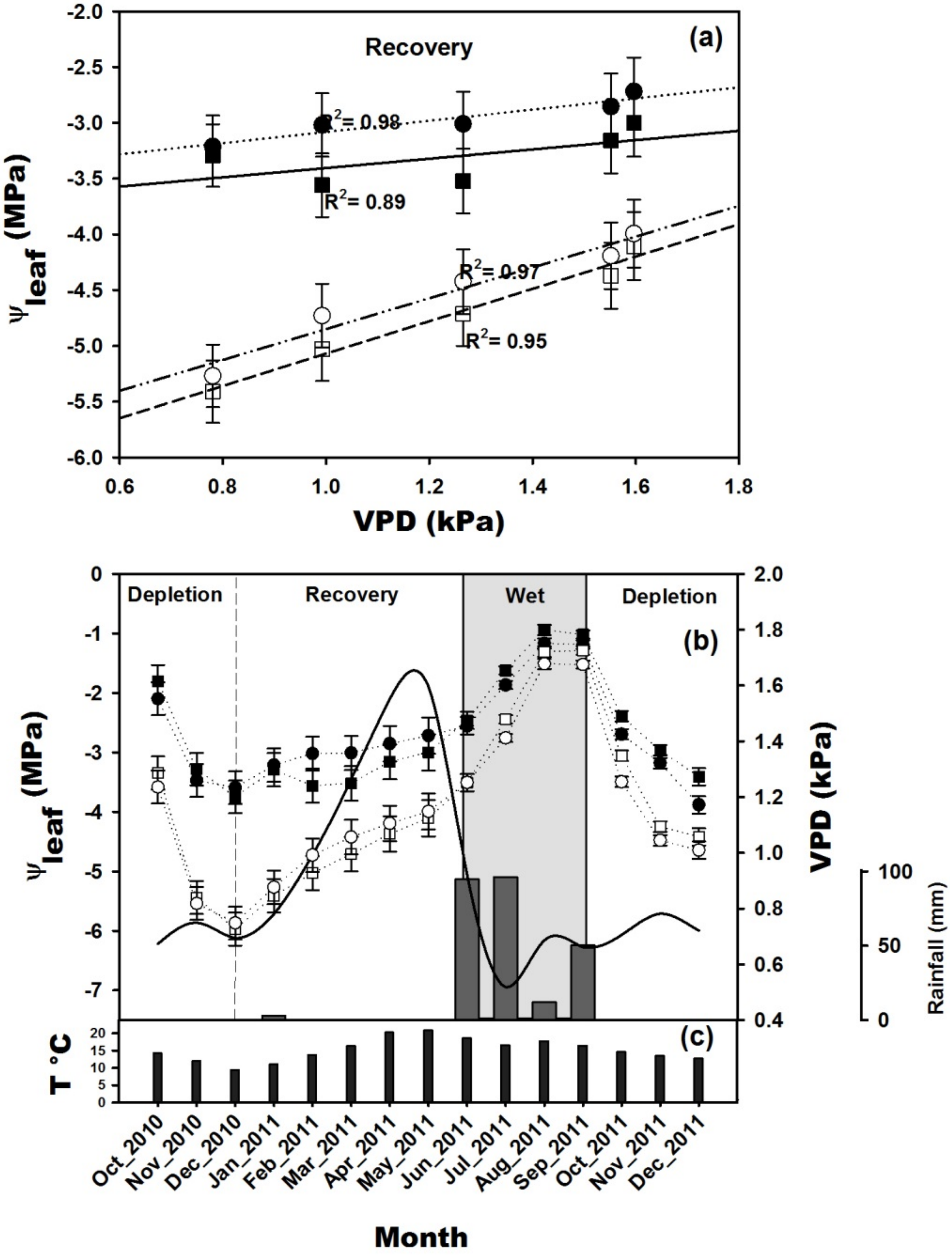

-2.0
-2.5
-3.0
-3.5
-4.0
-4.5
-5.0
-5.5
-6.0
Recovery
(a)
R² = 0.98
R² = 0.89
R² = 0.97
R² = 0.95
ψleaf (MPa)
0.6
0.8
1.0
1.2
1.4
1.6
1.8
VPD (kPa)
0
-1
-2
-3
-4
-5
-6
-7
Depletion
Recovery
Wet
Depletion
(b)
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
VPD (kPa)
100
50
0
Rainfall (mm)
ψleaf (MPa)
T °C
20
15
10
5
0
(c)
Oct_2010
Nov_2010
Dec_2010
Jan_2011
Feb_2011
Mar_2011
Apr_2011
May_2011
Jun_2011
Jul_2011
Aug_2011
Sep_2011
Oct_2011
Nov_2011
Dec_2011
Month

Figure 1.5.

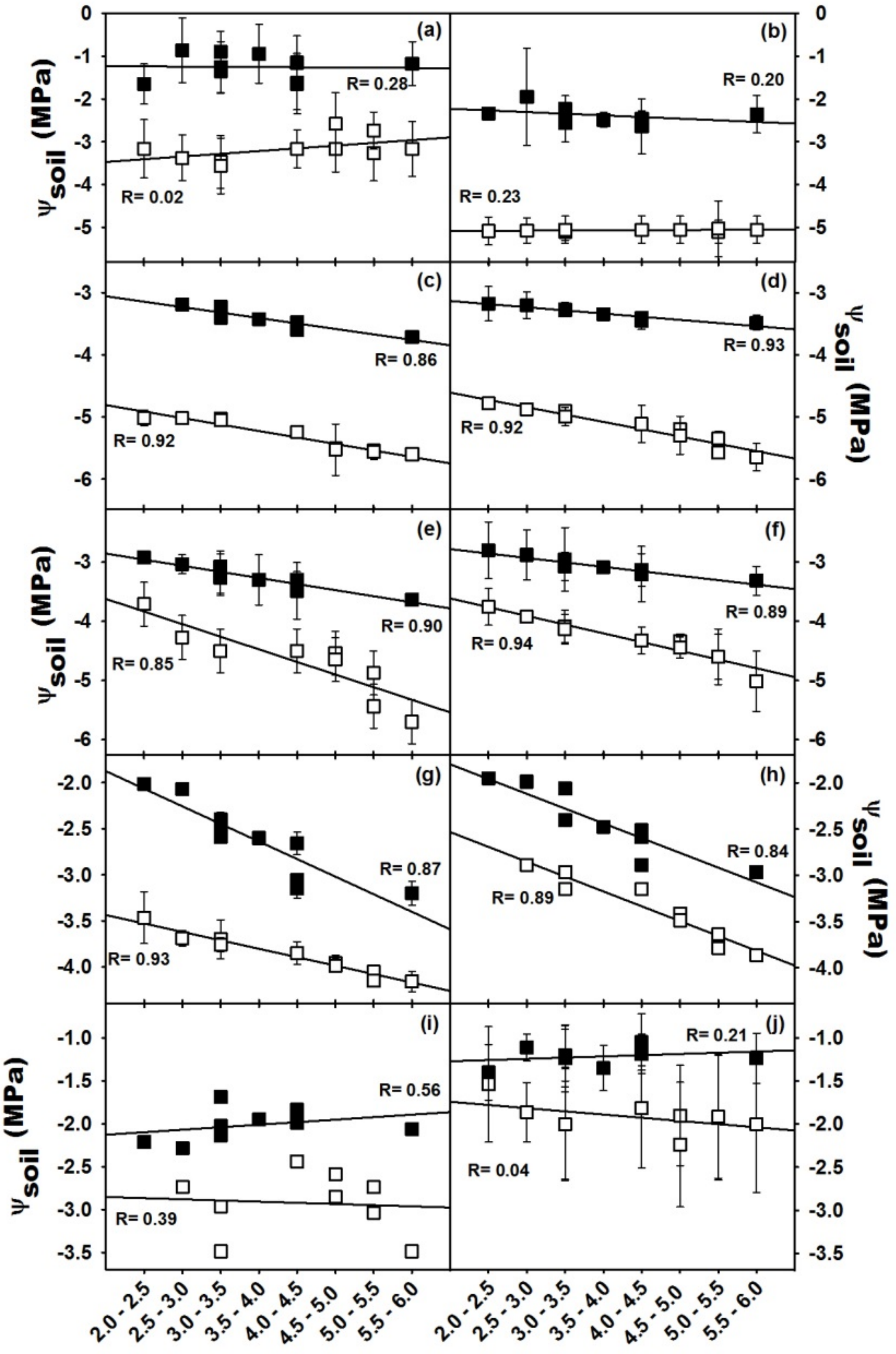

(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
R= 0.28
R= 0.02
R= 0.20
R= 0.23
R= 0.86
R= 0.92
R= 0.93
R= 0.92
R= 0.90
R= 0.85
R= 0.89
R= 0.94
R= 0.87
R= 0.93
R= 0.84
R= 0.89
R= 0.56
R= 0.39
R= 0.21
R= 0.04
ψ_{soil} (MPa)
2.0 - 2.5
2.5 - 3.0
3.0 - 3.5
3.5 - 4.0
4.0 - 4.5
4.5 - 5.0
5.0 - 5.5
5.5 - 6.0

Figure 1.6.

1.7. Supporting Information

Table S1.1. Intercepts, slopes, regression coefficients and observed probabilities of linear regressions between leaf water potential (Ψ_l) and soil water potential (Ψ_s) for *Pinus cembroides* and *Quercus potosina* in North and South expositions.

Exposition/Species	**Intercept ± 1SE**	**Slope ± 1SE**	**R^2**	***P***
North Pine	-0.6902 ±0.1153	0.9377 ±0.0458	0.94	<0.0001
South Pine	-0.8359 ±0.1163	0.9193 ±0.0277	0.98	<0.0001
North Oak	-0.6393 ±0.0891	0.9995 ±0.0391	0.96	<0.0001
South Oak	-0.8999 ±0.1335	0.9257 ±0.0334	0.96	<0.0001

Table S1.2. Repeated measures ANOVA for soil and leaf water potential (Ψ_s and Ψ_l) comparing aspect (North, South), tree species (*Pinus cembroides*, *Quercus potosina*) and sampling date in a tropical semiarid forest ecosystem in Central-North México. Analysis was run separately for the whole dry and the wet seasons.

	Ψ_s			Ψ_l		
Effect	df	*F*	*P*	df	*F*	*P*
a) Dry season						
Exposition	1	4601.28	<0.0001	1	4601.28	<0.0001
Species	1	0.03	0.8533	1	0.03	0.8533
Date	29	390.32	<0.0001	29	390.32	<0.0001
Exp*Sp	1	0.58	0.4504	1	0.58	0.4504
Exp*Date	29	32.19	<0.0001	29	32.19	<0.0001
Sp*Date	29	5.95	<0.0001	29	5.95	<0.0001
Sp*Exp*Date	29	0.68	0.9703	29	0.68	0.8999
b) Wetseason						
Exposition	1	1183.68	<0.0001	1	516.95	<0.0001
Species	1	60.33	<0.0001	1	70.69	<0.0001
Date	8	569.99	<0.0001	8	462.75	<0.0001
Exp*Sp	1	9.87	0.0034	1	0.32	0.5734
Exp*Date	8	82.66	<0.0001	8	20.23	<0.0001
Sp*Date	8	0.72	0.6762	8	2.85	0.0046
Sp*Exp*Date	8	1.55	0.0212	8	0.56	0.8079

df= degrees of freedom, *F* = Fisher´s statistics, *P* = probability value

Table S1.3. Repeated measures ANOVA for water use efficiency and stomatal conductance (WUE and G_{sw} respectively) comparing aspect (North, South), tree species (*Pinus cembroides*, *Quercus potosina*) and sampling date in a tropical semiarid forest ecosystem in Central-North México. Analysis was run separately for dry and wet seasons.

	WUE			G_{sw}		
Effect	df	*F*	*P*	df	*F*	*P*
a) Dry season						
Exposition	1	1.66	0.2216	1	10.02	0.0081
Species	1	11.83	0.0049	1	67.90	<0.0001
Date	6	37.90	<0.0001	6	252.09	<0.0001
Exp*Sp	1	5.81	0.0328	1	16.73	0.0015
Exp*Date	6	19.77	<0.0001	6	13.47	<0.0001
Sp*Date	6	12.84	<0.0001	6	4.07	0.0016
Sp*Exp*Date	6	8.46	<0.0001	6	8.05	<0.0001
b) Wet season						
Exposition	1	7.94	0.0155	1	2.99	0.1095
Species	1	134.27	<0.0001	1	17.86	0.0012
Date	1	6.66	0.0256	1	35.17	<0.0001
Exp*Sp	1	0.31	0.5896	1	13.79	0.0030
Exp*Date	1	0.01	0.9399	1	1.16	0.3040
Sp*Date	1	1.36	0.2676	1	6.54	0.0267
Sp*Exp*Date	1	15.43	0.0024	1	4.40	0.0599

df= degrees of freedom, *F* = Fisher´s statistics, *P* = probability value

Table S1.4. Intercepts, slopes, regression coefficients and observed probabilities of linear regressions between stomatal conductance (G_{sw}) and water user efficiency (WUE) with leaf water potential (Ψ_l), for both *Pinus cembroides* and *Quercus potosina* in North and South aspects. Regressions were run separately for dry and wet seasons.

	intercept (y0) ± 1SE	slope (a) ± 1SE	R^2	*p*
a) G_{sw}/Ψ_l	Dry season (*recovery perid*)			
North Pine	0.0275 ±0.3276	-0.0387 ±0.0946	0.01	0.6892
North Oak	1.2084 ±0.3260	0.3307 ±0.1031	0.48	0.0083
South Pine	0.6642 ±0.1341	0.1065 ±0.0258	0.58	0.0014
South Oak	0.4094 ±0.0809	0.0663 ±0.0176	0.61	0.0045
b) *WUE*/Ψ_l				
North Pine	7.9174 ±2.2103	0.1166 ±0.6383	0.00	0.8579
North Oak	-5.0423 ±3.2986	-4.4772 ±1.0430	0.62	0.0013
South Pine	8.3825 ±2.6342	-0.1792 ±0.5056	0.01	0.7296
South Oak	11.4763 ±2.8079	0.5092 ±0.6118	0.07	0.4268
c) G_{sw}/Ψ_l	Wet season			
North Pine	0.3958 ±0.0356	0.1879 ±0.0386	0.79	0.0028
North Oak	0.5952 ±0.0898	0.2149 ±0.0917	0.47	0.0575
South Pine	0.4540 ±0.0226	0.0940 ±0.0182	0.81	0.0021
South Oak	0.7080 ±0.1665	-0.2934 ±0.1321	0.45	0.0681
d) *WUE*/Ψ_l				
North Pine	3.4927 ±0.9195	-2.7636 ±0.9959	0.56	0.0322
North Oak	9.5371 ±1.6232	-0.3542 ±1.6235	0.00	0.8379
South Pine	8.3825 ±2.6342	-0.1792 ±0.5065	0.01	0.7296
South Oak	11.4763 ±2.8079	0.5092 ±0.6118	0.07	0.4268
e) G_{sw}/Ψ_l	Dry season (*depletion period*)			
North Pine	0.1371 ±0.0180	0.0189 ±0.0058	0.51	0.0083
North Oak	0.3156 ±0.0508	0.0549 ±0.0153	0.56	0.0050
South Pine	0.3042 ±0.0269	0.0436 ±0.0065	0.83	<0.0001
South Oak	0.2336 ±0.0156	0.0279 ±0.0036	0.88	<0.0001
f) *WUE*/Ψ_l				
North Pine	10.4776 ±1.6055	-0.8463 ±0.5142	0.21	0.1308
North Oak	16.9389 ±1.3038	1.5250 ±0.3938	0.59	0.0031
South Pine	6.8764 ±1.0533	-0.6832 ±0.2559	0.44	0.0256
South Oak	13.9709 ±0.8446	0.6887 ±0.1957	0.60	0.0079

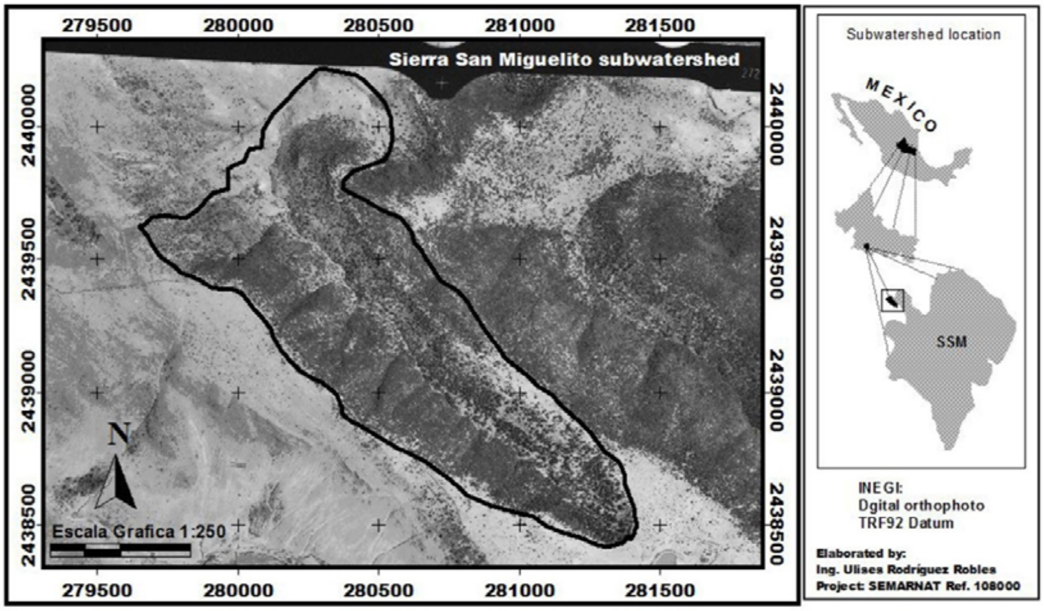


Figure S1.1. Geographic location of Sierra San Miguelito and the study site, in San Luis Potosí, México.

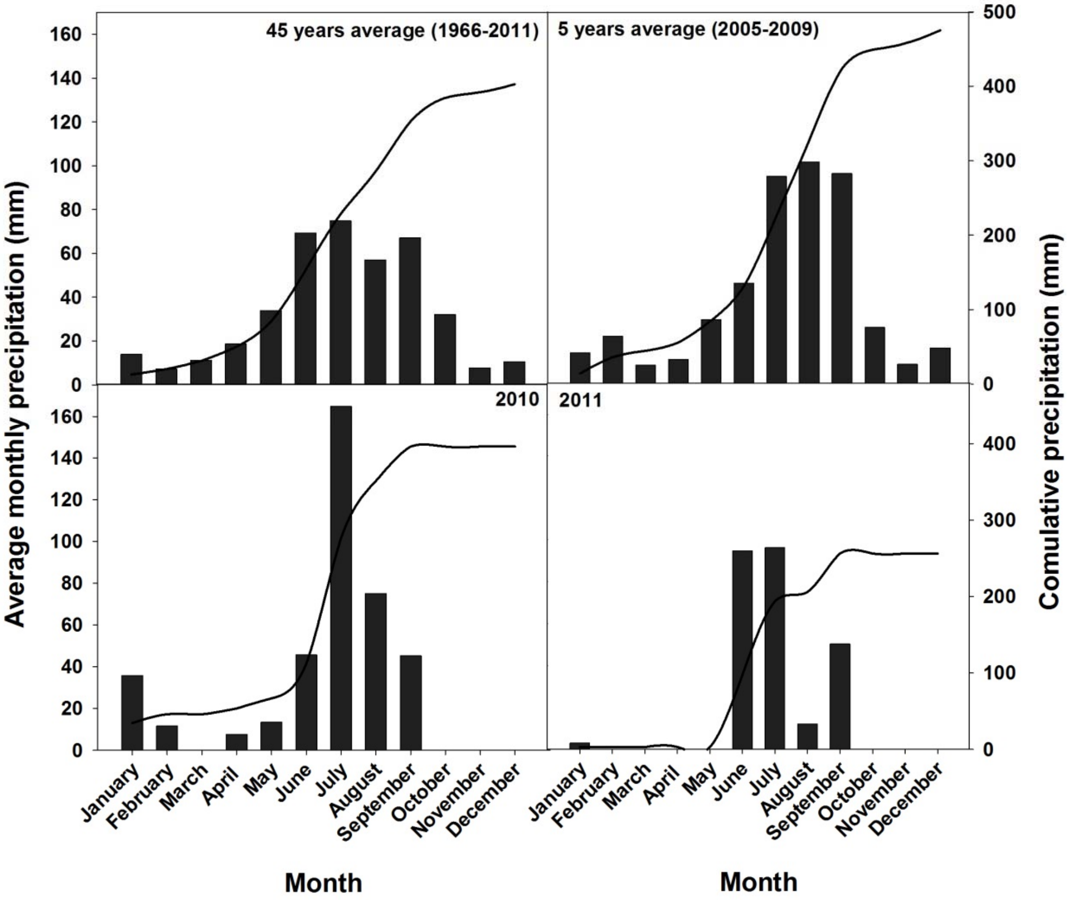


Figure S1.2. Monthly yearly average and annual cumulative precipitation for the last 45 and 5 yr period (top left and right, respectively). Total monthly and cumulative precipitation in 2010 (bottom, left) and 2011 (bottom, right) including the study period October 2010 – December 2011, in Sierra San Miguelito, SLP, México.

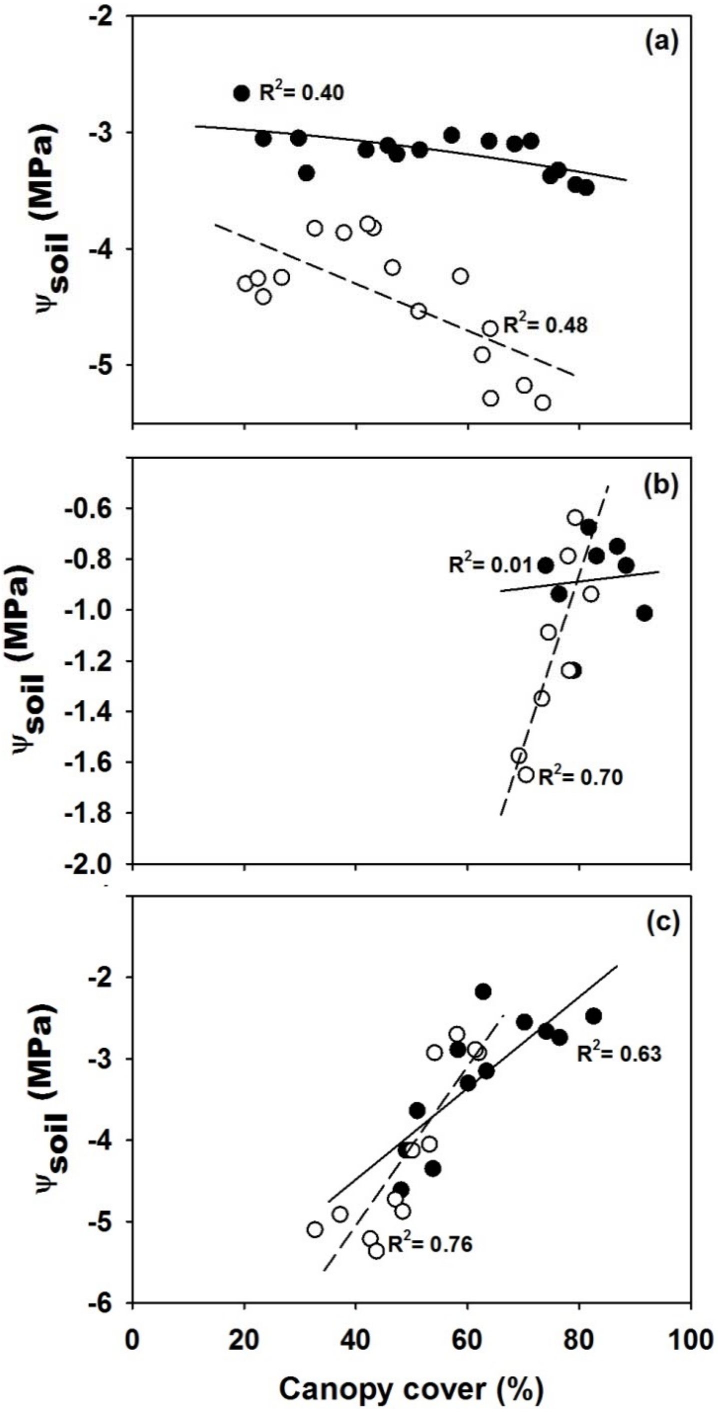


Figure S1.3. Linear relationships between Ψ_s and canopy cover of *Quercus potosina* in North and South aspect for the three periods defined in the study: recovery period from January to May **(a)**, wet season from June to September **(b)** and depletion period from October to December **(c)**. All regressions were statistically significant at $P < 0.05$, with exception of the North exposition in the wet season.

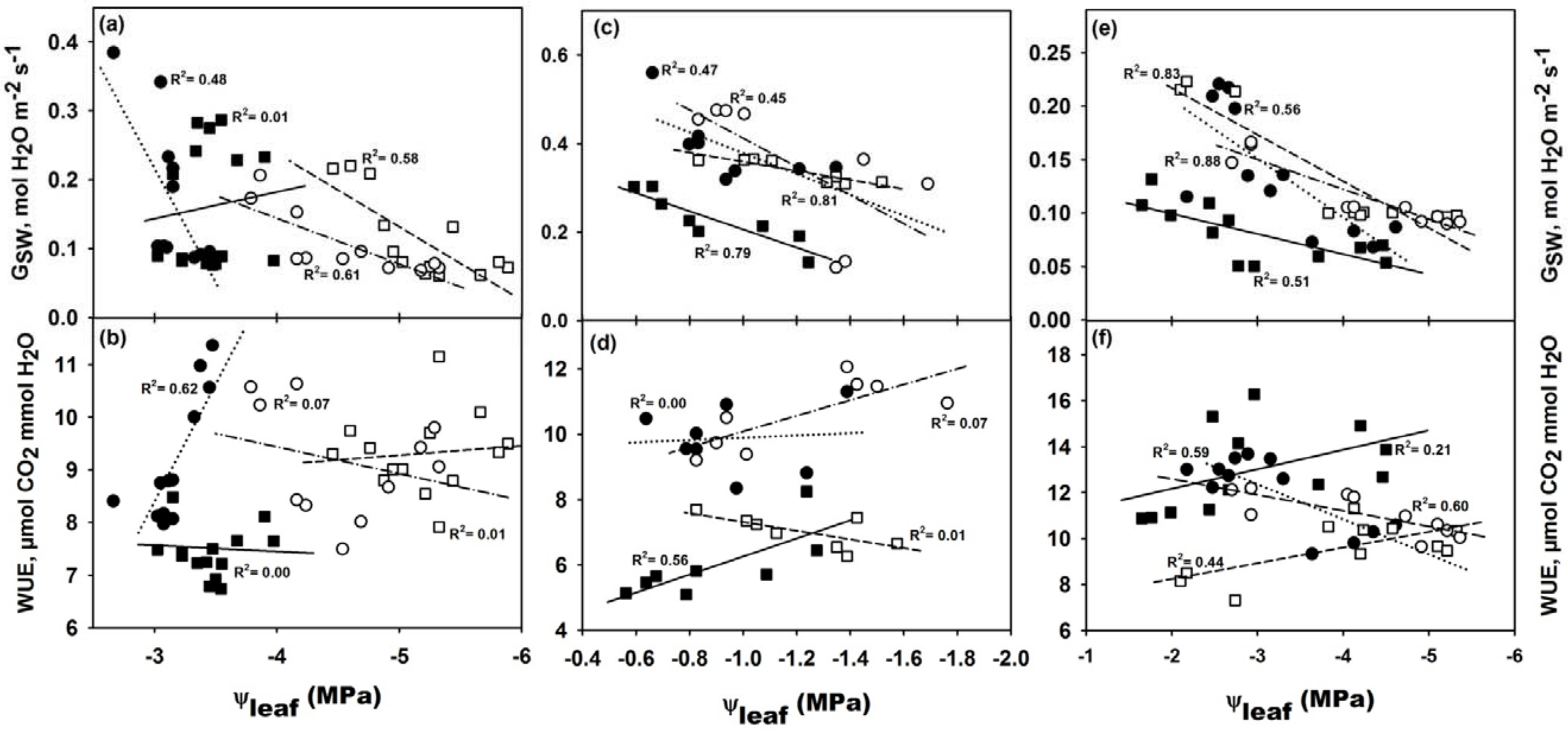


Figure S1.4. Linear relationships between estimated stomatal conductance, water use efficiency and leaf water potential for *Pinus cembroides* and *Quercus potosina* located in North and South expositions. Pine-North (─■─), Pine-South (---□---), Oak-North (···●···) and Oak-South (─○─). Relationships correspond to the three periods defined in the study for the dynamics of *Ψ*; recovery (**a** and **b**), wet (**c** and **d**) and depletion (**e** and **f**).

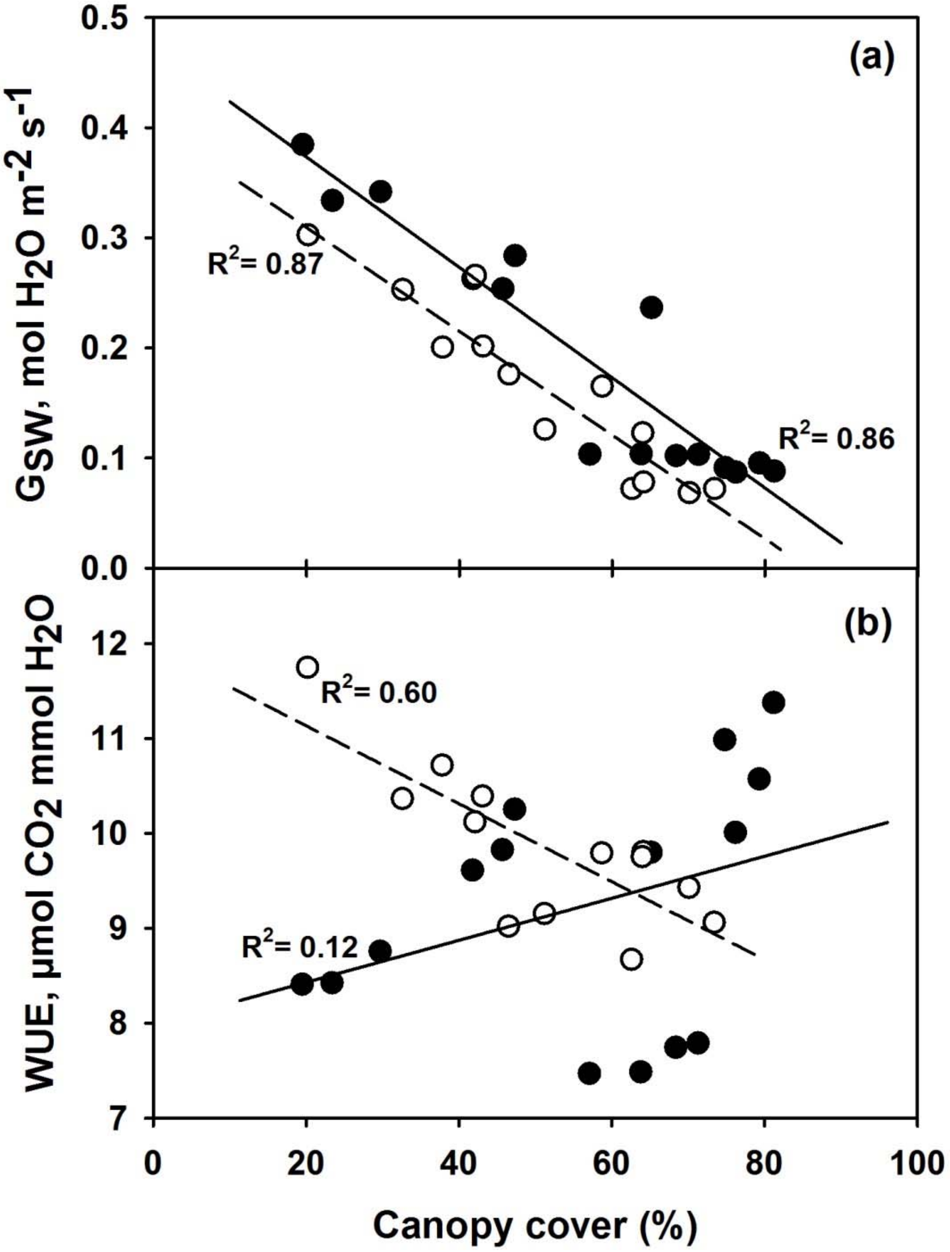


Figure S5. Linear relationships between stomatal conductance (Gsw) **(a)**, water use efficiency (WUE) **(b)** and canopy cover of *Quercus potosina* (n = 4) in North (open circle) and South (closed circle) aspects, during the recovery period. All regressions were statistically significant at $P < 0.05$.

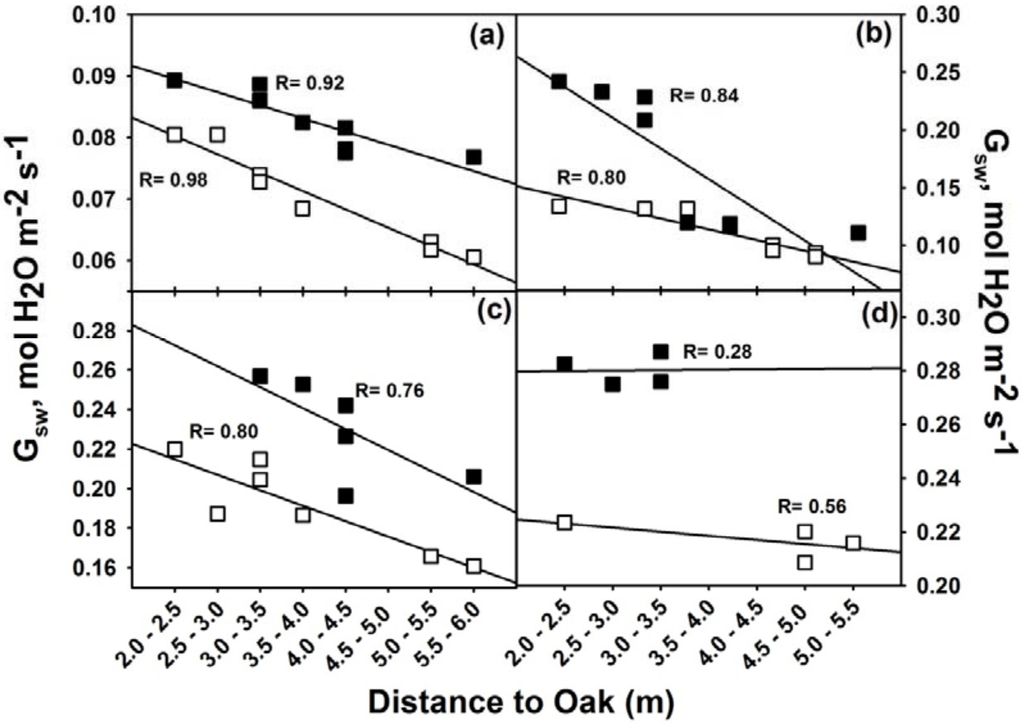


Figure S6. Linear relationship between *Pinus cembroid*es stomatal conductance (G_{sw}) and distance to the closest tree of *Quercus potosina* between January and April 2011. Closed symbols indicate North exposed trees whereas open symbols correspond to South exposed Pine. Each point represents the mean ±1 SE (*n*=4).

2

CHAPTER

GEOPHYSICAL TOOLS FOR TREE ROOT STUDIES: A CASE STUDY OF A SEMIARID FOREST ON SHALLOW ROCKY SOILS

Abstract

In semiarid environments, tree rooting depth and distribution may vary substantially depending on site characteristics. The Sierra San Miguelito Volcanic Complex is a mountainous area where extremely shallow soils (< 30 cm deep) and rock outcrops of rhyolitic rock (impermeable). It is generally assumed that shallow soils over solid bedrock restrict vertical root growth beyond the soil matrix, as it impedes downward soil water and root movements.

However, physical weathering of this volcanic rock may favor root growth; in particular, rock fractures, exfoliations and soil pockets allow preferential movement of soil and water, and positioning of roots. In semiarid environments, woodlands and open forest ecosystems frequently colonize rocky substrates, yet there exists a huge gap in our knowledge with respect to root distribution within and water uptake from fractured rocky substrates.

This study responds to the scientific needs suggested by Jayawickreme et al. (2014) and the opportunity of using geophysical methods (ground penetrating radar, GPR and electrical resistivity tomography, ERT) to better understand root ecology in shallow rocky soils in semiarid forests.

With the GPR method we identified root diameter categories ranging from 6 to 70 mm of different tree species and at different depth. Hence, with this method we could demonstrate that pine and oak distribute their fine and coarse roots at different depth suggesting they occupy complementary functional spatial niches. With the 800 MHz antenna, we have observed that the trees in these shallow soils, use of the weathered rock outcropping to anchor the trunk and distribute the roots. With monthly observations using the ETR method, we could identify areas of high and low humidity as well as the soil/bedrock interface, which together explain the vertical and horizontal root distribution.

Once geophysical images are calibrated with *in-situ* measurements of roots and soil depth, they can then be used to extrapolate findings over larger areas, as shown in the present work. Further advances in geophysical instrumentation have great potential to fill gaps in our understanding of shallow subsurface plant – water relations and should be integrated more broadly in interdisciplinary research such as root ecosystem ecology, ecohydrology, biogeosciences, etc.

Keywords: ground penetrating radar, electrical resistivity tomography, geophysical imaging, RadExplorer software, pine-oak forest, root detection, soil/bedrock interface, impermeable volcanic rock

2.1. Introduction

Water use strategies of plants and water transport in the soil–plant–atmosphere continuum are critical to understand ecosystem functioning in arid and semiarid regions, where plant productivity is primarily limited by soil moisture (Burgess & Bleby, 2006; Li et al., 2007; Prieto, I. et al., 2012). Roots have the major functions of absorbing water and inorganic nutrients, and of anchoring the plant body to the ground (Prieto, Iván et al., 2012). Growing roots change the soil texture, displace pore water and gas, and increase the porosity (Jackson et al., 1996). Water balance and the physiological process in soils and plants depend on the water uptake by absorbing roots, subsequent water redistribution and hydraulic lift, sap flow, transpiration, and photosynthesis (Anderegg & HilleRisLambers, 2016). Placement of roots at different soil depths favors spatial and temporal resource partitioning, greater potential for effective exploitation of whole profile water acquisition and enhanced biomass production with the same annual precipitation (Fernandez et al., 2000; Brooks et al., 2002; Hultine et al., 2003; Renee et al., 2010). Many of the areas with shallow soils (<1 m) are located in water-limited climatic regions with seasonally highly variable precipitation, where adequate storage capacity is critical for maximizing plant water status (Rose et al., 2003; Schwinning, 2010; Rodríguez-Robles et al., 2015). So far, there exist a good number of studies addressing hydrologic aspects of plants from semiarid regions in particular, from places where root development is not restricted by hardened soil layers (Lebourgeois et al., 1998; Schwinning & Ehleringer, 2001; Poulos et al., 2007). Few studies, however have examined semiarid forest ecosystems growing on shallow soils over bedrock, cemented horizons, or strongly developed argillic horizons that impede downward water movement and root growth (Andrews et al., 2005; Katra et al., 2008; Rodriguez-Robles et al., 2015).

In semi-arid climates, poorly developed shallow soils over water-impermeable surfaces rarely exhibit water storage capacity sufficiently high to maintain forest ecosystems. Empirical evidence suggests that trees and shrubs growing on this type of substrates are able to access water from weathered bedrock once water supply from top soil becomes exhausted (Querejeta et al., 2007; Schwinning, 2008). Still, the geological implications of shallow soils on plant-water relations are controversial in terms of the source of water and the adaptive mechanisms to live under limited water availability. This has been the focus of recent ecohydrological studies (Estrada-Medina et al., 2013; Schwinning, 2013; Tokumoto et al., 2014; Rodriguez-Robles et al., 2015). Due to difficulties and impracticality of bedrock excavation and thus lack of research tools to study root distribution in-situ, little is known about rooting patterns and growth strategies of forest ecosystems colonizing shallow soils over bedrock. Hence, alternative methods are needed that permit the simultaneous study of vertical root distribution and seasonal soil humidity patterns to understand potentially diverse species-specific adaptations to these complex ecohydrological conditions.

With surface geophysical methods, such as electrical resistivity tomography (ERT), it is possible to monitor soil water content at soil depths ranging from 2.5 to 17 m at weekly or monthly intervals. ERT is a nondestructive method, which produces two- and/or three-dimensional images depicting the spatial and temporal variation in soil electrical resistivity, which basically corresponds to variations in volumetric soil water content (Cosentini et al., 2012). The resistivity of rocks/soil may vary depending on their water content, water salinity and mode of pore distribution, presenting a wide range of values (10-8 – 1015 Ω m−1); low values indicate low water content, high values high water content (Orellana & Silva, 1982). ERT has traditionally been used in geological prospecting (Wang et al., 1991; Sudha et al., 2009; Chrétien et al., 2014), but is now also often applied in hydrological, agricultural and environmental studies (Jackson et al., 2000; Srayeddin & Doussan, 2009). Ground-penetrating radar (GPR) is one of the most effective and rapid type of geophysical survey methods (Parsekian et al., 2015). The variety of its application is limited only by the availability of antennas with different frequencies of emitted radio waves. The application of GPR ranges from engineering applications (Adepelumi & Fayemi, 2012), geological investigations (Gomez-Ortiz et al., 2007), measures of soil water content (da Silva et al., 2004), determination of tree root diameter (with minimum diameter of 5 mm) in forest and urban settings (Hruska et al., 1999; Ow & Sim, 2012; Tanikawa et al., 2013). The depth of investigation and resolution depends not only on the physics of the method but also on the distribution of subsurface physical properties (Table 2.1).

To explore the potential of these methods, we examined ecohydrological processes at the soil/bedrock-plant root interface in a mixed forest ecosystem in the mountainous region of Sierra San Miguelito (SSM) at the transition between the arid desert scrub biome in the North and the semiarid grassland biome in the South of the Mexican Central Plateau. Since the presence of an extended pine-oak forest in this semiarid region cannot be explained by climate conditions alone, we used geophysical methods to elucidate the geological and edaphic conditions and potential root adaptations to these conditions to help explain the presence and ecohydrological functioning of this azonal forest. The forest of SSM, geologically, is established in a volcanic complex of impermeable rocks of rhyolitic type, highly weathered by exfoliation processes (peeling off in sheets) and shallow poorly developed soils with high litter and organic matter content (<25 cm deep) (Perez et al., 2009). Recent studies suggest that native tree species may be able to extract water directly from subsurface bedrock by physiological mechanism (Proust et al., 2011; Schwinning, 2013; Tokumoto et al., 2014), however, most of these studies focused on water-permeable rock types (e.g. limestones). Rodriguez-Robles et al. (2015) suggested that species colonizing shallow rocky soils have specialized root systems that allow them to explore large regolith rocky areas, increasing their chances of finding water stored in cracks. However, little is known if water stored in the cracks of this material fulfills the water demand of coexisting tree species during periods of extended seasonal droughts of this region. Also, little is known about the distribution of fine and coarse roots growing underneath the shallow soils and in weathered bedrock, mainly due to difficulties of excavating bedrock.

This study responds to the call for the application of new geophysical methods to advance the science of root ecology (Jayawickreme et al., 2014). Our study is presenting a novel approach that will permit to tackle several questions on diverse disciplines such as ecology, ecohydrology, biogeosciences, etc. Here we present the application of surface geophysical imaging tools for root research studies in mixed forests in an edaphically and geologically extreme environment. This will serve as exploration tools providing an alternative or complement to traditional methods to gather information on ecologically relevant subsurface variables across time and space. Our hypothesis was that weathered rhyolite bedrock in the Sierra San Miguelito Volcanic Complex (SSMVC) maintains humid microsites and that root distribution mirrors this spatial and temporal heterogeneity in this growth limiting resource. In particular, we aimed at: (1) characterizing the weathered rock by exfoliation processes with a 800 MHz antenna; (2) detecting roots of different diameter size classes at various depths in a pine-oak forest growing in volcanic fractured rocks, using two antennas of different frequencies (500 and 800 MHz); and (3) developing ERT profiles describing the functionality of weathered rock in forest systems that grow on shallow rocky soils.

2.2. Materials and methods

2.2.1Site description

The site is situated in the SSM in a semiarid pine-oak forest ecosystem in the Southern region of the SSMVC (Fig. 2.1a). The SSMVC represents the remnants of one of the most voluminous rhyolitic volcanic events on Earth (McDowell & Keizer, 1977), formed by massive lava spills of rhyolitic composition (Portezuelo Latite and San Miguelito Rhyolite). This volcanic complex is affected by punctual fracturing at small scale at a scale that is directly influencing pine-oak forest establishment (Fig. 2.2a-b) because of its control on local pedogenesis and hydrology. Soils are poorly developed and overall extremely shallow (<25 cm) and rocky; hence tree roots commonly anchor in weathered rocks to get support (Fig. 2.2c-d). Lithological profiles show a high density of vertical roots in rock fractures and soil pockets (Fig. 2e-f). According to the World Reference Base for Soil Resources (WRB) classification system, soil at this site correspond to lithic–paralithic Leptosols (LPlip) (FAO, 2006). Organic matter content is very high (60%) in these soils (Perez et al., 2009). The climate is semiarid; for the last 65 years mean annual precipitation (MAP) has accounted for 408 mm (Weather station “La Purisima”, 22° 5' 22.4'', 101° 12' 28.9''), where in 64% of the years MAP has been below average and only in 12% MAP has been above 500 mm (Fig. 1b). In general, summer precipitation falls between July and October and accounts for 90% of MAP, the rest falls between December and February.

In October – December 2012 (dry year, 15 mm) and October –2013 (wet year, 54.4 mm) We examined root spatial distribution in the highly organic soil and under exfoliated rocks, as well as water displacement in rock fractures and soil resistivity for Pinus cembroides and Quercus potosina in pure and mixed stands. We monitored along 8 and 25 m long transects using near-surface geophysical tools, in particular electrical resistivity tomography (ERT) and ground penetrating radar (GPR).

2.2.2 Principles of ERT

ERT is a method that generates images of the variation of electrical resistivity in either two or three dimensions below a line or grid of electrodes placed on the soil surface. The method is based on measurements of voltage differences between electrode pairs in response to current injection between additional electrode pairs. This is a minimally invasive method, because it only requires inserting electrodes only a few centimeters into the ground to create electrical contact. The resulting resistivity structure describes variations in the ability of subsurface soils and rocks to conduct electrical current (Fig. 2.3b). The measured resistivity is a function of the water content of the substrate (rock or soil), its chemical composition of the pore water and the soil surface area/grain particle size distribution. The relations of these variables are summarized in Archie's law, an empirical equation of resistivity, ρ [Ω m−1], of a rock (König et al., 2007).

$$\rho = \frac{a}{\phi^m S^n} \rho_w$$

Φ (porosity) and S (saturation factor) are fractions between 0 and 1, ρ_w [Ω m^{-1}] is the resistivity of groundwater, and the parameters a (tortuosity), m (cementation factor), and n (saturation exponent) are empirical constants that need to be determined for each study. Measurements were performed using the SYSCAL KID SWITCH-24 (IRIS instruments) with a 24-multi-electrode switch box.

2.2.3 Principles of GPR

GPR is an impulse radar system designed for shallow and subsurface investigations of 1 a 25 m depth. A transmitting antenna of a certain frequency sends an electromagnetic pulse from the ground penetrates the soil and a boundary layer is reflected when this pulse crosses two objects with different physical values. Then, the reflected wave returns to the ground surface and it is intercepted by the receiving antenna that measures the reflected signal as a function of time. Reflections and diffractions of electromagnetic waves occur at boundaries between rock strata and objects that show differences in their electrical properties. It is known that most soils and rocks have extremely low conductivity (about < 10-2 S/m), thus the propagation of electromagnetic waves is mainly affected by electrical dielectric constants of soils and rocks. Electric permittivity Ɛ and electric conductivity σ are the petrophysical parameters which determine the reflectivity of boundary layers and the penetration depth. Generally, the reflection of an electromagnetic wave occurs at boundary layers and its strength is shown by the reflection coefficient r which is given by (Blindow et al., 2007):

$$r = \frac{\sqrt{\varepsilon_1} - \sqrt{\varepsilon_2}}{\sqrt{\varepsilon_1} + \sqrt{\varepsilon_2}}$$

In this equation, Ɛ1 and Ɛ2 are the dielectric constants of root and soil, respectively. Specifically, the contrast in dielectric constants between a root and the surrounding soil determines root radar reflectance (Fig. 3a). The larger r and the stronger the reflected wave at the boundary layer, the size and bow of the resulting hyperbola vary according to the amplitude of the reflected wave. We have worked with waveform parameters of the time interval between zero crossings (ns) of the maximum and minimum reflected waves (Guo et al., 2013).

GPR profiles were performed using a MALÅ RAMAC system with 500 and 800 MHz antennas. The 500 MHz antenna allowed us to estimate the size, position and depth of roots with 2 to 6 cm diameter range, while the 800 MHz antenna served to differentiate the exfoliated rock base from potential roots (0.6 to 4 cm diameter) present underneath the rock. The position and diameter of roots identified in the radar profiles were manually compared in situ with the vertical distribution of excavated roots as calibrations points. Finally, 15 liters of water were injected into a shallow fracture of 35 cm length in an oak stand. 150 minutes later, we conducted radar profiles of 330 cm along the slope with the 800 MHz antenna to trace percolation and flow water profiles.

2.2.4. Data processing

Electrical resistivity tomography was conducted using a wenner-switch configuration with 1 m electrode spacing. Inversion and forward simulations were performed with EarthImager2D software for later manipulation of data files with the ArcMap module applying an Empirical Bayesian Kriging method. The radargrams (radar profiles) background removal, filtration, and Stolt F-K migration routines in addition to other interpretation tool parameters were performed with RadExplorer v1.42 Software (Mala GeoScience, USA Inc). The radar profiles (raw data) in this study are presented in 2D sections (radargrams). The field profiles (that come without any type of processing) are then imported into RadExplorer software for radargram processing. The waveform parameter of the time interval between zero crossings (ns) of the maximum and minimum reflected wave was calculated and extracted using this software.

Filtering of radar data is used as an attempt to remove unwanted signals (noise) and correcting the position of reflectors on the radar record. The steps to apply the filters depend upon the accuracy of collected profiles and the study's aim. For each case, the profiles have different processing procedures. All profiles in this study were processed with the same range of filter values, because the whole study area contained a layer of organic soil and weathered rock underneath, which have similar characteristics throughout the study site. The background removal filter eliminates parallel bands resulting from plane reflectors such as ground surface, leaf litter, soil horizons, and bands of low-frequency noise (Butnor et al., 2003; Dahboosh Al-Shiejiri, 2013). Stolt F-K Migration routine was used to correct object positions and collapsed hyperbolic reflections (diffracted waves) based on signal geometry (Dahboosh Al-Shiejiri, 2013). In the radargrams, roots were identified manually according to where hyperbolas of high amplitudes of reflected waves were observed compared to the surrounding area (Cui et al., 2011). The time interval between zero crossings (ns, time interval of maximum reflected wave) were extracted at the points where roots were identified in the radargram.

Analysis of variance for a two-way ANOVA was used to examine differences in root diameter. The model included as classification variables forest stands with three levels (pure and mixed pine and oak stands, fixed effect), soil depth with three levels (10, 20 and 30 cm, fixed effect). We ran Type I regression analyses to examine the relationships between root diameter and time interval between zero crossings (ns) in both radar systems.

2.3. Results

All resulting geophysical images shed light on the spatial distribution of tree roots in soils and rocks and rocky soil characteristics. Raw radargrams (unfiltered radar profiles) were difficult to interpret, because they included noise and ghost's areas, caused by material characteristics of organic and rocky soils. However, radargrams highlight clear hyperbolic reflectance which corresponds to the position of roots at different depths (Fig. 2.3a). ETR imaging results (Fig. 2.3b) for the top 50 cm depth refer to the areas of greatest drainage (200 – 450Ω m−1) and fracturation (400 -700Ω m−1) and correspond with resistivity values. However, ETR image outputs of EarthImager2D software did not reveal the exfoliated rocks that occur in the study area.

2.3.1. GPR detection of tree roots and diameter estimation

We examined the relationships between root diameter and time interval between zero crossings (ns) using 500 MHz signals ($P < 0.0001$, $R^2 = 0.93$, Fig. 2.4a, Table 2.2). With this antenna we detected roots as thin as 2.5 cm diameter and as thick as 7.5 cm in different tree stands. In pure pine stands, the finest roots (2-3 cm) were preferentially located in the top 10 cm of the soil, while roots with thicker diameters occurred mostly at 30 cm depth (Fig. 2.4b). In contrast, in pure oak stands root diameter tended to decrease with increasing soil depth (Fig. 2.4b). Also in mixed stands, deeper roots had smaller diameters (Fig. 2.4b). It is important to remark that pure pine stands showed no roots below 30 cm depth. Figure 5a shows an interpretation of radar profiles resulting from the antenna 500 MHz applying band pass filtering and background removal filter. In mixed forest stands, the radargram reveals the largest congregation of coarse roots near tree bases and adjacent areas as well as a high heterogeneity of root diameters (Fig. 2.5a). Radargrams also revealed the soil boundary layer and soil pockets (dotted line).

The 2-D radar profile overlaps were made in a 8.5 m x 6 m tracking quadrant with the 500 MHz antenna; in this case pine and oak roots (uppercase letters) were validated in situ (Fig. 2.6). In this root mapping survey along 7 radar profiles, we identified a total of 386 roots in their vertical distribution. Root diameter was highly variable (2-6 cm) as well as the signal output of deep roots (5 – 30 cm). For the horizontal distribution of roots, for instance the root marked as "B", the different radargrams (Figure 2.6b – g), showed the variation in diameter observed along a 6 m transect (radar profiles: a; 6.5, b; 4.8, c; 5.2, d; 5.8, e; 6.4, f; 4.6, g; 3.8 cm, respectively) in accordance to the size of signals amplitude (radar profiles: a; 1.16, b; 0.78, c; 0.84, d; 0.94, e; 1.09, f; 0.73, g; 0.61 ns, respectively). Roots with larger diameters had higher signal amplitude whereas smaller diameter roots had lower amplitude.

With a combination of concentric transects around a tree, using the 800 MHz antenna and applying background removal routines, we could identify pine trees anchored under exfoliated rocks (Fig. 2.7). The radargram also revealed (uppercase letters) roots under exfoliated rocks that we used to calibrate the radargram. This technique allowed us to differentiate the base of exfoliated rocks (about 35 cm deep) and the presence of thin roots under the rock (0.6 to 4 cm in diameter). For instance, along the transect at 50 cm three hyperbolas were reflected suggesting root presence under the exfoliated rock. By increasing the transect length, we also increased the number of reflected hyperbolas under the rock (i.e. transect at 100 cm distance) and the rock limits, permitting to follow root distribution in shallow rocky soil. Also, it is possible to observe the signal amplitude of pine trees anchored in exfoliated rocks (letter "B") and how they distribute their roots (arrows). In spite of filtering routines, it is very difficult to completely remove the noise in radargrams, therefore there was some noise due to excess leaf litter under the exfoliated rock. With this antenna, we observed a significant relationship between root diameter and time interval between zero crossings ($P < 0.0001$, $R^2 = 0.97$, Fig. 2.4a, Table 2.2).

2.3.2. Distribution of roots and resistivity profiles

Figure 5b presents electrical resistivity tomography profile for fourteen trees. The vertical and horizontal resistivity profiles of 2 m depths showed a wide range of values with maxima > 1000 Ωm at the profile bottom and minima of 250 – 650 Ωm at surface horizons. The ERT profile exhibited a layered structural organization that is characteristic of weathered rocks with exfoliation processes. For the first meter, we observed the largest variation in rock moisture content ranging from 250 - 1450 Ωm. Overlapping root vertical distributions (Fig. 2.5a), we observed that resistivity profiles were related to root distribution and vegetation cover at the measurement points. In the upper horizons (<0.5 m), the observed low resistivities (<450 Ωm) corresponded to islands of higher root densities beneath vegetation patches and associated with water extraction zones, while high resistivities (>450 Ωm) were associated with bedrock outcropping.

2.3.3. Fracturing as a secondary water supply to the forest

Upon water injection into a rock fracture close to oak trees on exfoliated rocks (Fig. 2.8), we observed a response signal in form of a wave amplitude equivalent to those observed underneath vegetation patches (Fig. 2.8b). Radargrams also showed an infiltration signal in the first 50 cm. The signal appeared 150 minutes after water injection and it was not homogeneous for all vegetation patches.

2.4. Discussion

In semiarid environments, forest ecosystems that develop on young volcanic bedrock and poorly developed soils face two independent growth limitations, 1) highly variable precipitation and increasing frequency of droughts and 2) extremely low water storage capacity of soils. Hence, insight into the distribution of different tree root types at the soil/rock interface and the spatiotemporal availability of water for plant uptake is fundamental for understanding tree ecophysiology, tree population dynamics, tree species interactions, and forest ecosystem function. Lack of instruments and technology to study belowground rock root ecology has delayed scientific advances in forest ecosystem ecology in semiarid regions. However, with interdisciplinary efforts and the employment of geophysical tools together with standard methods of ecosystem science (e.g. use of natural abundance and tracer stable isotopes) great advances have been achieved in our understanding of the underlying geoecohydrological mechanisms that explain tree species coexistence in extreme water-limiting environments (Rodriguez-Robles et al., 2015). Here, we demonstrate the enormous potential of applying geophysical tools to examine non-destructively and in real-time soil-rock-water and root characteristics. We clearly detected pine and oak roots of 0.6 – 6cm in diameter using GPR under soil in natural conditions (Fig. 2.4). Typically such kind of studies have been carried out in homogeneous soils, such as forest plantations, gardens, parks, backyards, crop fields, or under controlled conditions (Cermak et al., 2000; Cox et al., 2005; Dannoura et al., 2008; Zenone et al., 2008; Ow & Sim, 2012), because of the difficulties in detecting reflected signals (hyperbolic). The application of high and low frequency antennas gave complementary information in these shallow rocky soils. Using the 800 MHz antenna the detection efficiency of fine roots decreased at sites with higher litter accumulation under exfoliated rocks (Fig. 2.7). Hirano et al. (2009) reported that soil water content is a major factor that limits reflected wave detection originating from roots. Still, although our GPR survey was carried out in the dry period, we also had difficulties to accurately differentiate hyperboles of roots as some of them were overlapped.

2.4.1 Dynamics of weathered rocks and spatial distribution of roots

In forests growing on shallow soils and impermeable volcanic rock, it appears that water availability depends largely on the soil/weathered rock interaction. Thus, the water from a 56 mm rain event (accumulation) infiltrated and percolated down only the top 50 cm of substrate responded to the event (Fig. 5b, 250-550 Ωm). Although volcanic rock is characterized by low permeability, rock fracturation functions as secondary substrate porosity in impermeable rock, thus allowing water flow and storage (Carrillo-Rivera et al., 1996). The analysis of ERT profile images revealed a clear detachment of rock layers (exfoliation) and soil pockets; these conditions appear to promote the establishment and anchorage of tree plants under otherwise highly limiting soil water conditions (Fig. 2.5). Several studies have reported that trees can get established in rock fractures (mainly permeable rocks) (Poot & Lambers, 2008; Estrada-Medina et al., 2010) and locate their roots inside of this permeable material to exploit stored water (Querejeta et al., 2007; Schwinning, 2013). Combining ERT and GPR profile images (Fig. 2.5) suggests that in this shallow layer of weathered rock, species get established, forming vegetation patches. Oak and pine exhibit complementary strategies to access different water sources. Oak distributes its fine roots in both the soil organic layer and in the soil/weathered rock interface (Fig 2.4a, 5a). This strategy may enable oak to access water retained in weathered rock during the dry periods. Pine, in contrast, gathers water from soil pockets that exist within weathered rock. The difference in horizontal root distribution and its geological niches determines that these two species may persist in these ecosystems.

Our assay with the injected water into the rock fracture in the dry period, we observed the rapid response to water retention that exhibited oak roots to this water supply, taking a time of 150 minutes for this 15 liters to move 300 cm, indicating that there is communication between fractures and exfoliated rocks (Fig. 2.8). These exfoliated rocks in addition, can also serve as a support for trees (Fig. 2.7) and function as vital water reservoirs during dry periods. Root anchorage at this site can be considered as a survival strategy since trunks and horizontal roots located below exfoliated rocks permit to have support in these particularly shallow soils.

2.5. Conclusion

The geophysical images application as tools for research ecohydrology in forest, shows potential for estimating of diameters and water reservoirs, have also revealed scale-field spatial information of using GPR non-invasive mapping of the use ERT to characterize the interface soil/rock weathered which are traditionally assessed using coring and excavations methods. The spatial information obtained by combining ERT and GPR would have been difficult to get using standard sampling techniques. Our work therefore suggests that ERT and GPR have a significant role to play in capturing the spatial and temporal characteristics of moisture redistribution by root zone processes at the field scale.

However, while these tools offer many advantages and RadExplorer software has allowed us to emphasize areas of interest in the radargrams applied processing routines and other interpretation technique parameters, the main limitations observed in this study were: field soil conditions i) had dramatic impacts on the practicality of coarse root detection and quantification by GPR 500 MHz antenna; ii) it degraded the ability of 800 MHz GPR to delineate reflection signals emitted by the roots; iii) increases in soil moisture decreased the electromagnetic gradient between roots and soils, such that the reflected signals were weakened, making the delineation of roots more difficult under wet conditions.

We have no doubt that these geophysical images in field of ecology, are a valuable and promising tool for those who work with hydrologic processes and ecology of roots.

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2.7. Tables and Figures

Radar frequency (MHz)	Tree species	Soil type	Site Condition	Detected root diameter (cm)		Detected root depth (cm)		Reference
				min	max	min	max	
400	*Pinus taeda*	Gergeville soil	Plantation	3.7	10	-	130	*Butnor et al., 2001*
400	*Melaleuca quinquenervia*	Flat sandy soil	Controlled, root segments	3	13	-	50	*Nga et al., 2014*
450	*Quercus petrae*	Loamy deluvium soil	Plantation	3	5	-	200	*Hruska et al., 1999*
500	*Larixkaempferi L.*	Forest soil	Plantation	-	10	10	30	*Zhu et al., 2014*
500	*Quercus potosinaPinus cembroides*	Shallow soils and rocky	Semiarid tropical forest	2	7.5	3	40	**This study**
500	*Ulmuspumila, Artemisia ordosica*	Dry sandy	Controlled, fixed sand dunes	-	3.5	10	80	*Cui et al., 2013*
800	*Eucalyptus sp.*	River sand	Plantation	-	5	-	50	*Barton and Montagu, 2004*
800	*Quercus potosinaPinus cembroides*	Shallow soils and rocky	Semiarid tropical forest	0.6	4	1	40	**This study**
900	*Prunuspersica*	Faceville fine sandy loam	Controlled in a peach orchard	2.5	8.2	11	114	*Cox et al., 2005*
900	Different tree species	Red-yellow and marshy soils	Subtropical evergreen forest	1	3	1	60	*Yan et al., 2013*
1,000	*Eucalyptus sp.*	River sand	Plantation	1	10	-	50	*Barton and Montagu, 2004*
1,000	*Quercus douglasiiPinus sabiniana*	Auburn-exchequer soil	Semi-arid savanna	1.3	10	8	30	*Raz-Yaseef et al., 2013*
1,500	*Populusdeltoides*	Lakeland soil	Plantation	0.6	1.7	11	27	*Butnor et al., 2001*
2,000	*Ulmuspumila Artemisia ordosica*	Dry sandy	Controlled, fixed sand dunes	0.5	3.5	-	30	*Cui et al., 2011*

Table 2.1. A cross-study comparison of the detection capacity (minimum and maximum) of tree root diameter and depth in different soil types using GPR systems with various radar frequencies.

Table 2.2. Coefficients and least square residuals (R^2) of linear relationships between *root diameter* and *time interval*.

Frequency antenna	**intercept (y0) ± 1 S.E.**	**Slope (a) ± 1 S.E.**	**R^2**	***p***
500 MHz	0.1964 ±0.2006	5.7482 ±0.2223	0.93	<.0001
800 MHz	-2.0910 ±0.1273	6.2450 ±0.1839	0.98	<.0001

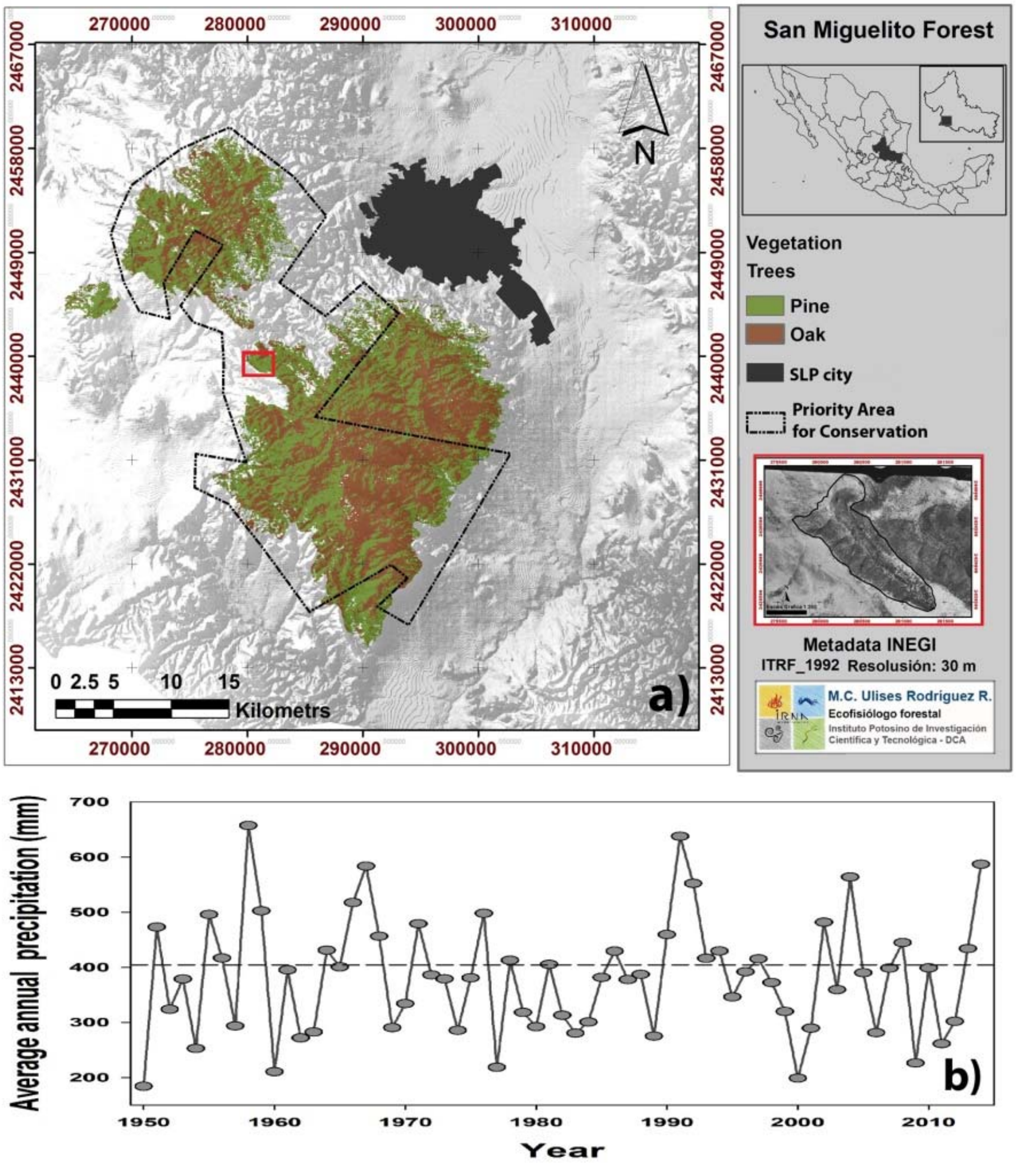
270000
280000
290000
300000
310000
2467000
2458000
2449000
2440000
2431000
2422000
2413000
N
0 2.5 5 10 15
Kilometrs
a)
San Miguelito Forest
Vegetation
Trees
Pine
Oak
SLP city
Priority Area for Conservation
Metadata INEGI
ITRF_1992 Resolusión: 30 m
M.C. Ulises Rodriguez R.
Ecofisiólogo forestal
Instituto Potosino de Investigación Científica y Tecnológica - DCA
Average annual precipitation (mm)
700
600
500
400
300
200
1950
1960
1970
1980
1990
2000
2010
Year
b)

Figure 2.1.

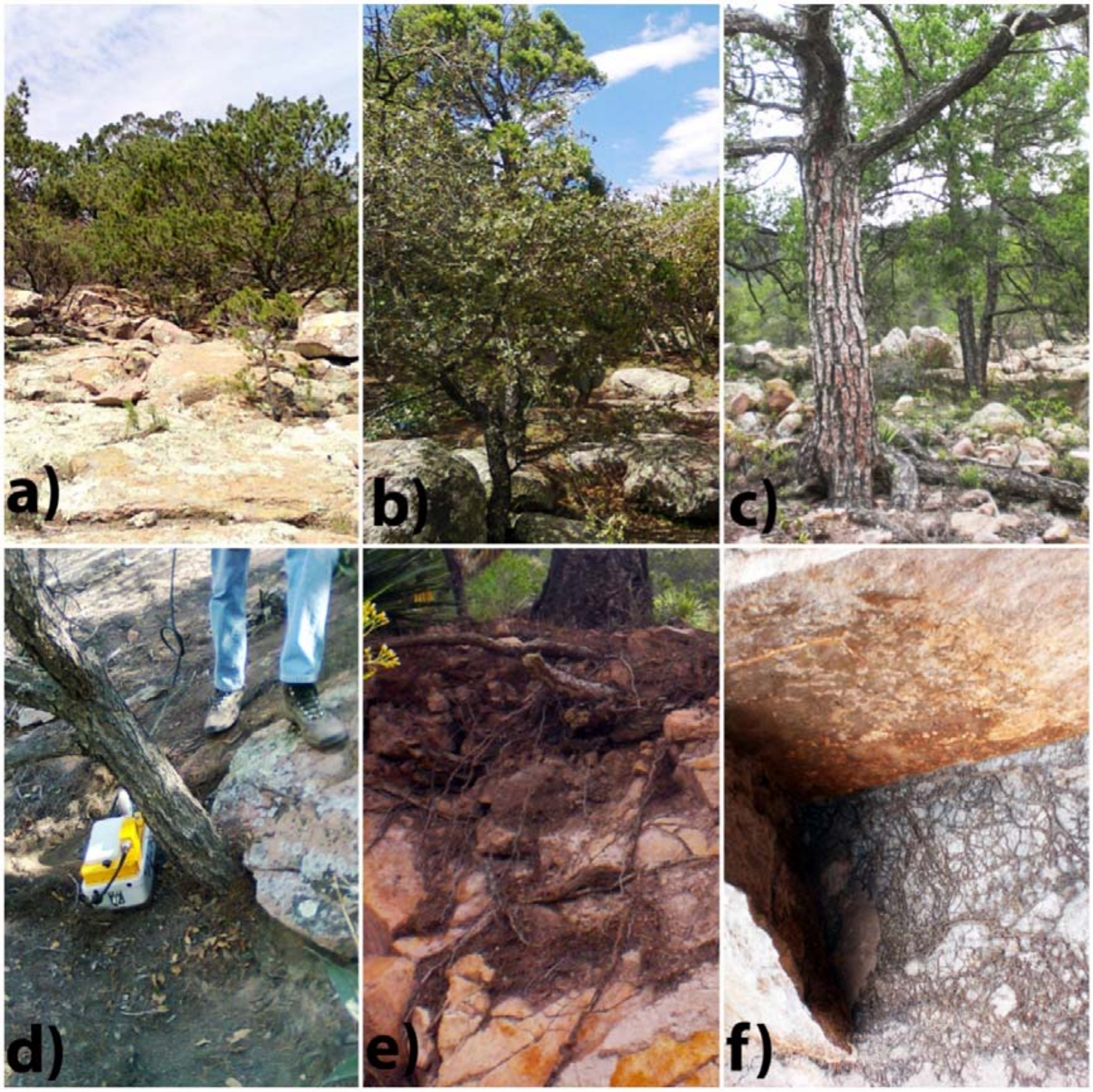

Figure 2.2

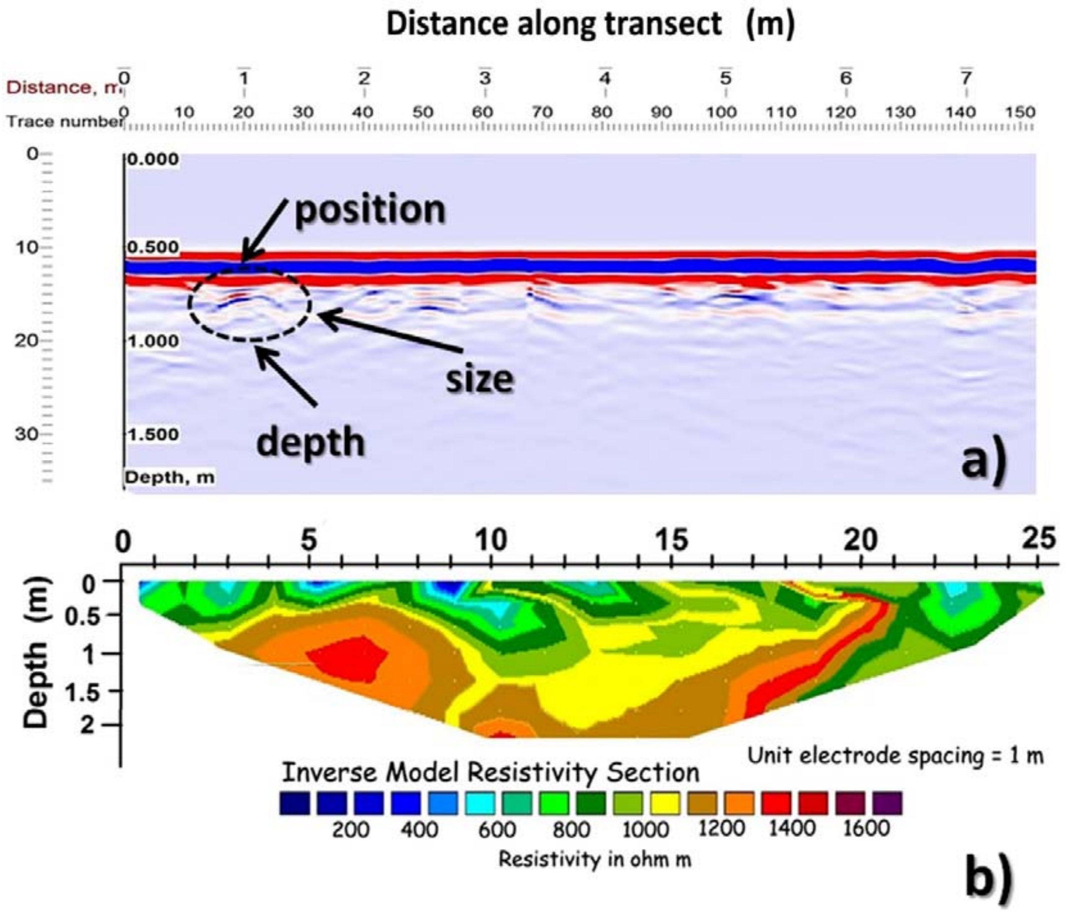
Distance along transect (m)
Distance, m
0
1
2
3
4
5
6
7
Trace number
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
0
10
20
30
0.000
0.500
1.000
1.500
Depth, m
position
size
depth
a)
0
5
10
15
20
25
Depth (m)
0
0.5
1
1.5
2
Unit electrode spacing = 1 m
Inverse Model Resistivity Section
200
400
600
800
1000
1200
1400
1600
Resistivity in ohm m
b)

Figure 2.3.

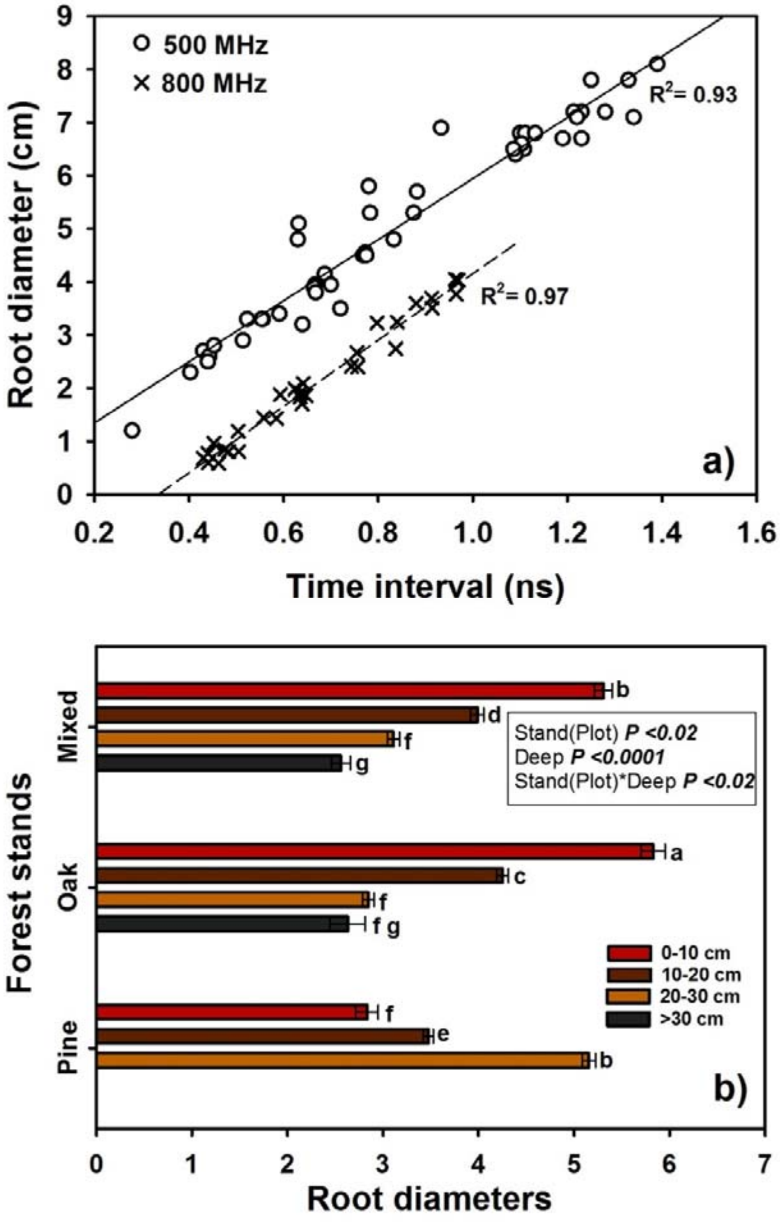
500 MHz
800 MHz
R²= 0.93
R²= 0.97
a)
Root diameter (cm)
0
1
2
3
4
5
6
7
8
9
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
Time interval (ns)
Mixed
b
d
f
g
Stand(Plot) P <0.02
Deep P <0.0001
Stand(Plot)*Deep P <0.02
Oak
a
c
f
f g
0-10 cm
10-20 cm
20-30 cm
>30 cm
Pine
f
e
b
b)
Forest stands
0
1
2
3
4
5
6
7
Root diameters

Figure 2.4.

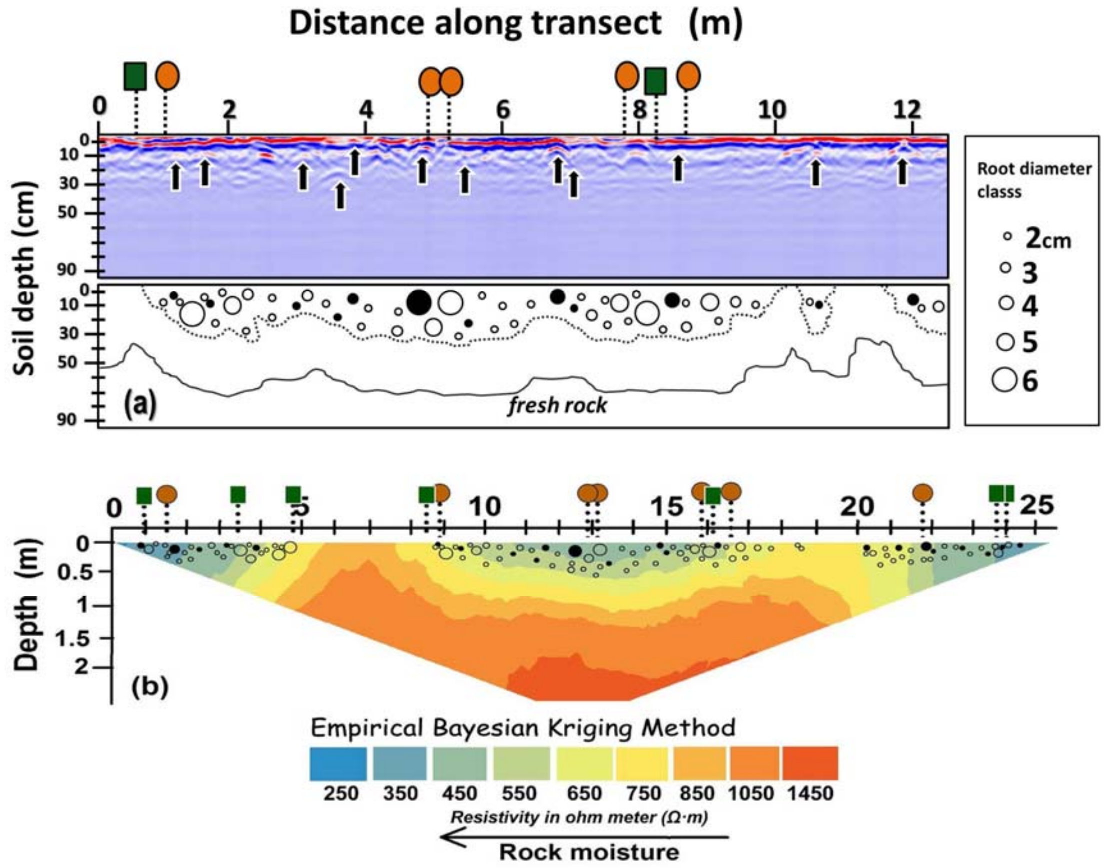
Distance along transect (m)
0
2
4
6
8
10
12
Soil depth (cm)
0
10
30
50
90
Root diameter classs
2cm
3
4
5
6
(a)
fresh rock
0
5
10
15
20
25
Depth (m)
0
0.5
1
1.5
2
(b)
Empirical Bayesian Kriging Method
250
350
450
550
650
750
850
1050
1450
Resistivity in ohm meter (Ω·m)
Rock moisture

Figure 2.5.

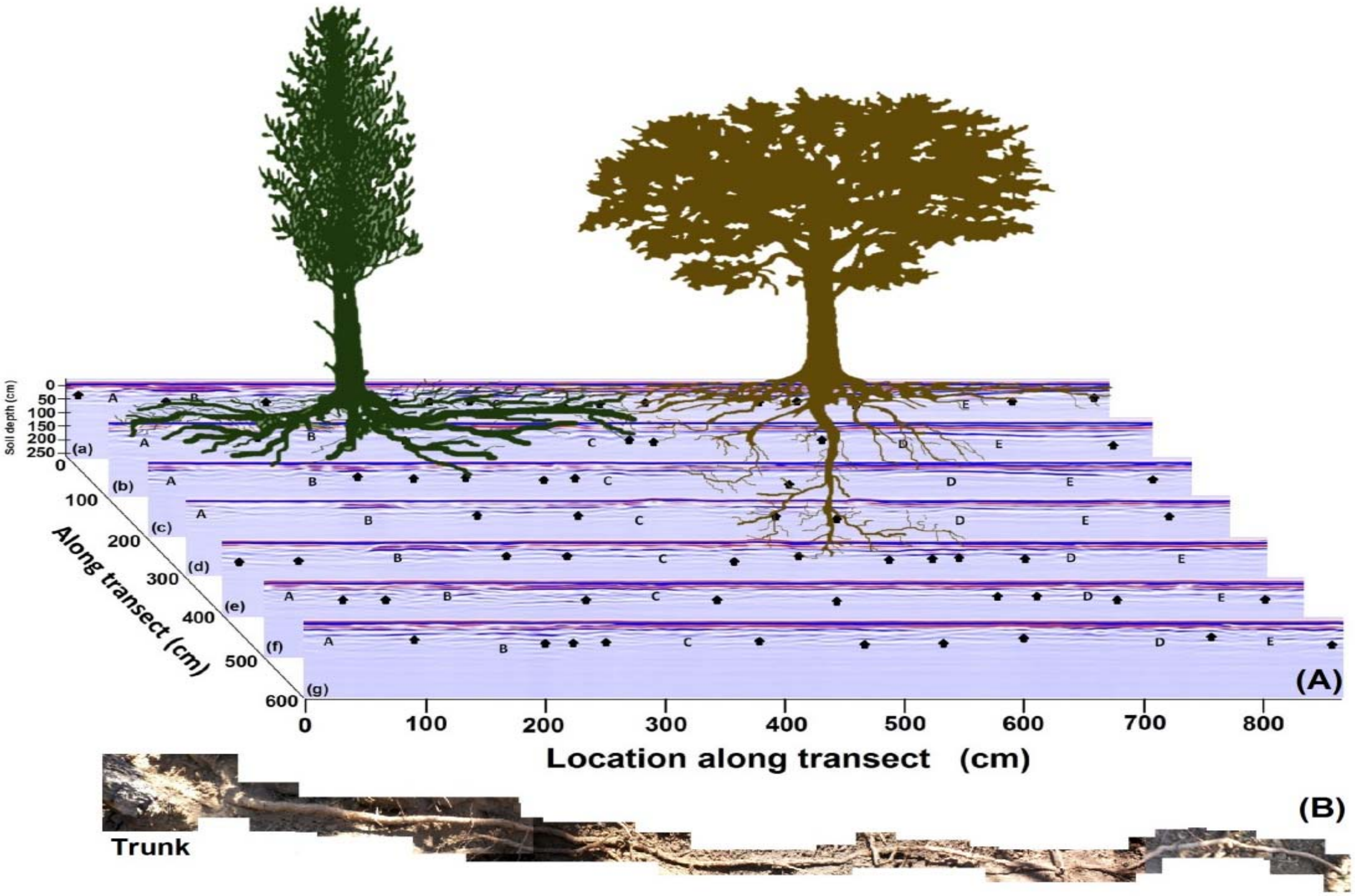
Soil depth (cm)
0
50
100
150
200
250
(a)
(b)
(c)
(d)
(e)
(f)
(g)
A
B
C
D
E
Along transect (cm)
0
100
200
300
400
500
600
(A)
Location along transect (cm)
0
100
200
300
400
500
600
700
800
(B)
Trunk

Figure 2.6

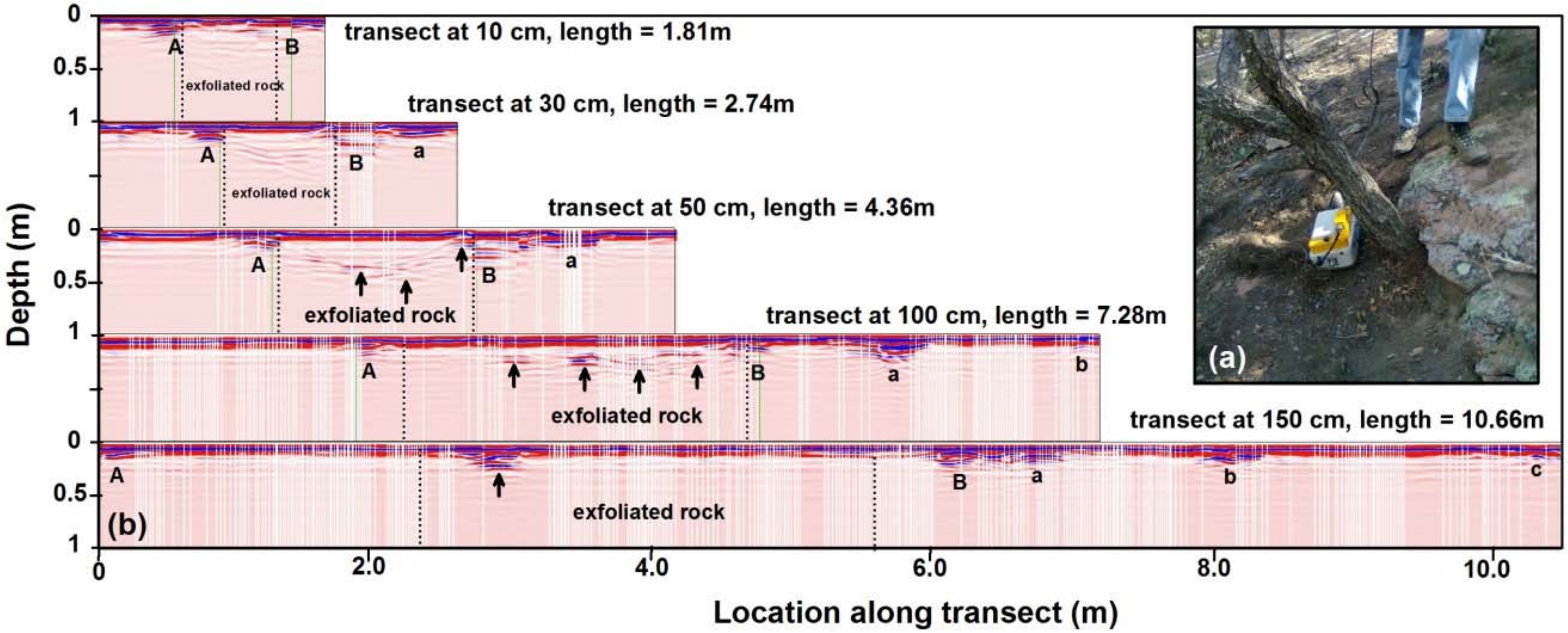
transect at 10 cm, length = 1.81m
transect at 30 cm, length = 2.74m
transect at 50 cm, length = 4.36m
transect at 100 cm, length = 7.28m
transect at 150 cm, length = 10.66m
A
B
a
b
c
exfoliated rock
(a)
(b)
Depth (m)
0
0.5
1
Location along transect (m)
0
2.0
4.0
6.0
8.0
10.0

Figure 2.7.

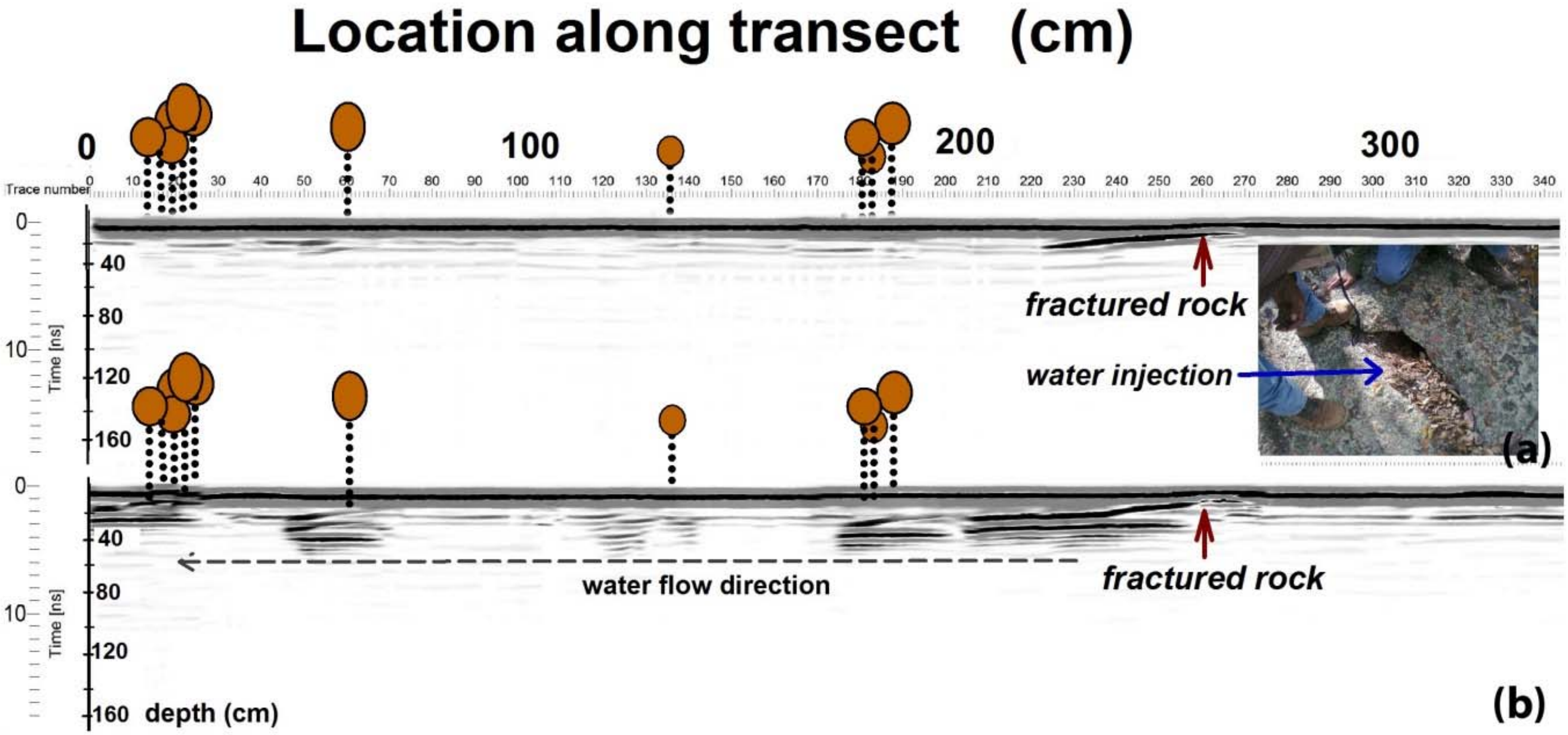
Location along transect (cm)
0
100
200
300
Trace number
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
190
200
210
220
230
240
250
260
270
280
290
300
310
320
330
340
Time [ns]
0
10
40
80
120
160
fractured rock
water injection
(a)
water flow direction
fractured rock
depth (cm)
(b)

Figure 2.8.

3
CHAPTER

GEOECOHYDROLOGICAL NICHES FACILITATE TREE SPECIES COEXISTENCE IN WATER-LIMITED ENVIRONMENTS

Abstract

In semiarid environments, geoecohydrological niches may determine which species coexist and how species respond to extreme hydrologic events such as drought. An important dimension of the geoecohydrological niche concept includes both the spatial and temporal partitioning of potential water sources, and plant adaptations, in particular roots in highly constrained landscapes characterized by shallow soils over fractured bedrock. In this study, we examined niche differentiation as well as adaptation mechanisms of Pinus cembroides and Quercus potosina to explore and exploit emerging spatial and temporal niches of water availability in a semiarid tropical forest that extends over large geographical areas, using ecophysiological and geophysical exploration techniques. Results showed that niche differentiation does exist for soil and rock water accessible to both species during the dry period. These geoecohydrological niches are spatially differentiated however there are also temporal and physiologic elements. Radargrams revealed, one that there exist two differentiated niches and second that in pine and oak stands finest and thickest roots were distributed over different depths (for pine; at 10 vs 15-25 cm depth; for oak; at 20-30 vs 10 cm depth, respectively). Use of labeled water injected in rock fractures also revealed that only oak was able to uptake this rock water while pine used only water pulses on the shallow soil. The difference in root distributions and alternations in accessing different water sources in the limited water and soil/rock depth system, determines where tree species can persist and ensure the coexistence of these two species.

Keywords: Hydrological niche, pine-oak coexistence, fractured rocky soils, noninvasive root research, ERT, GPR, hydraulic lift, water alternative sources.

3.1. Introduction

Most plant species require the same resources and acquire them through similar mechanisms, thus causing interspecific competition (Aarssen & Epp 1990; Goldberg & Barton 1992; Gurevitch et al. 1992). Yet, plant species co-occurrence appears to be the rule rather than the exception (Silvertown 2004) even under extremely limiting growing conditions. Potential coexistence mechanisms have been reviewed previously and empirical evidences in support of most of them have been presented (Silvertown 2004; Harmon et al. 2005; Eklöf et al. 2013). The Lotka-Volterra competition model (Gauze 1934), the regeneration or complementary niche theory (Grubb 1977), the resource ratio model (Tilman 1982), the storage effect (Chesson 2000), or the unified neutral theory (Hubbell 2001) are just a few concepts that describe the mechanisms to elucidate plant species coexistence. The principle of Gauss's competitive exclusion, which is derived from Lotka-Volterra's classical ecological theory, states that stable coexistence among species requires them to occupy and use differential niches to minimize competition. The concept of niche was originally proposed by Joseph Grinnell and Charles Elton and applied for the first time to explain animal coexistence (Chesson 1994).

In plant communities, the concept of niche has resulted more challenging to demonstrate, as all plants require basically the same resources (light, carbon dioxide, water, mineral nutrients). This raises the question as to what mechanisms do competing plant species exhibit that allows them to coexist, as the classical niche concept apparently cannot fully explain species co-existence as postulated by classical resource complementarity theory (Butler 2011). However, if classical theory applies niche differentiation should exist, however in a more complex biotic and abiotic "nichescape" that has not been considered thus far. Several studies have presented evidences of niche differentiation in plant communities (Hector et al. 2002; Fridley 2003), however the dimensionality and identity of these niche axes involved still remains unresolved. Therefore, understanding plant species coexistence in highly resource limiting environments imposes the need to disentangle the respective niche axes.

For instance, marked differences in vertical and horizontal root distribution patterns among species have been interpreted as adaptations to partition temporal and spatial niches and minimize competition for water during prolonged periods when precipitation is scarce and upper soil layers become extremely dry (Brassard et al. 2009; David et al. 2013). Trees with dimorphic root systems for instance, access water resources with both superficial and deep roots at different times of the year (Scott et al. 2008; Prieto et al. 2011). In such a case, the dual root system remain physiologically active during the dry season by switching from superficial to deep soil water uptake; since the latter stores soil water for longer periods (Dawson 1995; Dawson & Pate 1996). Consequently, some semiarid woody species do not necessarily rely on water uptake from a single soil depth. This adaptation also enables the extraction of water from a larger soil volume during dry conditions facilitating spatio-temporal niche partitioning among species (Phillips 1963; Rose et al. 2003; Bleby et al. 2010).

In shallow fractured rocky soils (i.e. rhyolitic composition), it is not well established how these can sustain tree water demands during dry seasons. Fine root foraging into fractured rocks, may be one adaptive mechanism to sustain continuous water supply. Hyphal foraging of ectomycorrhizal associations may be an alternative mechanism (Allen et al. 2002; Querejeta et al. 2012). Root water uptake from the top superficial soil layer appears only reliable in the rainy season. In contrast, the main water source for woody plants growing on karst systems, are soil pockets or clay layers within few meters of the soil surface (Estrada-Medina et al. 2013). Thus, our current understanding of the hydrology of shallow soils in semiarid forest ecosystems suggests that they function as a temporal water source in the wet period, yet remain decoupled from plant hydrology during the dry period (Kukowski et al. 2013). However, a recent study by Rodríguez-Robles et al. (2015) showed that throughout the year, tree water relations in two coexisting tree species remained coupled to the hydrology of shallow soils on top of fractured rocks, which were likely sustained by rock water supplied by mechanisms of hydraulic lift. Therefore, if niche differentiation may not occur at times we need to know the distribution and function of roots growing on these shallow soils and in rock fissures, in particular their role in accessing water in this potential reservoir

(Zwieniecki & Newton 1995; Estrada-Medina et al. 2010) and thereby controlling coexistence of tree species.

Geophysical exploration methods provide promising yet rarely explored opportunities for belowground ecological studies, as they are non-invasive and deliver high-resolution of spatial data and real time depth coverage (Rossi et al. 2011; Jayawickreme et al. 2014). Their use in ecological studies may help overcome challenges faced by researchers interested in identifying relationships among soil, water, vegetation, and other ecosystem components in shallow subsurface substrates (<30 cm). Ground-penetrating radar (GPR) is a geophysical and close-range remote sensing technique based on the use of radar pulses to obtain cross-section images of underground features (Blindow 2009). Electrical resistivity tomography (ERT) takes advantage of a fundamental property of rocks which is its electrical resistivity. It varies over a wide range from 10-8 to 1015 ohm m (Ω m−1) as a consequence of the physicochemical properties of soil-rock and is used to characterize the soil in terms of material type, lithology, alteration, water saturation and fracturing (Orellana & Silva 1982).

The semiarid forest ecosystem in Sierra San Miguelito (SSM) is located South of the desert scrub biome and southeast of the semiarid grassland biome in Central Mexico (Fig. S3.1). The SSM is a mountain massif of impermeable volcanic rocks (rhyolitic composition), highly weathered by exfoliation processes (peeling off in sheets) and characterized by extremely shallow soils (<25 cm). In spite of the thin substrate, these soils support a complex architecture typical of semiarid tropical pine and oak forests consisting of pure and mixed stands. Oak (*Quercus potosina*) seems to have access to rock water (Rodríguez-Robles et al. 2015) due likely to deeper roots than pine (*Pinus cembroides*), thereby allowing the exploration and acquisition of water from rock cracks. In mixed forest stands, oak seemed to have uplifted rock water from greater depth and deposit it on the surface soil, during 5 months of the drought period (Rodriguez-Robles et al., 2015). Yet, it is still unclear what precise mechanisms may underpin pine-oak coexistence. We suggested this species coexistence must be based on niche differentiation and thus complementary resource use by the two species. However, the existence of these potentially complementary niches first needs to be demonstrated for this “shallow soil over rocky substrate complex” with exceptionally low water storage potential.

Thus, using geophysical exploration methods (GPR and ERT) and considering the reported facilitation interaction between oak and pine during the dry season, we hypothesized that oak and pine coexist, because the long-term weathering process of rhyolite bedrock in the Sierra San Miguelito Volcanic Complex (SSMVC) generated geoecohydrological conditions for spatial and temporal niche differentiation (H_1). Complementarily, coexistence of species in this extremely adverse environment may have emerged as these tree species developed adaptations to access and use these resource niches. Consequently, oak with a deeper more vertical root system will preferentially occupy rocky substrate niches, while pine with its mostly horizontal root system will occupy shallow soils (H_2).

3.2. Materials and methods

3.2.1. Study site, geology and forest stand

The experimental area is a semiarid tropical forest located at the Southern part of the Sierra San Miguelito Volcanic Complex (SSMVC), in central México (Fig. S1, 2350 m.a.s.l.; latitude 22.25° and longitude -101.12°). The climate is semiarid, with summer precipitation lasting from June to September and with small winter rains between December and January accounting for 5% of total annual rainfall. For the last 40 years, average annual rainfall ranged from 380 to 640 mm (INEGI 2002). The topography is abrupt and irregular, representing a “complex terrain”. The landscape is characterized by slopes steeper than 30° and elevation ranges between 1900 and 2870 m.a.s.l.. According to the World Reference Base for Soil Resources (WRB) classification system, the extremely shallow soils and fractured rock 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 (Pérez et al. 2014). The dominant native tree species are *Pinus cembroides* Zucc. (1832) and *Quercus potosina* Trel. (1924), which form both pure and mixed forest stands with little understory. In general terms, it has been mentioned that Quercus species exhibit dimorphic roots, while Pinus species show horizontally spreading superficial roots (Kutschera & Lichtenegger 2002; Cermak et al. 2008).

3.2.2. Experimental plots

Along a 2.5 km long transect running parallel to a narrow watershed, where pine and oak trees are evenly distributed in pure and mixed stands (Table 3.1), we established 12 experimental plots of 25 m diameter (four plots per stand type). In September 2012, each plot was equipped with four (64 total) soil psychrometer sensors (TSP-55, Wescor Inc. USA) inserted at 12 cm depth (depending on the presence of soil pockets) near tree trunks to monitor soil water potential (Ψ_s). To determine plant water potential (Ψ_l) we harvested 2-3 leaf discs from healthy mature leaves and needles exposed to sunlight, allowing 25 minutes for stabilization in C-52 chambers (C-52, Wescor Inc. USA). Thus, soil and leaf Ψ were monitored every two weeks from September 2012 to June 2013, during the diurnal peak of water stress (from 11 to 14 hrs). Later, eight additional measurements (October 2013, December 2013, February 2014 and May 2014) were performed fortnightly (two per month) to compare Ψs data with ERT surveys.

3.2.3. Implementation of geophysical methods

In fall-winter 2012, we used a GPR with four frequency antennas (50, 250, 500 and 800 MHz) to characterize the weathered rocky soil, and the frequency and distribution of different root types. We established two parallel linear transects of 50 and 25 meters along the watershed crossing all experimental plots, as well as radial transects in each of the 12 plots (four directions: N-S, NE-SW, E-W and SE-NW). Different antenna frequencies were used for particular purposes. The 50 MHz antenna was used to differentiate between soil and bedrock depth. With the 250 MHz antenna, we obtained details on weathering and fracturation of volcanic rocks as a possible zone of water storage, while the 500 MHz antenna allowed us to estimate the size, position and depth of roots in the range between 2.5 to 6 cm diameter. Finally, with the 800 MHz antenna we differentiated the exfoliated rock base from potential roots (0.6 to 4 cm diameter) present underneath the rock. The radargrams (radar profiles) were manipulated applying background removal, filtration, and Stolt F-K migration routines with RadExplorer Software (Mala GeoScience USA Inc). In the radargrams, roots were identified manually according to where hyperbolas of high amplitudes of reflected waves were observed compared to the surrounding area (Cui et al. 2011). The time interval between zero crossings (ns, time interval for maximum reflected wave) were extracted at the points where roots were identified in the radargram. The position and diameter of roots identified in the radar profiles were manually compared in situ with the vertical distribution of excavated roots as calibrations points. The detection frequency for the number of roots identified in the radar profile was calculated along each transect for seven root diameter classes (2.5–3.0, 3.0–3.5, 3.5–4.0, 4.0–4.5, 4.5-5.0, 5.0–5.5, and > 6.0 cm).

Patterns of resistivity in the soil resulting from lithology, rock porosity, geologic structure, temperature, root density and water content (König et al. 2007; Kirsch & Yaramanci 2009; Brunet et al. 2010) were determined with ERT. During this 7-months period, we made 12 ERT profiles (four for each stand type) on different dates (October 2013, December 2013, February 2014 and May 2014). The resistivity of a rock is proportional to the resistivity of the dry material and is highly sensitive to saturated pore spaces (Chrétien et al. 2014). These observations are summarized in Archie's law, an empirical equation of resistivity, ρ [Ω m−1] of the rock (König et al. 2007).

$$\rho = \frac{a}{\phi^m S^n}\rho_w$$

Φ (porosity) and S (saturation factor) are fractions between 0 and 1, ρw [Ω m−1] is the resistivity of ground water, and the parameters α (tortuosity), m (cementation factor), and n (saturation exponent) are empirical constants that need to be determined for each study. We used SYSCAL KID SWITCH-24 with an array of 24 electrodes with 1 m spacing, and a Wenner-switch configuration, which provides reliable resistivity information to a depth of approximately 2.5 m (Iris Instruments, France). Inversion of the data was done with EarthImager2D for later manipulation with the ArcMap module.

For comparison among and within forest stands, four ERT determinations were carried out at different times of the year (October 2013, December 2013, February 2014 and May 2014), to detect both spatial and temporal patterns of soil moisture, based on the assumption that electrical resistivity decreases with increasing water content.

3.2.4. Testing niche utilization

To examine species root foraging into the two identified niches, we implemented an essay using labeled water (δD = -88.2‰, δ18O = -11.8‰). We choose either oak or pine (monospecific stands) as targets, selecting a tree that was neighboring a tree from the other species (oak → pine, pine→oak) at a range between 4 and 6 m. Within 30-50 cm of the target tree we located a rock fracture where we installed a 1.5 cm diameter hose down to 30 cm. Labeled water (δD = 485.1‰, enriched 6.5 times compared to natural abundance of deuterium) was slowly applied with a syringe (500 ml) into the hose, to avoid spreading labeled water on the soil surface. Presence of the D_2O tracer was detected by collecting seven branches from different regions of the crown. After the injection of D_2O (day 0), we collected every other day branches, wood cores from the target plant and its closest neighbour tree and soil during the next 10 days. In all cases, branches were collected at 12:00 hours.

3.2.5. Statistical analysis

Two-way nested analysis of variance with forest stands with three levels (pure and mixed pine and oak stands, fixed effect), soil depth with three levels (10, 20 and 30 cm, fixed effect) and plots number per stand as nested factor was performed to examine differences in root diameter and root detection frequencies. We also ran a nested ANOVA of repeated measures to examine differences in leaf and soil water potentials considering different stands with four levels (pine and oak trees in pure and mixed stands), and time (10 weekly sampling dates, random effect) as repeated factor and plots number per stand as nested factor. In both models, the plot effect was nested within forest stand effect. We run Type I regression analyses to examine the relationships between root diameter and time interval between zero crossings (time of maximum signal, ns), to calibrate the method. Polynomial quadratic regression analyses were implemented to examine the relationships between soil water potential (Ψ_s, MPa) and resistivity (Ω m−1). Spatial analysis of vertical root distribution at different depths and soil electrical resistivity were examined using the Kriging interpolation method (Empirical Bayesian Kriging Simulations). All statistical analyses were performed with SAS v. 9.2 for Windows (SAS System, Cary, NC 2002-2007), whereas geostatistical analysis were run with ArcGIS v. 10.1 for Windows (ArcGIS Desktop, ESRI 2011).

3.3. Results

3.3.1. Soil and leaf water potentials

Monitoring of leaf and soil water potentials started at the end of 2012 rainy season (September 2012, Fig. 3.1). There was a large variability in Ψ_s and Ψ_l with values oscillating from -1.2 to -5.9, however, following the end of summer Ψ dropped rapidly until a winter rain rewetted the soil (32 mm, Dec 2012– Jan 2013). Later, Ψ remained more or less stable until they recovered at the beginning of the rainy season (June). Ψ_l and Ψ_s time series were divided into three ecohydrological functional periods: depletion and recovery periods and the wet period. The depletion period corresponded to the time when soil humidity started declining at the end of the rainy season, from October 2012 to February 2013. The recovery period started once leaf and soil Ψ reached their lowest values and lasted until the beginning of the rain season (March to May 2013). The wet season corresponded to the months receiving monsoon precipitation in September 2012 and June 2013.

Observed differences in soil and leaf water potential in the course of the study depended on stand type (species x stand(plot), $P < 0.005$ for Ψ_l and $P < 0.0001$ for Ψ_s, Table 3.2). Overall, pine stands exhibited leaf and soil Ψ around 1 MPa ($P < 0.001$) more negative compared to those in oak stands, reaching their lowest Ψ_s and Ψ_l in February 2013 (Ψ_s: pure pine = -5.1 ± 0.052 MPa, mixed pine = -5.4 ± 0.052 MPa; Ψ_l: pure pine= -5.6 ± 0.050 MPa, and mixed pine = -5.8 ± 0.050 MPa, Fig. 3.1). Beginning March 2013, in both oak and pine stands Ψ_s and Ψ_l began to rise steadily, except in case of pure pine stands, which were most responsive to recent rain events (Fig. 3.1b, average difference 0.72 MPa in soil and 0.41 MPa in leaves, $P > 0.001$, Fig. 3.1).

3.3.2. Niche characterization

Radargrams derived from the GPR survey using antenna frequency of 50 MHz differentiated a 0.25m layer that corresponded to the shallow soil (Fig. 3.2a), with rock outcroppings at the surface (e.g. at 5, 12, 41, 45 m; Fig 3.2a). Underneath the soil, lays a highly fractured layer and regolith due to rock weathering with scattered soil deposits (between 0.25 and 0.75 m). Beyond 0.75m, the radargram showed fresh rock material of several meters thickness, without fissures or cracks. However, when using the 250 MHz antenna and applying background removal and Stolt F-K migration, we detected detached curved plates derived from belowground rock crusts (exfoliated rocks as a product of mechanical weathering processes) and the presence of coarse woody roots underneath exfoliated rocks (Fig. 3.2b,c).

3.3.3. Distribution and characteristics of roots

In radar profiles with the 500 MHz antenna (Fig. 3.3), band pass filtering and background removal allowed delineating and locating roots with different diameters in the rocky soil (0-0.45m). Amplitude of reflected hyperbolas derived from roots decreased with decreasing root diameter (Fig. 3.3). Hyperbolas detected with GPR in the different plots were validated and calibrated with the respective excavated roots in the field (Figs. 3.2e, S.3.2), showing diameters from 2.5 to 7.5 cm to a maximum depth of 40 cm. The strong positive relationship observed between the time interval with zero crossing and root diameter ($P< 0.0001$, $r^2= 0.93$, Fig. S3.2), indicate the high reliability of the method to estimate diameters. A total of 3218 roots in their vertical distribution were identified along 16 transects (Table 3.3). Mean root diameter was 4.67 cm with smallest diameters of about 2.5 cm and the largest of 7.5 cm. Of these, approximately 35% of detected roots measured less than 2.6 cm in diameter, with highest root frequencies depending on stand type and soil depth. In pure pine stands, the highest frequency of small diameter roots occurred in the top 10 cm of soil (Fig. 3.3 top and S3.3), which contrasted with pure oak stands where up to 70% of this root diameter class occurred at 20 cm depth. Pure pine placed roots thicker than 6 cm diameter preferentially between 10 and 30 cm depth, whereas pure oak showed a uniform distribution within the soil, however with overall lower frequencies (Fig. 3.3 bottom, S3.3).

Analyzing root spatial distribution for the different stands, we observed that root diameter tended to increase with increasing soil depth in the case of pure pine plots (r^2 = 0.72, Fig. 3.3a, b, c). In contrast, root diameter in pure oak stands tended to decrease with increasing soil depth (r^2 = 0.75, Fig. 3.3d, e, f), while in mixed stands we observed a trend of decrease in diameter in deeper roots (r^2 = 0.75, Fig. 3.3g, h, i). Another difference between mixed and oak stands was that in the upper soil layer there were no roots thicker than 5 cm in diameter (Fig. 3.3g).

3.3.4. Water dynamics in the pedothitic substrate as detected by ERT

The different forest stands exhibited similar structural organization for rock moisture content derived from ERT profiles. These consisted of higher resistivities for deeper layers (>2m) compared to surface horizons (Fig. 3.4). Basically, resistivity distribution profiles reflected the lithological characteristics of the study site, with low resistivity at 1 m depth corresponding to the fractured rock. Underneath the first meter, there was a clear increase in resistivity corresponding to fresh rock (not weathered). It was also observed that resistivity values got distributed along layers throughout the rock profiles, which is characteristic of exfoliated rocks (weathered type). Resistivity profiles were also related to vegetation cover at the measurement points. In the upper horizons (<0.5 m), the observed low resistivities (<450 Ωm) corresponded to islands of higher root densities beneath vegetation patches and associated with water extraction zones, while high resistivities (> 450 Ωm), occurred as a consequence of bedrock outcropping.

Following seasonal drying (Dec 2013 to May 2014), ERT profiles of all stands exhibited increasing resistivity between 0 to 1 m depth (Fig. 4.4), which was attributed to both tree water uptake and soil evaporation. Thus, in the first meter, we observed the largest spatial variation in rock moisture content ranging from 250 - 1450 Ωm. When comparing forest stands, both mixed and pure oak stands showed highest moisture content in all four monitored periods (Fig. 4.4d - i). There were also differences in geodiversity associated to the location of forest stands, with pure pine preferentially occurring in sites with deepest soils (up to 60 cm), while pure oak anchored mostly on exfoliated rocks.

Interestingly, a strong negative relationship (R^2 = 0.95) was observed between soil resistivity and soil water potential, including all observations from the different stands (P < 0.0001, Fig. S3.4). Thus, as resistivity increased Ψ_s dropped up to resistivities of around 750 Ωm being proportional to almost -6 MPa.

3.3.5. Essay with labeled water

When oak was the target plant, the signal of labeled water started to appear on woody tissue at the fourth day while the companion pine showed the label at day 6th (Fig. 3.5a). When pine was the target plant, oak required up to 7 days to show the D2O label whereas pine only exhibited the label after 9 days. Regarding the monitoring of D_2O on the soil around target and neighboring plants we could detect it at day seven in both target and neighboring oak. In soil around both pine trees we could not detect labeled water during the 10 days study (Fig. 3.5b).

3.4. Discussion

Conditions at our study site included shallow soil and a high proportion of volcanic rocks (Fig. 3.2a), both limiting water access to roots and hampering vertical penetration and percolation of tree roots and water, respectively. In spite of this, the forest ecosystem that developed over this shallow substrate harbors two coexisting tree species with proportional abundances and productivities (Perez et al. 2009) suggesting they have developed complementary mechanisms to acquire limiting resources. Based on these observations and a recent study by Rodríguez-Robles et al. (2015), we suggest that oak and pine species coexist in this azonal ecosystem, because of the interaction of meteorological events, inherent pedolithic properties of this young volcanic substrate, and tree species characteristics that have generated a unique geoecohydrological habitat with distinctive spatial and temporal niches for complementary resource use as fundamental driver for small-scale habitat differentiation.

While from a theoretical perspective, the concept of niche complementarity in the context of species coexistence and resource sharing is compelling, to empirically demonstrate plant species coexistence mechanisms coupled to niche segregation is highly challenging (Carroll et al. 2011). Those studies need to prove two fundamental aspects separately: first, the existence and biogeophysical nature of complementary niches and secondly, evidence that plant species have developed physiological, phenological, morphological and/or ecological adaptations that allow them to exploit the resources associated with these niches, which together facilitate coexistence (Silvertown 2004).

As mentioned earlier, several mechanisms have been proposed to explain plant coexistence (see synthesis by Silvertown 2004), one basic idea is that niche differentiation occurs and species can obtain resources along niche axes. Spatial and temporal heterogeneity are attributes that may contribute to create these niche axes. A fundamental aspect that accompanies niche differentiation is that this facilitates species coexistence. Silvertown (2004) suggested four tests to evaluate the existence and functionality of niches, including a) intraspecific competition is greater than interspecific, b) segregation on a resource or environmental axis, c) tradeoff in traits or in performance on different niche axes, and d) niche shifts in response to experimental manipulation of competition. In our study, although it was not designed with these tests on mind, we believe it addresses somehow most of them.

3.4.1. Intraspecific competition is greater than interspecific

Thus, to examine competition we used the physiological performance as a function of the distance between species. We attested from a previous study (Rodriguez-Robles et al., 2015) that oak did not show a decrease in Ψ_l and G_{sw} (Fig. S3.5) as it grew closer to pine, likely because it accessed both shallow soil and rock water. In contrast, as pine grew closer to oak it showed an improvement in the performance of Ψ_s and G_{sw} (lower water stress). This response (Fig. S3.5), suggests a greater water availability in the close range of oak (Rodríguez-Robles et al. 2015), therefore reduced or null interspecific competition. A previous study of forest productivity using literfall as a surrogate variable, showed that mixed forest stands showed overyielding respect to pure oak and pine stands with 19 and 49% more productivity (Perez-Suarez et al., 2009), respectively.

3.4.2. Segregation on a resource or environmental axis

According to soil water potential measurements at 10 cm deep, water availability dropped to the lowest values (about -5.3 MPa) by December. Later, between February and May soil water potentials increased by over 2.0 MPa, yet in the absence of additional rainfall events. This suggests that shallow soils maintain water availability not only by meteorological events but also through geoecohydrological mechanisms (Rodríguez-Robles et al. 2015). GPR and ERT temporal profiles indicate that fractured rocks occur within the top 70 cm of substrate profile (Fig. 3.2a, b), and this is the zone with greatest resistivity variation occurs (250-1050 Ωm) at a single date, where higher moisture zones are interspersed with rocks (Fig. 4). Although volcanic rocks are characterized by high impermeability, fracturation as a product of physical weathering induces a sort of porosity in impermeable rocks, which allows water percolation, storage and lateral flow. ERT profiles also indicate sub-hypodermical water flow running along the profile. This flow represents a more permanent water source for the forest than individual static reservoirs in rock cracks and soil pockets. Evidence for this sub-hypodermal water flow is provided in Figs. 3.4h and 4l, in which clusters of trees recorded at ~15 m along the transect are associated to zones of lowest resistivity suggesting a possible water uplift from fractured rocks to the soil surface facilitated by the roots located at the depth of the sub-hypothermal water flow. For pine stands (Fig. 4a - d), no such a development of low resistivity was observed with seasonal progress of drought but only for oak monocultures and mixed stands.

3.4.3. Tradeoff in traits or in performance on different niche axes

Niche differential use by the two forest species is inferred from radargrams identification of root size and distribution. According to this, in pure pine stands the thickest roots (4 - 7.5 cm diameter) occurred mostly at 15 to 25 cm depth (Fig. 3.3c), while fine roots that are those related to root foraging (< 3 cm) were mainly distributed in the top10 cm (Fig. 3.3a) suggesting that pine has developed adaptations to acquire water from small water pulses typically occurring in the rainy season (Fig. 3.1) or from hydraulic lift by oak (Prieto et al. 2011). In contrast, in pure oak stands, root diameter distribution was opposite to the one observed in pine (*P*<0.02, Fig. 3.3d - f). Oak placed thicker roots in the top 10 cm of soil (Fig. 3.3d), while small diameter roots occurred mostly at 20-30 cm depth (Fig. 3.3f), coinciding with humidity patterns observed in rock fractures at > 30 cm (Fig. 3.4l). These findings help to explain the recovery of oak water status during drought periods (recovery phase, March to May 2013, Fig. 3.1), as fine roots related to water uptake are placed in fractured rocks (Fig. 3.2d) that function as water reservoirs. The use of water from the fractured limestone rocks by woody vegetation has been reported in several other studies (Nadezhdina et al. 2008; Estrada-Medina et al. 2010; Kukowski et al. 2013; Schwinning 2013; Tokumoto et al. 2014).

To attest whether forest species can differentially acquire water from any of the two geologic niches during the dry period, we examined responses to labeled water (δD = 485‰) applied on rock fractures (>30 cm). For paired trees 2 to 4 m apart, oak required 3 days to show the label on its branches tissue water, when this species was the target, while the partner pine reported the label up to 6 days later from the time of injection (Fig. 3.5a). Our test indicates that for pine, this water was not directly taken from the fractured rock but from the remobilized labeled water by oak to the soil surface (Fig. 3.5b). We concluded this, because when pine was the target of labeled water, pine did not show labeled water in its branches tissue even after 10 days (Fig, 3.5a), the accompanying oak showed water tissue enriched at day 7th. In addition, the soil on the surface close to pine did not get enriched with labeled water through mechanisms of water remobilization whereas in all cases for oak, the soil surface got enriched after 7 days (Fig. 3.5b). These results suggest that oak was able to get the water from the rock fractures and that is also able to remobilize it to the top soil. In contrast pine showed no adaptations to acquire water rock, however it took advantage of water uplifted by oak (Fig. 3.5a) during the dry season. This observation coincides perfectly with the identification of the two niche domains mentioned earlier (top soil and rock fractures, Fig. 3.2) and with root functional types distribution associated to substrate depth and niche types (Fig. 3.3). For pine, this seems as a good strategy for two reasons, 1) these are sites, where 60% of the rain occurs as events smaller than 5mm just wetting the soil surface (Perez et al. 2009), and 2) these surface roots will also take advantage of passive water transfer by oak roots from the rock reservoirs to the top soil as was suggested by Rodríguez-Robles et al. (2015).

3.4.4. Niche shifts in response to experimental manipulation of competition

Finally, we can no prove niche shifts since we did not manipulate competition. Still we can invoke the natural occurrence of the two forest species where monospecific pine stands are established on sites presenting the deepest soils (30 to 60 cm, Fig. 3.4, contrast pine vs. oak and mixed forest) and a lower degree of rock fracturation. Mixed and monospecific oak sites showed a shallower soil on top of a high rock presence. In pine sites, oak appeared incapable to get establish likely through competitive exclusion mechanisms with pine. Whereas in oak sites, it appears that pine is acting as an opportunist species profiting from water remobilization by oak in shallowest soils.

Thus, based on the radargrams, rooting strategies include a dimorphic system for oak with thin roots exploring water sources in rock fractures and at the transition to healthy rock as well as superficial thick roots for anchorage and support. In contrast, pine exhibits a rooting strategy emphasizing water acquisition in the soil surface (top 10 cm) profiting from small wetting events, while thick roots served as anchorage in the deepest rock layers (> 25 cm). Rooting strategies by pine and oak appear complementary adaptations for niche use in this shallow rocky soil, as fine roots involved in water and nutrient uptake are spatially segregated. These differences in rooting patterns determine where tree species can persist and thrive ensuring the long-term coexistence of these two tree species forming important semiarid forest-ecosystems in this region otherwise dominated by scrubland and grassland.

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3.6. Tables and Figures

Table 3.1 Number of trees monitored (*n*) at all sampling dates, as well as mean and standard error for tree diameter at breast height (DBH), estimation of tree age based on growth rings and total tree height of four forest stands at Sierra San Miguelito, San Luis Potosi, Mexico 2013.

Species / stand	*n*	DBH (cm)	Age (years)	Sample height (m)
Pine/pure	16	14.67 ±3.19	79.05 ±3.42	6.24 ±1.74
Oak/pure	16	8.93 ±1.49	63.17 ±5.21	5.65 ±2.77
Pine/mixed	16	14.72 ±5.37	82.22 ±2.86	7.89 ±1.86
Oak/mixed	16	8.13 ±1.43	76.44 ±4.88	6.42 ±1.96

Table 3.2 Nested repeated measures ANOVA for soil (Ψ_s) and leaf (Ψ_l) water potentials in different stands (pure pine, pure oak, mixed pine and mixed oak), tree species (*Pinus cembroides*, *Quercus potosina*), plots (four per stand type) and sampling date in a tropical semiarid forest ecosystem in Central-North México.

	Soil wáter potential			***Leaf wáter potential***		
Effect	df	*F*	*P*	df	*F*	*P*
Species	1	4422.60	<0.0001	1	3902.70	<0.0001
Stand	1	0.65	0.4190	1	0.17	0.6839
Species*Stand	1	1.11	0.2925	1	0.64	0.4230
Species*Stand(Plot)	12	2.45	0.0037	12	3.32	<0.0001
Date* Species*Stand	36	441.03	<0.0001	36	418.39	<0.0001
Date* Species*Stand(Plot)	108	0.65	0.9976	108	0.78	0.9501

df= degrees of freedom, *F* = Fisher´s statistics, *P* = probability value

Table 3.3 Total number of detected roots and mean root diameter (±1S.E.) for each root diameter class of pine, oak and mixed forest stands, estimated from GPR profiles along 25 m transect.

	Pinus cembroides			***Quercus potosina***			**Mixed forest**		
Root diameter class (cm)	Number of radar detected roots[a]	Number of transects in which roots occurred[b]	Mean diameter ±SE (cm)	Number of radar detected roots[a]	Number of transects in which roots occurred[b]	Mean diameter ±SE (cm)	Number of radar detected roots[a]	Number of transect in which roots occurred[b]	Mean diameter ±SE (cm)
2.5-3	204	16	2.65 ±0.05	412	16	2.63 ±0.12	500	16	2.65 ±0.12
3-3.5	36	16	3.28 ±0.01	56	16	3.28 ±0.36	27	12	3.28 ±0.07
3.5-4	19	15	3.92 ±0.01	43	14	3.87 ±0.14	104	16	3.92 ±0.15
4-4.5	13	4	4.63±0.44	19	7	4.25 ±0.08	16	6	4.13 ±0.50
4.5-5	103	13	4.58 ±0.02	122	9	4.55 ±0.11	169	13	4.60 ±0.08
5.-5.5	12	4	5.23 ±0.02	17	9	5.20 ±0.68	62	16	5.22 ±0.08
5.5-6	17	13	5.88 ±0.01	23	14	5.84 ±0.03	53	15	5.84 ±0.26
>6	458	8	7.57 ±0.97	160	13	7.67 ±0.87	573	14	7.61 ±1.00
All diameter classes	862	16	4.71±1.54	852	16	4.66±1.58	1504	16	4.65 ±1.56

[a] Along a total of 16 transects.

[b] Number of transects in which roots of each diameter class were found (out of 16 transects).

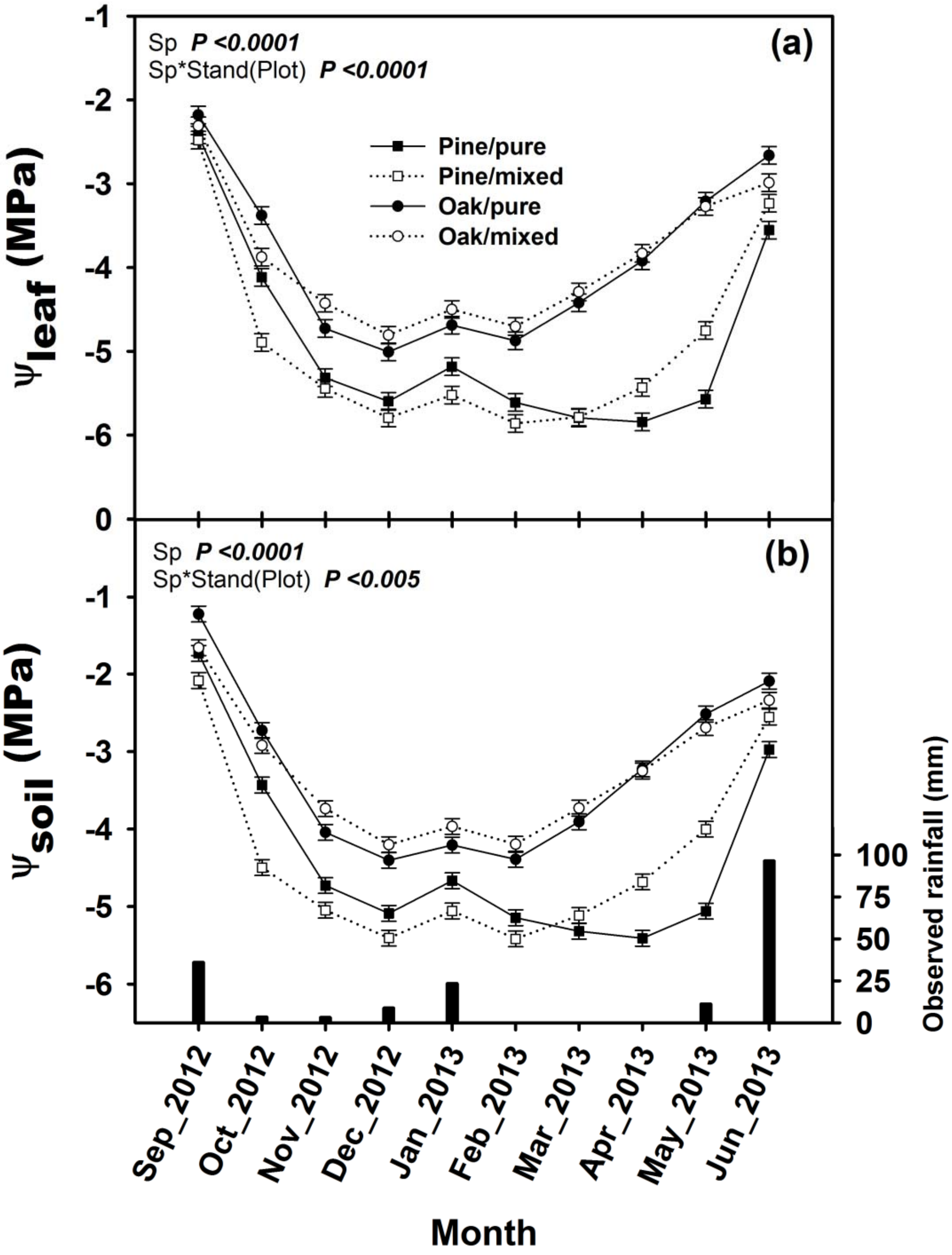
(a)
Sp P <0.0001
Sp*Stand(Plot) P <0.0001
Pine/pure
Pine/mixed
Oak/pure
Oak/mixed
Ψ_{leaf} (MPa)
-1
-2
-3
-4
-5
-6
0
(b)
Sp P <0.0001
Sp*Stand(Plot) P <0.005
Ψ_{soil} (MPa)
-1
-2
-3
-4
-5
-6
Observed rainfall (mm)
100
75
50
25
0
Sep_2012
Oct_2012
Nov_2012
Dec_2012
Jan_2013
Feb_2013
Mar_2013
Apr_2013
May_2013
Jun_2013
Month

Fig. 3.1

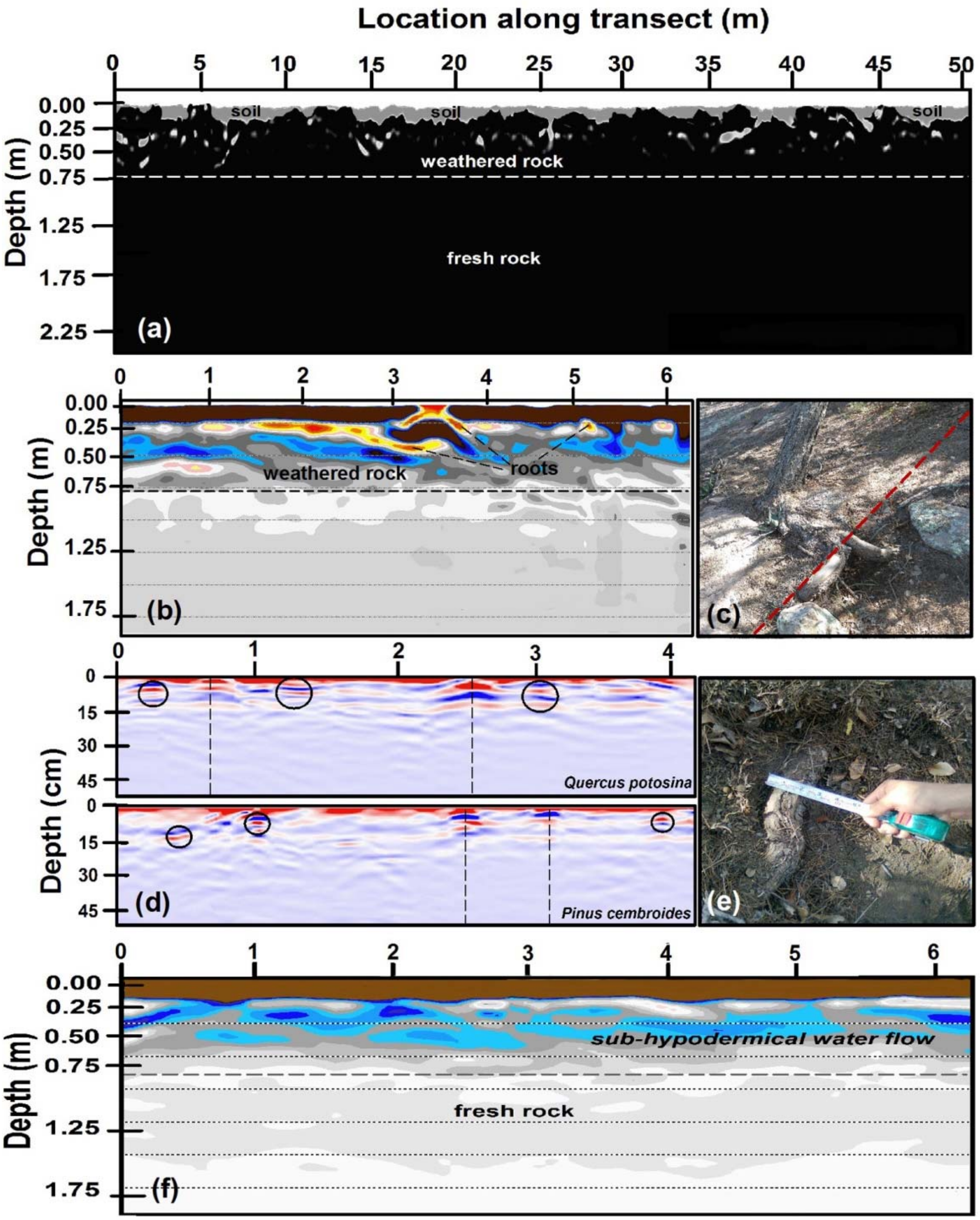
Location along transect (m)
0
5
10
15
20
25
30
35
40
45
50
Depth (m)
0.00
0.25
0.50
0.75
1.25
1.75
2.25
soil
soil
soil
weathered rock
fresh rock
(a)
0
1
2
3
4
5
6
Depth (m)
0.00
0.25
0.50
0.75
1.25
1.75
roots
weathered rock
(b)
(c)
0
1
2
3
4
Depth (cm)
0
15
30
45
Quercus potosina
0
15
30
45
Pinus cembroides
(d)
(e)
0
1
2
3
4
5
6
Depth (m)
0.00
0.25
0.50
0.75
1.25
1.75
sub-hypodermical water flow
fresh rock
(f)

Fig. 3.2

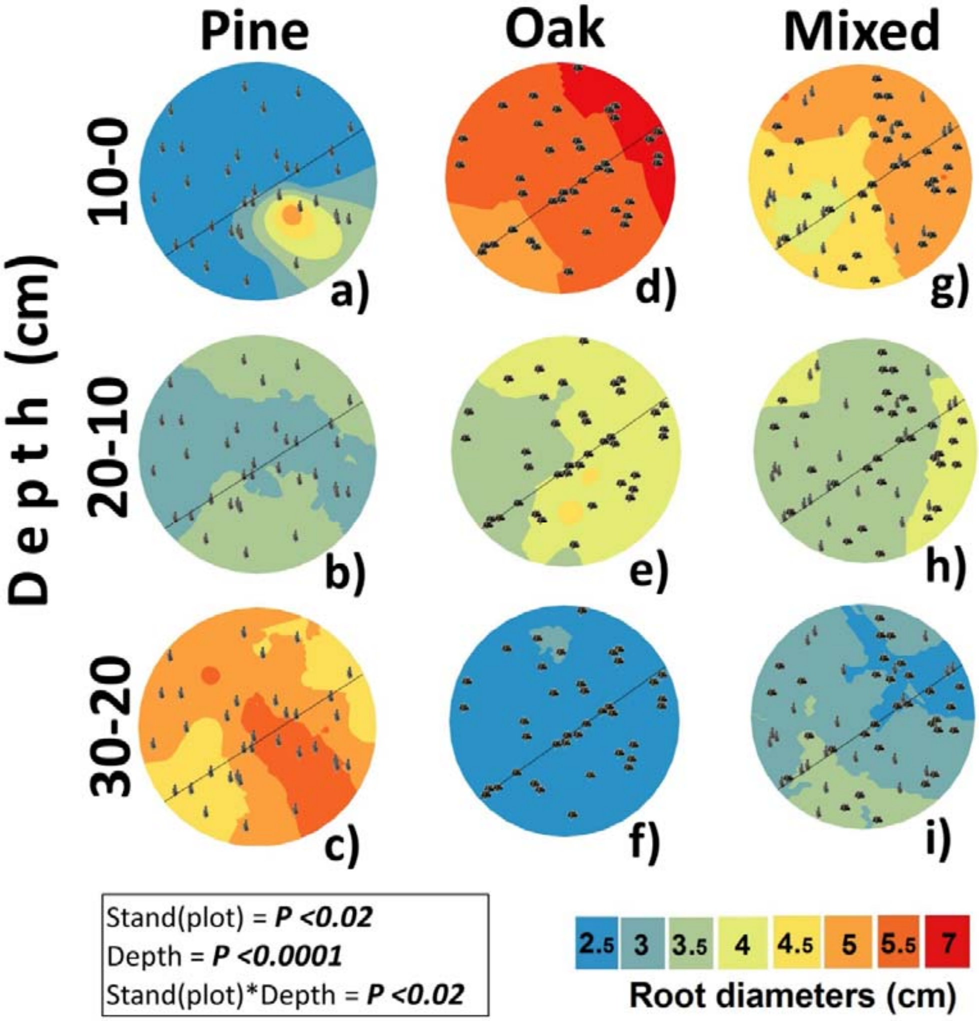
Pine
Oak
Mixed
Depth (cm)
10-0
20-10
30-20
a)
b)
c)
d)
e)
f)
g)
h)
i)
Stand(plot) = P <0.02
Depth = P <0.0001
Stand(plot)*Depth = P <0.02
2.5
3
3.5
4
4.5
5
5.5
7
Root diameters (cm)

Fig. 3.3

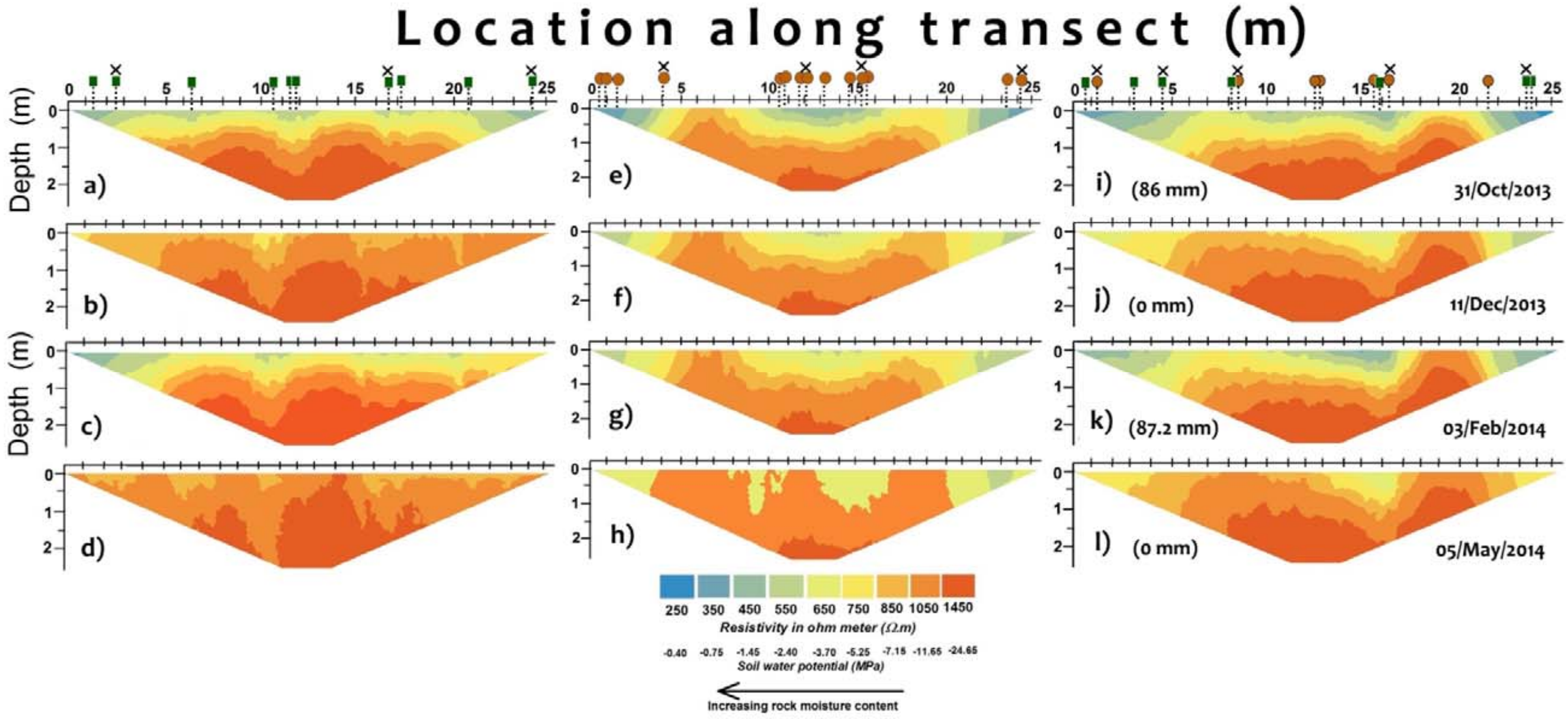
Location along transect (m)
0
5
10
15
20
25
Depth (m)
0
1
2
a)
b)
c)
d)
e)
f)
g)
h)
i) (86 mm)
31/Oct/2013
j) (0 mm)
11/Dec/2013
k) (87.2 mm)
03/Feb/2014
l) (0 mm)
05/May/2014
250
350
450
550
650
750
850
1050
1450
Resistivity in ohm meter (Ω.m)
-0.40
-0.75
-1.45
-2.40
-3.70
-5.25
-7.15
-11.65
-24.65
Soil water potential (MPa)
Increasing rock moisture content

Fig. 3.4

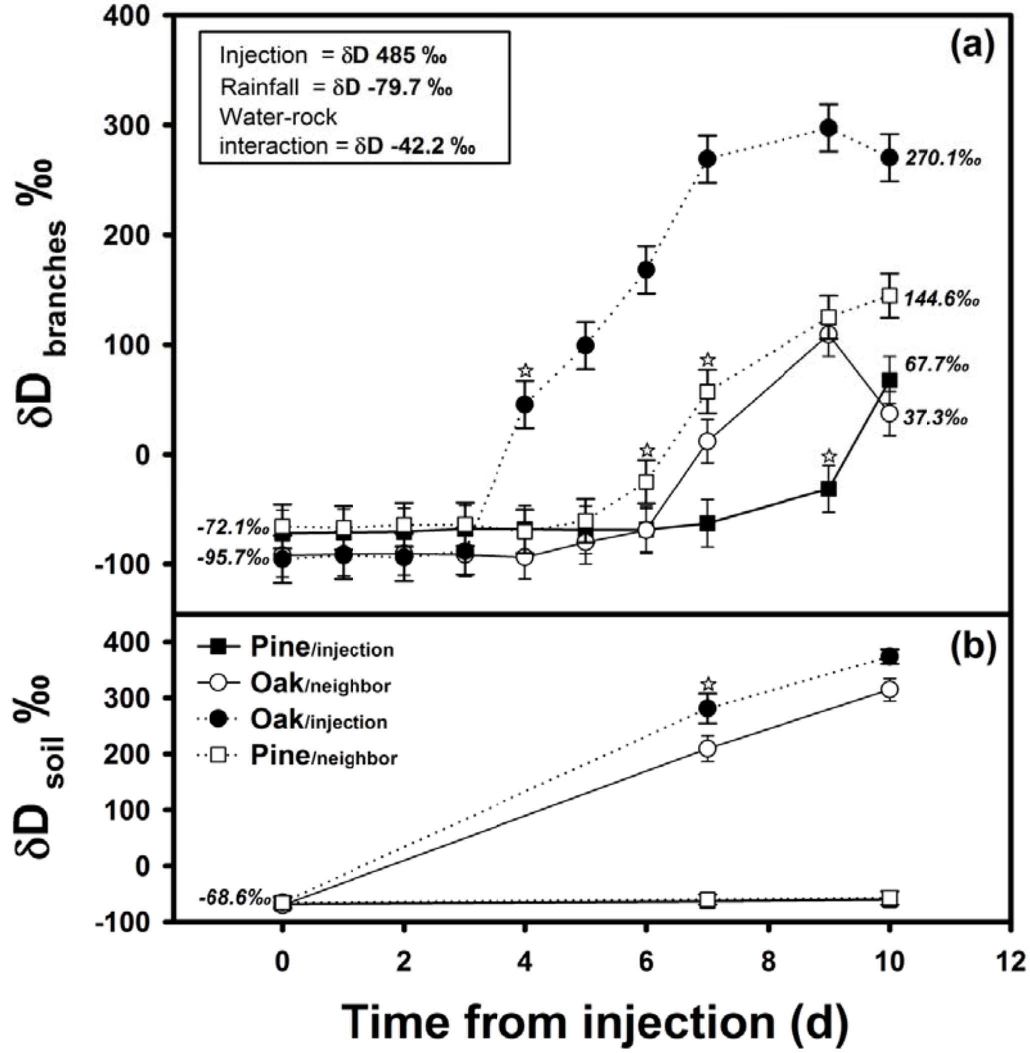
Injection = δD 485 ‰
Rainfall = δD -79.7 ‰
Water-rock interaction = δD -42.2 ‰
(a)
δD branches ‰
400
300
200
100
0
-100
270.1‰
144.6‰
67.7‰
37.3‰
-72.1‰
-95.7‰
(b)
Pine/injection
Oak/neighbor
Oak/injection
Pine/neighbor
δD soil ‰
-68.6‰
0
2
4
6
8
10
12
Time from injection (d)

Fig. 3.5

3.7. Supporting Information

3.7.1. Figures

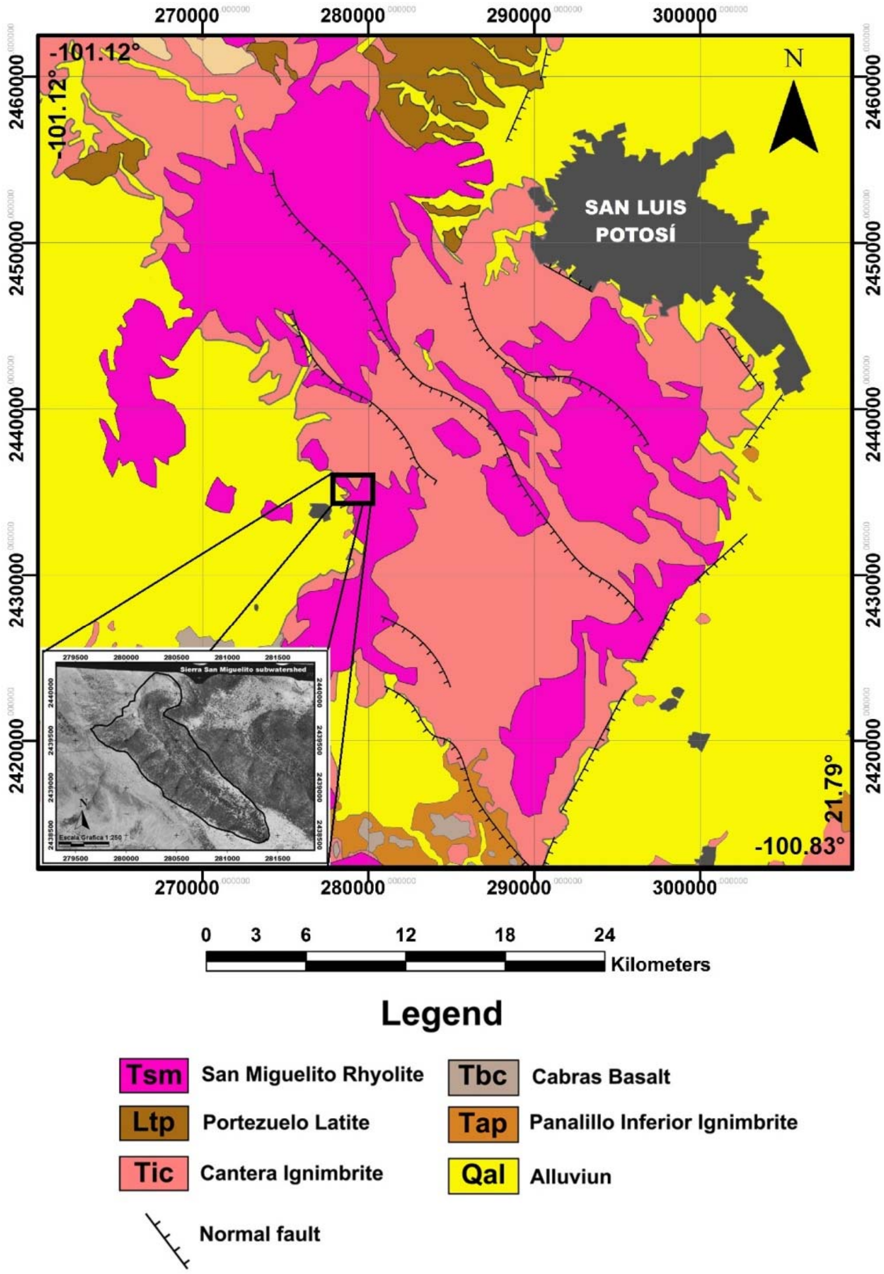

Figure S3.1. Geologic map of SSMVC showing the study area, San Miguelito rhyolite outcropping and structural features.

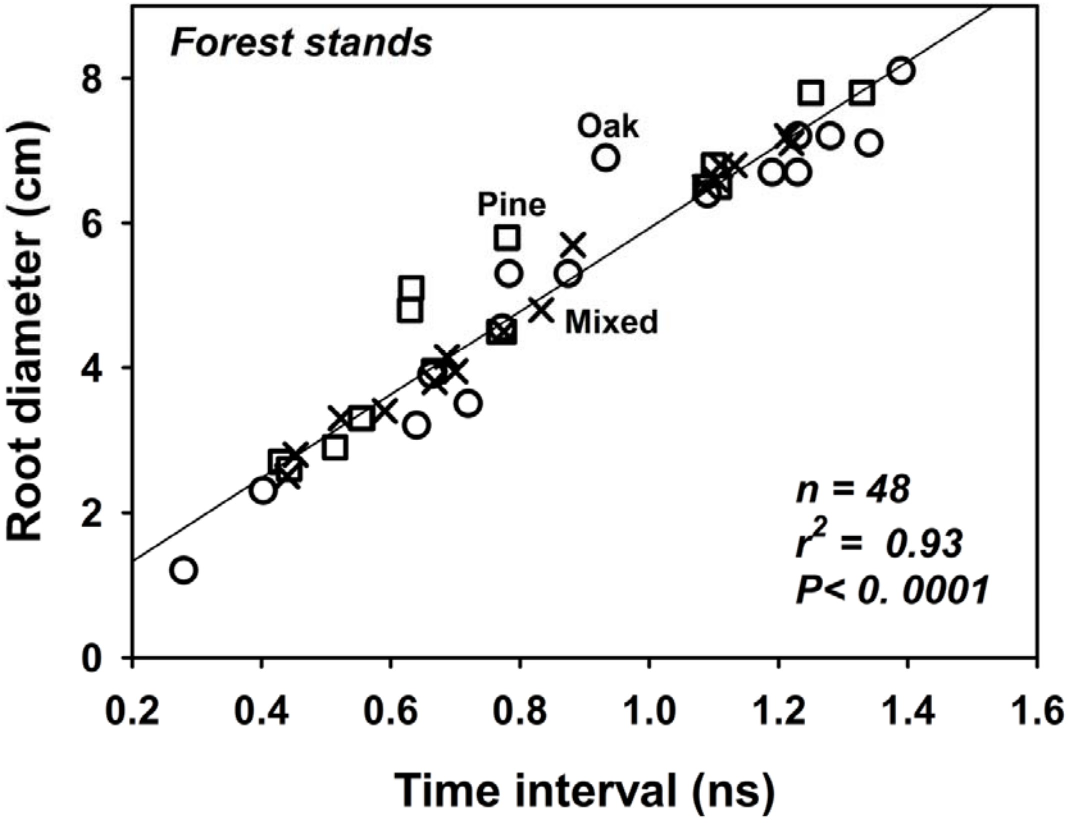

Figure S3.2. Relationship between root diameter of different stands and time interval with zero crossing (point of maximum signal). *n* = the number of roots detected by GPR.

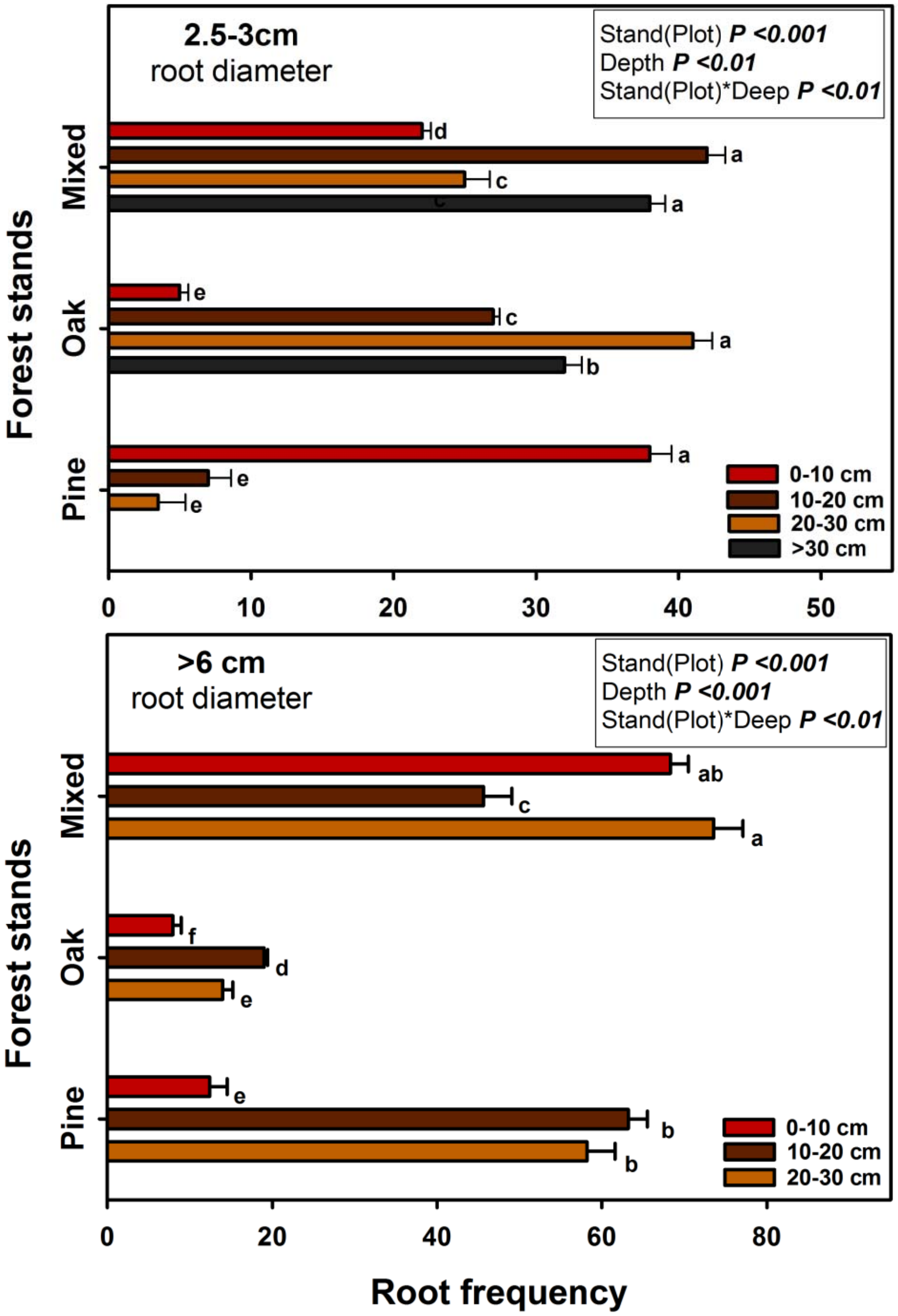

Figure S3.3. Root frequency (%) of two root diameter classes 2.5 – 3 cm (top) and > 6 cm (bottom), observed for each forest stand at three different soil depths. Different letters next to each column indicate statistical differences at a probability value of *P <0.005.*

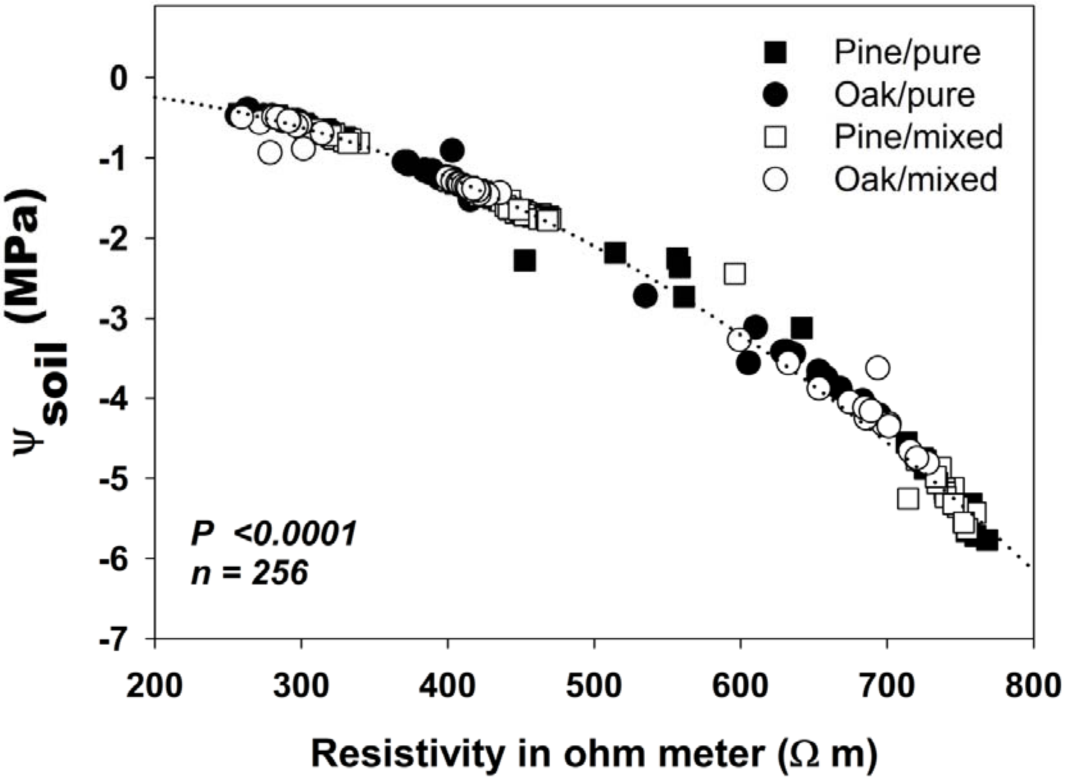

Figure S3.4. Relationship between soil water potential and soil resistivity for pine, oak and mixed stands. Global relation corresponds to the four periods defined in the study (October 2013, December 2013, February 2014 and May 2014) for both the spatial and temporal dynamics of soil resistivity.

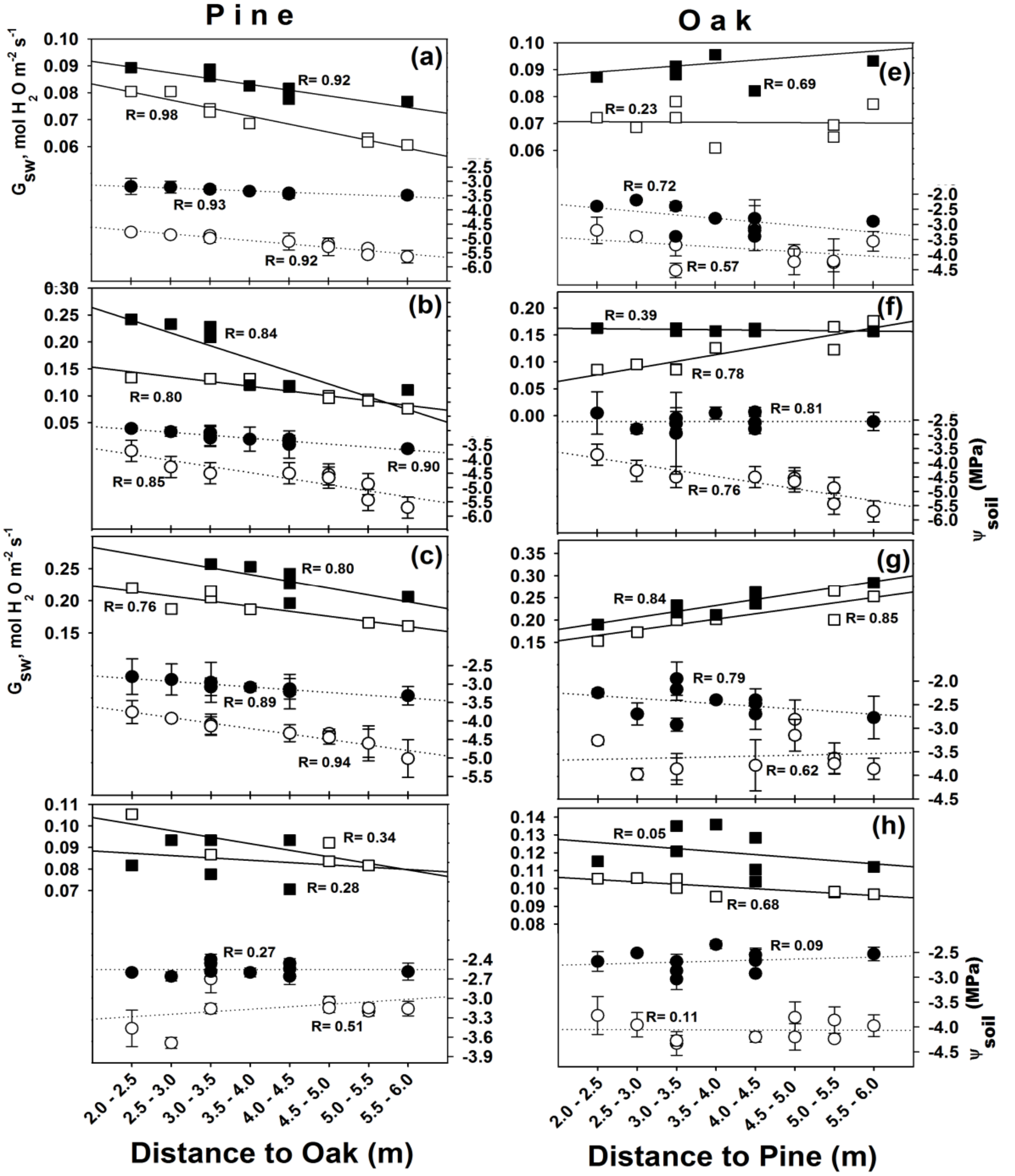

Figure S5. Linear relationship between stomatal conductance (G_{sw}), soil water potential (Ψ_{soil}) associated to *Pinus cembroides* and distance to the closest tree of *Quercus potosina* and the other way around, *Quercus potosina* to tree of *Pinus cembroides* between **a)** January; **b)** February; **c)** March and **d)** November 2011. Squares, G_{sw}; circles, Ψ_{soil}. Closed symbols indicate North exposed trees whereas open symbols correspond to South exposed Pine. Each point represents the mean ±1 SE (*n*=4).

4

CHAPTER

MULTIDIMENSIONALITY NICHE IN SPECIES COEXISTENCE

Keywords: niche, coexistence strategies, resource partitioning, functional traits, pine-oak forest, hydraulic lift, water-rock interaction, geodiversity

4.1. Introduction

Understanding the mechanisms that allow for species co-existence within plant communities has long been a focus of ecological research (Valladares et al. 2015). During the last seventy years, many studies on species coexistence mechanisms patterns and their potential niches have been reported. Several theories have arisen from all this work (Gause 1934; Hutchinson 1957; MacArthur 1968; Whittaker 1969; Whittaker et al. 1973; Grubb 1977; Noble & Fagan 2015). Whittaker (1969) for instance, suggested that community diversity results from habitat partition, i.e. a diversification of the habitat-niche. Complementary resource use has been suggested as an explanation for higher productivity observed in mixed plant communities compared to monospecific communities. Resource use complementarity has been attributed to functional traits and/or niche differences among species, suggesting that species access resources unavailable to others or differ in spatial and temporal uptake of the same resource (Soliveres et al. 2014). Niches are central to ecological thinking because they represent convenient shorthand for many of the concepts used by ecologists to approach a variety of important problems, including resource use, geodiversity, and many aspects of community composition and structure (Valladares et al. 2015). One of the intriguing wiched problems of theoretical ecology has been to understand and pinpoint in what sense a given species become identified with its ecological niche.

Almost 50 years ago, G. E. Hutchinson (1957) formalized the ecological niche concept as an abstract n dimensional set of points in a space whose axes represent environmental variables (this has been the most influential concept). In subsequent elaborations, Hutchinson (1978) established a useful distinction between scenopoetic and bionomic niche axes. After Hutchinson’s original formulation, the niche concept has undergone many changes, but all alternative contemporary definitions retain the formalization of the niche as a multidimensional space. How many dimensions (trait-axes) are required to predict whether two species interact? This unanswered question originated with the idea of ecological niches, and yet bears relevance today for understanding what determines co-existence.

The debate on whether co-existence in species-rich plant communities is determined by niche has gained renewed impetus over the last decade, resulting in many studies on distribution patterns of diversity (Grubb 1977; Martorell et al. 2015). Will two individuals of different species interact if given the opportunity? If the two species have matching traits, then a co-existence interaction based on sharing resources is possible. For example, two species with different root system architectures (homorhizic *versus* allorhizic) may coexist, since their roots are located at different soil depths, such that plants may access the same resource at different times and space, otherwise, the interaction may be averted. Clearly, several traits might need to match for a species co-existence to occur. Thus, we can envision species being embedded in a multi-dimensional time and space continuum, where each axis represents the expression of a given trait (e.g. size, phenology, root distribution, life history, resource use, geodiversity, etc.) along different environmental gradients and each interacting species falls within or occupies a certain space and time domain. This is the classic idea of a multidimensional ecological niche posed by pioneers as Grinnell, Elton and Hutchinson (Box 1). Most ecologists will agree, that a niche includes conditions in both the physical environment and resource availability as important axes of ecological space and time. It has long been argued that differences among species in their niche use (or niche partitioning) promote competitive coexistence in a spatially heterogeneous environment in a variety of ecological communities (Goldberg & Barton 1992; Castro-Arellano & Lacher 2009). However, in this type of studies it is assumed that sites are homogeneous even though they are actually geodiverse, which is why we speak of competitive coexistence (February et al. 2013). The pine-oak forest of Sierra de San Miguelito Volcanic Complex (SSMVC) is an ideal system to address the multidimensional niche concept to elucidate the mechanisms of species coexistence. In a study conducted in 2010 and 2011, Rodriguez-Robles et al. (2015) demonstrated a unique geoecohydrological mechanism that tightly couples the hydrology and water relations of shallow rocky soils and trees, respectively. The mechanism that explains species coexistence in this mixed forest is based on oak trees facilitating water access to pine in extreme dry periods (Rodriguez-Robles et al. 2015). It was suggested that rock water constitutes a potentially critical water source for trees, particularly during periods of drought, marking temporary geohydrological niches. This suggestion was consistent with the observed phenology in some shallow-rooted plants growing on karst soil, which remain active even under intense drought (Tokumoto et al. 2014). However, the possibility that plants could use water of fractures from impermeable rock remains unexplored.

Here, we directly explore the association between species root traits of *Pinus cembroides* and *Quercus potosina*, which enable their coexistence in environments with a high microgeodiversity. Trait differentiation allows them to cope with extreme drought detonating one neutralism-competitive interaction mechanism (facilitation). It has been long understood that trait differences between species such as rooting depth, can maintain diversity in communities, promoting coexistence and reducing competition. We tested the hypothesis that phenotypic and biophysical properties drive niche differentiation which in turn promotes species coexistence. This type of studies requires multidisciplinary techniques and tools. To fulfill this goal, we drew on ecophysiology, anatomy, stable isotope ecology, hydrogeology and geophysical exploration tools (images) (explained in Materials and Methods, *supplementary material*), to ultimately differentiate functional species traits representing multiple ecological dimensions.

4.2. Alternate life-history strategies in species coexistence

The SSMVC, is characterized by a low annual rainfall (408 mm, average of the last 65 years, Figure S4.1 top). In the last five years of the study, the month with the most precipitation (July) has been two months delayed (September), prolonging drought (Figure S4.1 bottom). However, this mountainous tropical semi-arid climate hosts a pine-oak forest with particular biophysical characteristics, supporting the survival of these two species. The forest colonizes shallow rocky soils over impermeable volcanic material with frequent occurrence of fractures and fissures (at 35 to 75 cm depth), exfoliated rock (0 to 45 cm depth), soil pockets and regolith (5 to 38 cm) and a very thin layer of soil (<25 cm) (Figure S4.2). In accordance to its geographical location, the orography of both Sierra Madre Oriental and Sierra Madre Occidental play an important role regulating the incoming humidity fronts from either Pacific and Atlantic ocean basins. Of these, the Atlantic basin is nearer to the study site (355.5 vs. 463.5 km) resulting in well-defined rain isotopic signatures. We examined ^{18}O and ^{2}H of each rainfall event, from water springs (water-rock interaction) to generate our Local Meteoric Water Line (LMWL, Figure 4.1). We collected continuously soil and tissue water from tree twigs in response to the dynamics of transport and storing water (Figure 4.2). The natural abundance analysis of water in xylem confirmed that trees used different water sources throughout the year, which permitted us to identify niches (in space and time) and functional traits of species.

We monitored both soil and plant water potential (Ψ_{leaf} and Ψ_{soil}) in 12 plots (64 trees) for 28 months, highlighting the ecophysiological responses of these two species (Fig. 4.3). To help interpreting plant responses to soil water availability, Ψ_{leaf} and Ψ_{soil} time series were divided into three ecohydrological periods: two dry periods that we named depletion and recovery and one wet period (wet season).The Ψ_{leaf} response is practically a mirror of Ψ_{soil} (stand x date, P <0.0001 for all cases). For the first depletion period, a marked variation in a 4 months period was observed in both Ψ, with a decline of up to 4 MPa (September - December 2012). Overall, the most negative Ψ was observed in pine in particular in the mixed stands (-5.45 MPa), while oak Ψ dropped by ~ 3 MPa. In these 5 months we recorded less than 30 mm rain followed by a recovery period, when Ψ of oak exhibited a significant recovery (pure and mixed), while pine in mixed stands showed only partial recovery (1.5 MPa difference. The water potential recovery can be explained by the isotopic signature of oak's xylem sap that shows an isotopic signal closer to the water-rock interaction line than to free soil water (Figure 2e). The isotopic composition of *Q. potosina* trees was similar to that of coexisting *P. cembroides* in the same community. This suggests that species from the mixed forests shared the same temporal hydrological niche, being partitioned by functional traits of two species and biophysical characteristics. Supported by geophysical images (GPR, Figure 4.4), we observed differential root distribution for pine and oak in relation to the geological characteristics of the terrain. Radargrams showed that oak distributed the finest roots in the deeper layers (soil / regolith and fractures, Figure 4.4c), unlike pine, that distributed its finest roots in the surface (top 10 cm, Figure 4.4a). In an injection test of deuterated water (δD = 366‰) in pine stems of mixed and pure stands, we observed that mixed pine renewed water constantly, reaching up to 50% more efficiency than in trees in pure pine stands (average 3 days, $P < 0.0001$, Figure 4.5). In pine trees in mixed stands, stem water originated from rock fractures (δD = -38.6‰), unlike in trees in pure stands, which used available soil water from most recent rain events (δD = -78.6‰). Even though pine trees from mixed stands do not distribute their roots in fractures, they are still able to access this source of water through facilitation mechanism (hydraulic lift) by oak. In this scenario, the co-existence theory mentions the occurrence of interspecific competition for the same resource, however, the differentiated functional traits of pine and oak, allowed the acquisition of the same resource yet from different spatial niches. This results in a neutralism-competitive interaction, indicating that the use of water from fractured rocks is a mechanism to shallow-rooted trees growing on fractures of shallow rocky soils.

In wet periods corresponding to the months receiving monsoon precipitation, leaf and soil Ψ had fully recovered (June–October 2013 and May-October 2014, Figure 4.3). A consistent trend in the increase of Ψ_{leaf} in response to Ψ_{soil} for the first wet period (June 2013), showed a significant difference between species in mixed ($P < 0.05$) and pure stands ($P < 0.001$), with less negative Ψ in oak. For pure pine, the recovery of ~ 2 MPa in Ψ was associated to its parenchyma surrounding the tracheids (structural anatomy), that resulted in a greater efficiency of soil water supply and therefore the pumping of water to the canopy (Figure S4.3). The isotopic composition of xylem sap revealed that trees during the wet period only used meteoric water, alternating water coming from the two ocean basins (Figure 4.2f). A test consisting of excluding shallow roots (access only to the rocky substrate) revealed that only oak had access to water deposits found in the fractured rock, through its deepest roots, suggesting that this mechanism might contribute to mitigate competition in mixed stands in summer (June-October 2013), alternating water resources into the spatial and temporal niches (Figure 6a-b). The δ^{18}O isotope ratios revealed these small changes resulting from the use of water from different sources, supporting the hypothesis of presence of oak fine roots in rock fractures (Figure 4.6b). The δ^{18}O isotope curve for oak showed that its value moved across the line of water-rock interaction, unlike pine plots where the evaporation line indicates isotopic fractionation in the stem, since the water is not renovated (Figure 4.6c).

We also observed another physiological strategy, in the second depletion period (November 2013 –April 2014, Figure 4.3). Overall, stands reached the lowest Ψ_{soil} in April (pure pine = -3.3 ±0.098, mixed pine = -3.5 ±0.098 MPa, pure oak = -3.1 ±0.110 and mixed oak = -3.15 ±0.110, $P > 0.5$), in contrast to Ψ_{leaf} where only pine stands showed an average decline of 3 MPa (-4.2 ±0.105 and -4.6 ±0.105, for pure and mixed pine, respectively). In comparison oak stands maintained Ψ_{leaf} partially stable throughout the period (pure oak = -1.1 ±0.087 and mixed oak = -1.2 ±0.087). The response by oak can be explained with isotopic analysis of xylem water (Figures 4.2g-i) and records of water entry to the system (Figure 4.1). In December 2013 and January 2014, abundant rainfall was recorded (85 mm FF31+T16, $\delta^{18}O$= -15.05, $\delta^{2}H$= -106.8730), that promoted an average increase of 0.52 ±0.05 MPa for both Ψ in oak and pine. Xylem water isotopic signal revealed that both species used this winter resource (Fig 2g). Following the rise of water potentials (January 2014), in the following three months there was a decline of Ψ_{leaf} in pine while oak was unaffected (February-April 2014, Figure 4.3). Oak used gradually winter rainfall (FF32+T16) that was stored in their trunks, while pine used water coming from the Atlantic, thus avoiding temporal niche overlap and interspecific competition. Using structural anatomy techniques, we could identify fibretracheids (specialized tissues to store water, Figure S4.4c), connecting the vessal tissues (conductive structures, Figures S4.4b, d) and a considerable number of mesic and xeric vessels (Figures S4.4a) throughout the trunk. In addition, we observed that oak trees shrank their trunk at the end of each ecohydrological period (Figure S4.5a) as they used stored trunk water. Thus, in wet ecohydrological periods (408 mm, wet period 2013) oak trunk hydrated up to 68 ±6.1% of its weight, unlike pine that only hydratated 37 ±4.8% ($P < 0.0001$, Figure S4.5b). By April 2014, trunk water in oak decreased and switched its route of water acquisition from fractures, tracing this to the water-rock interaction line (Figure 4.2i). The survival strategies in resource use complementarity, helped oak to maintain a constant Ψ_{leaf} (-1.25 MPa), contrasting to the first dry period, when a hydraulic lift mechanism was observed (March-April 2013, Figures 4.3, 2e). It is well known that hydraulic lift mechanism, increases survival in dry soil and increases nutrient uptake by the plant under extended dry periods (Nadezhdina et al. 2010; Prieto et al. 2012). Alternative pathways such as a direct hydraulic redistribution from the rock (non-stop on the top soil), might fulfill the water demand of the canopy, however other biologically relevant processes might be impeded (e.g. nutrient supply).

With the arrival of the monsoon in 2014 (2nd wet period), there was a slow Ψ increase in both species. In addition, forest species exhibited significant difference in Ψ_{leaf} (average difference 1.71±0.105 MPa, $P<0.0001$). Ψ_{soil} pine have shown a better response than oaks to rain events, same as has been reflected in Ψ_{leaf} (pine-mixed= 2.56 ±0.110, oak-mixed= 0.35 ±0.06 Mpa, February-April, Figure 4.3). Intraspecific competition for water was clearly observed in the community during the wet period (520 mm rainfall), reflects overlap of hydrological niches, suggesting that the dimension of its niches is reduced during wet season. By lowering available water in the system, pine and oak reduced intraspecific competition using a different water source (Figure 4.2k).

Altogether, our results indicate that *Quercus potosina* uses fractured volcanic rock water, particularly during drought, moving through the substrate profile when in association with *Pinus cembroides*, thus avoiding competitive exclusion. Well differentiated functional traits such as the distribution of their roots (spatial niche) and their anatomical and physiological adaptations (biological niche), allowed coexistence of pine and oak in semiarid conditions. Biophysical characteristics of the system, such as the geospatial axis (microgeodiversity), also promoted the facilitation of the most limiting resource, predominantly through big niche overlap (dimensionality), resulting in an expansion in the axes. *Pinus cembroides*, a species operating closer at its functional limits is apparently entering the geospatial niche of oak. Through water redistribution mechanisms, pine benefits from co-existence with oak standing prolonged periods of drought. We have strong evidence to discard alternative explanations.

First, differences in root distribution and anatomical structures, with oak fine roots located in fractures (Figure 4.4e, c). These roots show a series of adaptations to break through fractures (triple layer of epidermal tissue and druzes of calcium oxalate) and water bombing (mesic and xeric vessels). When humidity is very limited, reduction in vessel size with tyloses (Gottwald 1972), conducting little water and preventing cavitation (Figure 4.7). In addition, a comparative study comparing *Q. potosina* superficial and deep roots within fractures and regolith (not shown in this paper), revealed up to 60% more druzes and 83% of xeric vessels in deep roots. We have considered the possibility that pine roots can access the water reservoir, located in fractures, but this was not the case. Although *P. cembroides* was supplied 1/2 L of labeled water (δD = 485‰) in the fracture (33 ±5.2 cm depth) closest to the trunk (45 ±8.2 cm distance), we did not record the presence of the tracer in the xylem water. Oak in contrast showed the tracer on the third and fourth day after starting the treatment. We observed ^{2}H-enriched values in the xylem water as well as in soil samples, which is also an evidence of hydraulic lift mechanism (Figure 4.8).

Second, the different fractionation processes described between soil and xylem water do not match with our observations. Isotope fractionation for ^{2}H during water uptake has been described for some xerophytic plants (Ellsworth & Williams 2007), but in the opposite direction to our study, that is, water becoming ^{2}H-depleted. It has been suggested that water uptake mediated by mycorrhiza may cause an additional fractionation, based on water extracted from ectomycorrhizal fungi, but the effect was considered to be negligible (<0.5% for δ^{18}O) (Lilleskov et al. 2009), since most of such transport is apoplastic, without mixing with the cytoplasm (Barzana et al. 2012). Xylem water could also become progressively ^{18}O and ^{2}H-enriched through bark evaporation. However, this is mainly associated with young stems exposed to high evaporative demand, together with long residence times for xylem water (Dawson & Ehleringer 1993). This was not the case, since we sampled at the base of the twig, which had a thick and highly hydrophobic bark. Furthermore, due to differential fractionation factors for ^{18}O and ^{2}H, in case of evaporation occurring in the xylem, we would expect a parallel slope of the δ^{18}O/δ^{2}H relationship to the soil values line, similar to the behavior of excluded pine roots (Figure 4.6c). In our study, the slope of the δ^{18}O/δ^{2}H relationship in oak xylem water in the dry period was perpendicular to both rock water and the meteoric water line (Figure 4.2e, i).

Third, it can be argued that the highly complex geological structure (weathered rock; outcrops, exfoliation, pockets, fractures, fissures, Figure S4.2) facilitates distribution and storage of water spatially and temporally, allowing species coexistence with different traits (Figure 4.9). The presence of mixed and monospecific stands in this forest ecosystem at the landscape scale, reflects aspects of geodiversity at larger spatial scales, resulting in geospatial niches at the landscape scale. Thus, sites with greater vertical micro geodiversity permit the co-existence of both species whereas less diverse sites are dominated by pure stands. These results significantly modify the current paradigm of water use by plants, as water held in rocks has not been regarded as a potential source. Here, we demonstrated that rocky soils also generate a high degree of variability in water content and large offsets in the physiological status of trees. Incorporating geospatial niches as a major aspect of ecosystem structure may clarify some of the apparent paradoxes of forest covered rock-dominated landscapes, such as variability in the spatial patterns of tree mortality under drought conditions.

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4.3. References

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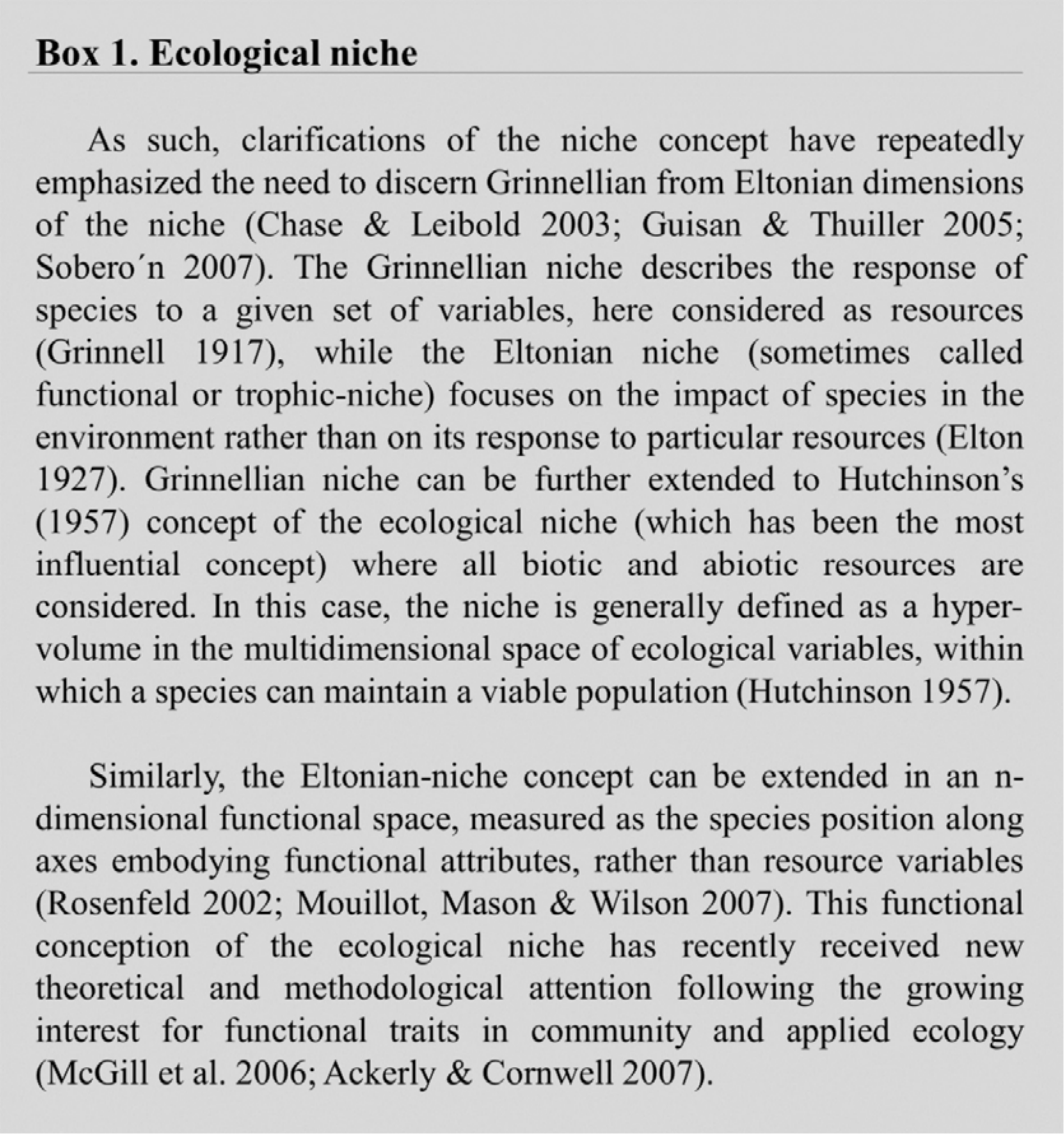
4.4. Box and Figures



Box 1. Ecological niche

As such, clarifications of the niche concept have repeatedly emphasized the need to discern Grinnellian from Eltonian dimensions of the niche (Chase & Leibold 2003; Guisan & Thuiller 2005; Sobero´n 2007). The Grinnellian niche describes the response of species to a given set of variables, here considered as resources (Grinnell 1917), while the Eltonian niche (sometimes called functional or trophic-niche) focuses on the impact of species in the environment rather than on its response to particular resources (Elton 1927). Grinnellian niche can be further extended to Hutchinson's (1957) concept of the ecological niche (which has been the most influential concept) where all biotic and abiotic resources are considered. In this case, the niche is generally defined as a hyper-volume in the multidimensional space of ecological variables, within which a species can maintain a viable population (Hutchinson 1957).

Similarly, the Eltonian-niche concept can be extended in an n-dimensional functional space, measured as the species position along axes embodying functional attributes, rather than resource variables (Rosenfeld 2002; Mouillot, Mason & Wilson 2007). This functional conception of the ecological niche has recently received new theoretical and methodological attention following the growing interest for functional traits in community and applied ecology (McGill et al. 2006; Ackerly & Cornwell 2007).

Box 1.

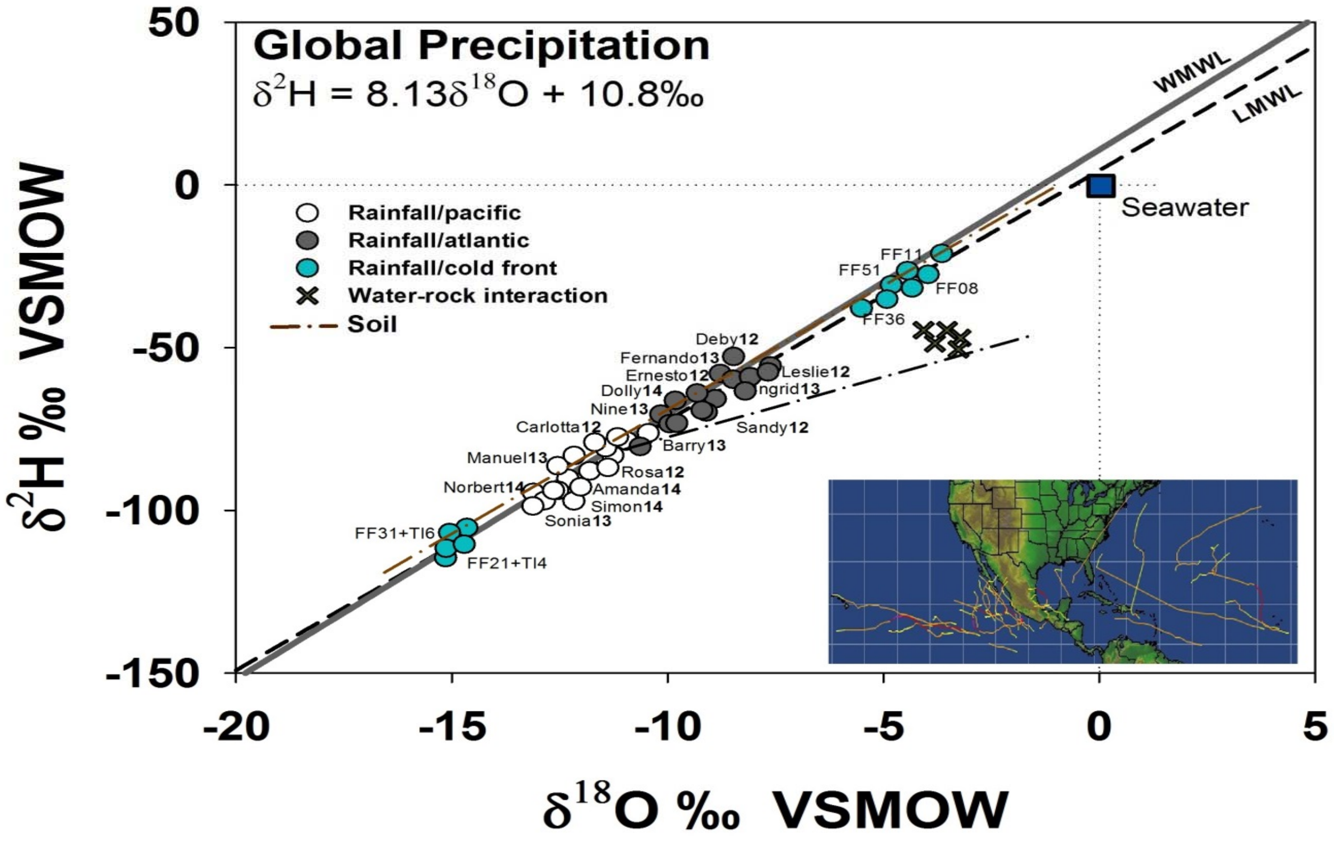

Global Precipitation
$\delta^2H = 8.13\delta^{18}O + 10.8‰$
WMWL
LMWL
Seawater
Rainfall/pacific
Rainfall/atlantic
Rainfall/cold front
Water-rock interaction
Soil
FF11
FF51
FF08
FF36
Deby12
Fernando13
Ernesto12
Leslie12
Ingrid13
Dolly14
Nine13
Sandy12
Carlotta12
Barry13
Manuel13
Rosa12
Norbert14
Amanda14
Simon14
Sonia13
FF31+TI6
FF21+TI4
50
0
-50
-100
-150
-20
-15
-10
-5
0
5
δ^2H ‰ VSMOW
$\delta^{18}O$ ‰ VSMOW

Fig. 4.1

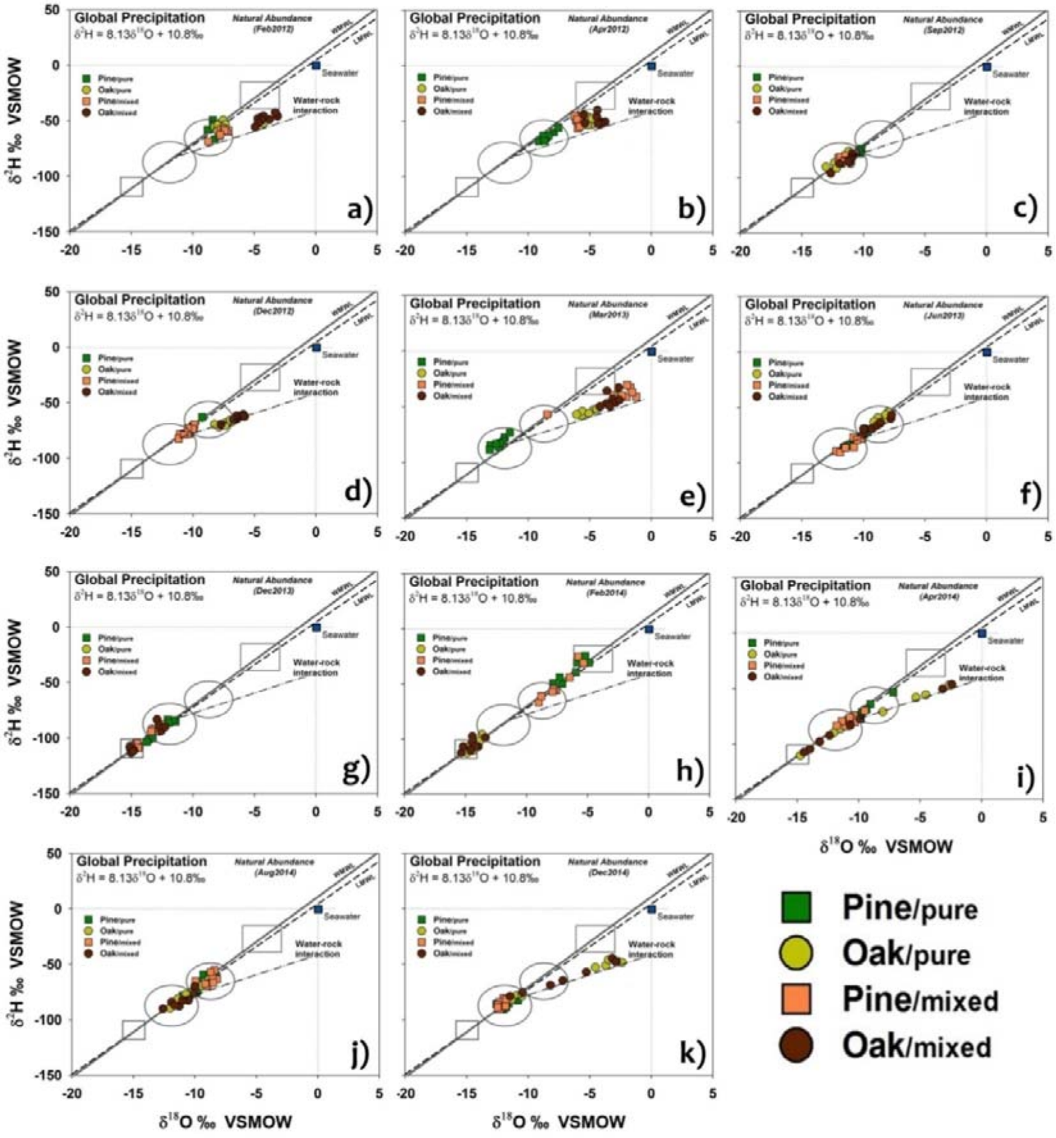
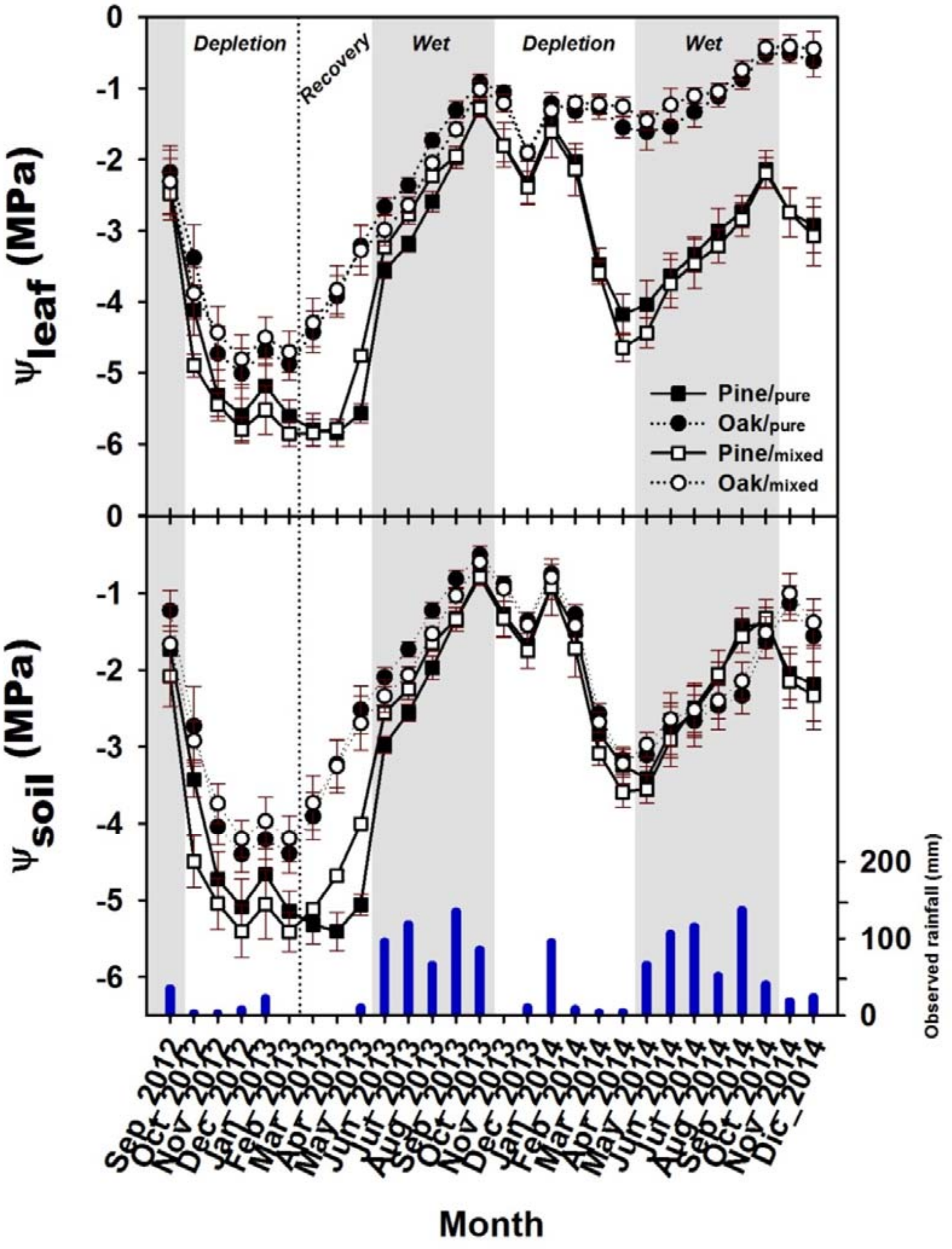

Global Precipitation
$\delta^2H = 8.13\delta^{18}O + 10.8‰$
Natural Abundance (Feb2012)
Natural Abundance (Apr2012)
Natural Abundance (Sep2012)
Natural Abundance (Dec2012)
Natural Abundance (Mar2013)
Natural Abundance (Jun2013)
Natural Abundance (Dec2013)
Natural Abundance (Feb2014)
Natural Abundance (Apr2014)
Natural Abundance (Aug2014)
Natural Abundance (Dec2014)
WMWL
LMWL
Seawater
Water-rock interaction
Pine/pure
Oak/pure
Pine/mixed
Oak/mixed
a)
b)
c)
d)
e)
f)
g)
h)
i)
j)
k)
δ^2H ‰ VSMOW
$\delta^{18}O$ ‰ VSMOW
50
0
-50
-100
-150
-20
-15
-10
-5
0
5

Fig. 4.2


Depletion
Recovery
Wet
Depletion
Wet
ψleaf (MPa)
ψsoil (MPa)
0
-1
-2
-3
-4
-5
-6
Pine/pure
Oak/pure
Pine/mixed
Oak/mixed
Observed rainfall (mm)
200
100
0
Sep_2012
Oct_2012
Nov_2012
Dec_2012
Jan_2013
Feb_2013
Mar_2013
Apr_2013
May_2013
Jun_2013
Jul_2013
Aug_2013
Sep_2013
Oct_2013
Nov_2013
Dec_2013
Jan_2014
Feb_2014
Mar_2014
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Jun_2014
Jul_2014
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Sep_2014
Oct_2014
Nov_2014
Dic_2014
Month

Fig. 4.3

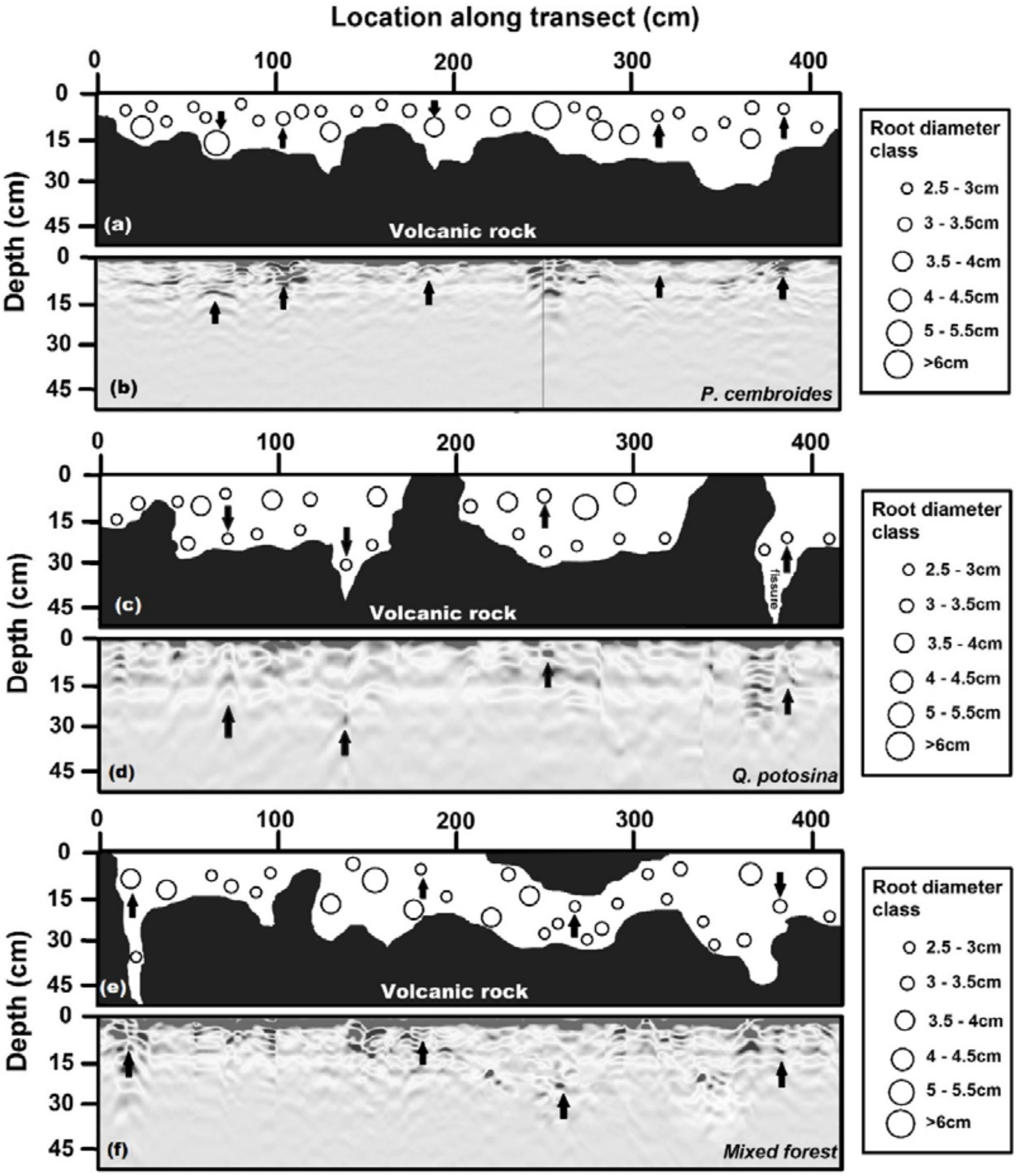
Location along transect (cm)
0
100
200
300
400
Depth (cm)
0
15
30
45
(a)
Volcanic rock
(b)
P. cembroides
(c)
fissure
(d)
Q. potosina
(e)
(f)
Mixed forest
Root diameter class
2.5 - 3cm
3 - 3.5cm
3.5 - 4cm
4 - 4.5cm
5 - 5.5cm
>6cm

Fig. 4.4

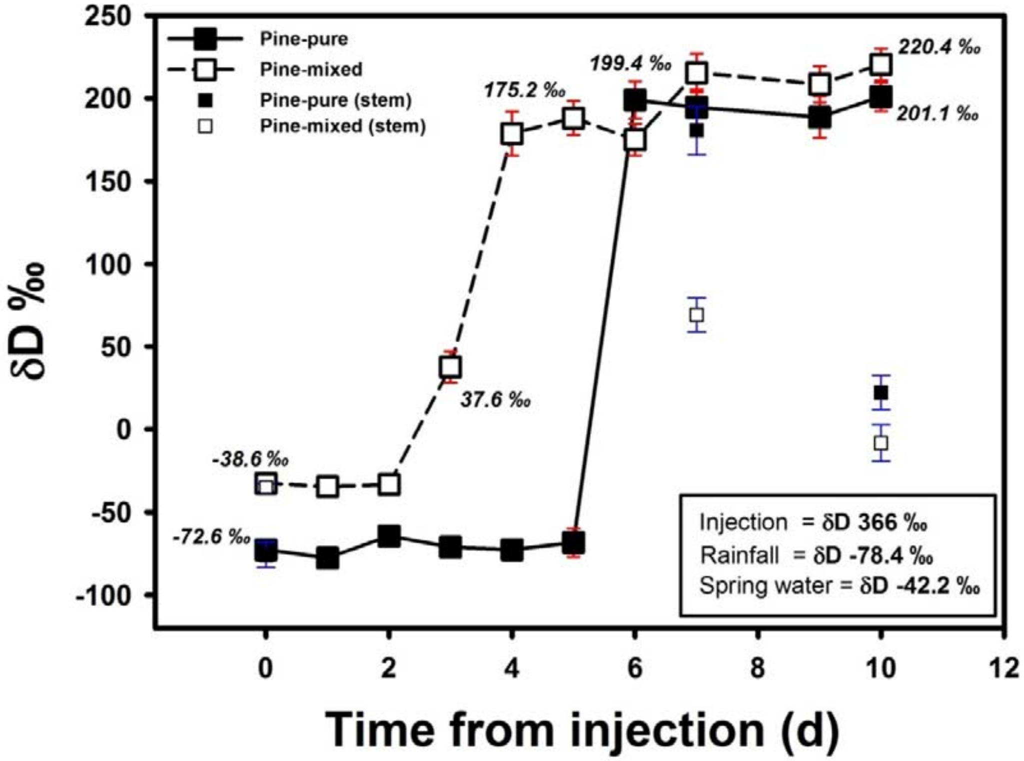
Pine-pure
Pine-mixed
Pine-pure (stem)
Pine-mixed (stem)
175.2 ‰
199.4 ‰
220.4 ‰
201.1 ‰
37.6 ‰
-38.6 ‰
-72.6 ‰
Injection = δD 366 ‰
Rainfall = δD -78.4 ‰
Spring water = δD -42.2 ‰
δD ‰
250
200
150
100
50
0
-50
-100
0
2
4
6
8
10
12
Time from injection (d)

Fig. 4.5

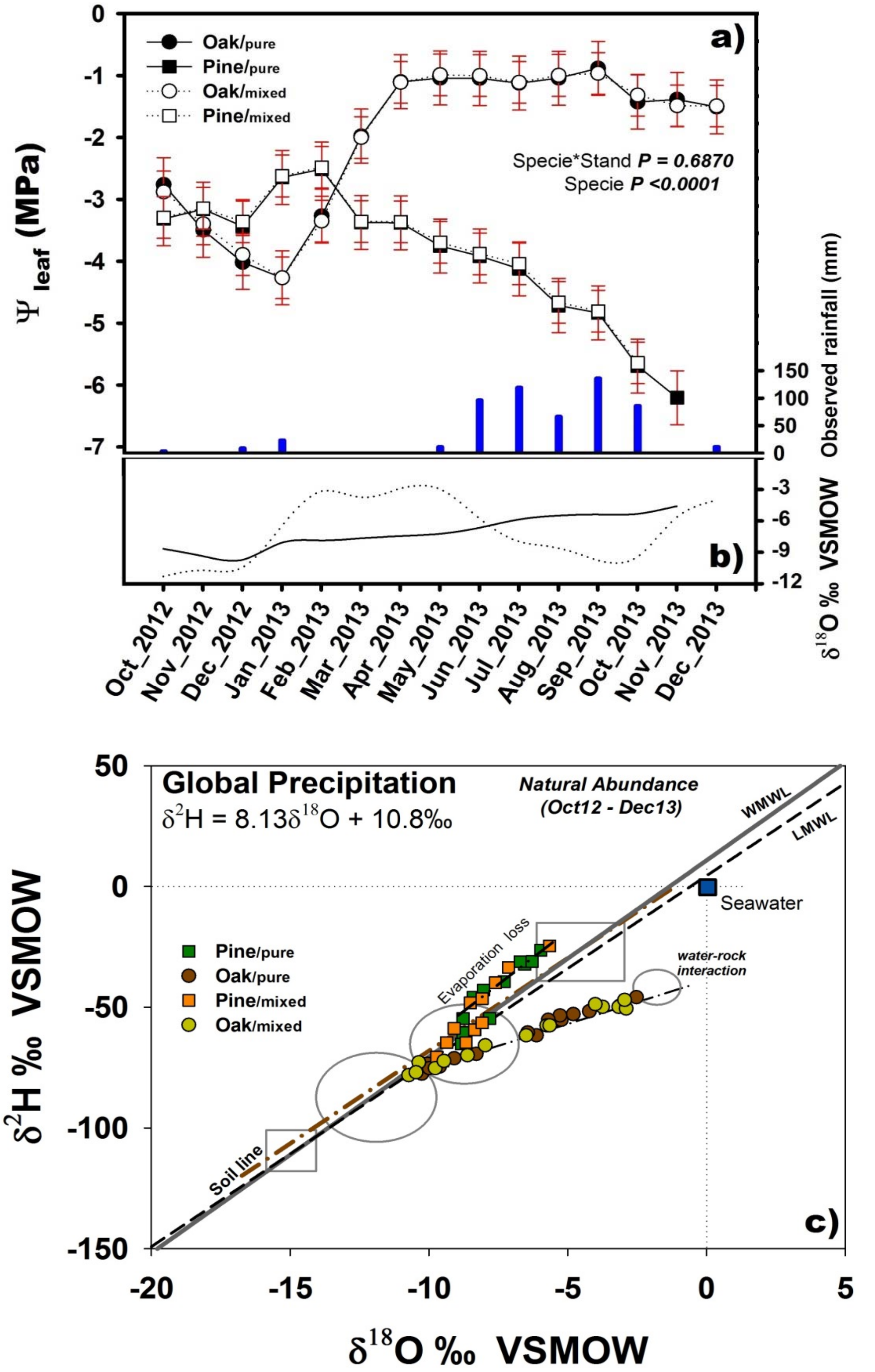
a)
Oak/pure
Pine/pure
Oak/mixed
Pine/mixed
Specie*Stand P = 0.6870
Specie P <0.0001
Ψ leaf (MPa)
0
-1
-2
-3
-4
-5
-6
-7
Observed rainfall (mm)
150
100
50
0
b)
-3
-6
-9
-12
δ18O ‰ VSMOW
Oct_2012
Nov_2012
Dec_2012
Jan_2013
Feb_2013
Mar_2013
Apr_2013
May_2013
Jun_2013
Jul_2013
Aug_2013
Sep_2013
Oct_2013
Nov_2013
Dec_2013
Global Precipitation
δ2H = 8.13δ18O + 10.8‰
Natural Abundance
(Oct12 - Dec13)
WMWL
LMWL
Seawater
Evaporation loss
water-rock interaction
Pine/pure
Oak/pure
Pine/mixed
Oak/mixed
Soil line
c)
δ2H ‰ VSMOW
50
0
-50
-100
-150
-20
-15
-10
-5
0
5
δ18O ‰ VSMOW

Fig. 4.6

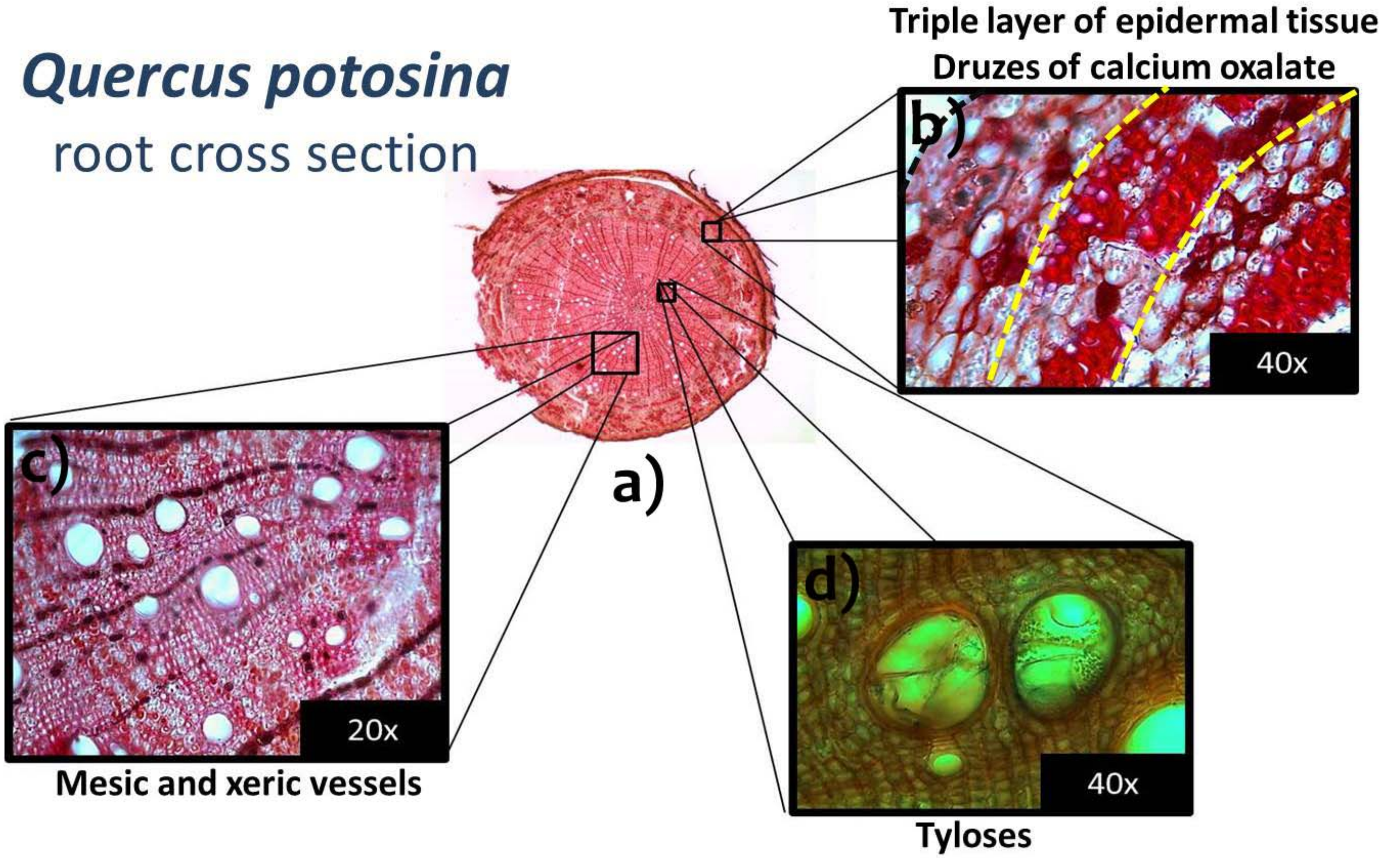
Quercus potosina
root cross section
Triple layer of epidermal tissue
Druzes of calcium oxalate
b)
40x
a)
c)
20x
Mesic and xeric vessels
d)
40x
Tyloses

Fig. 4.7

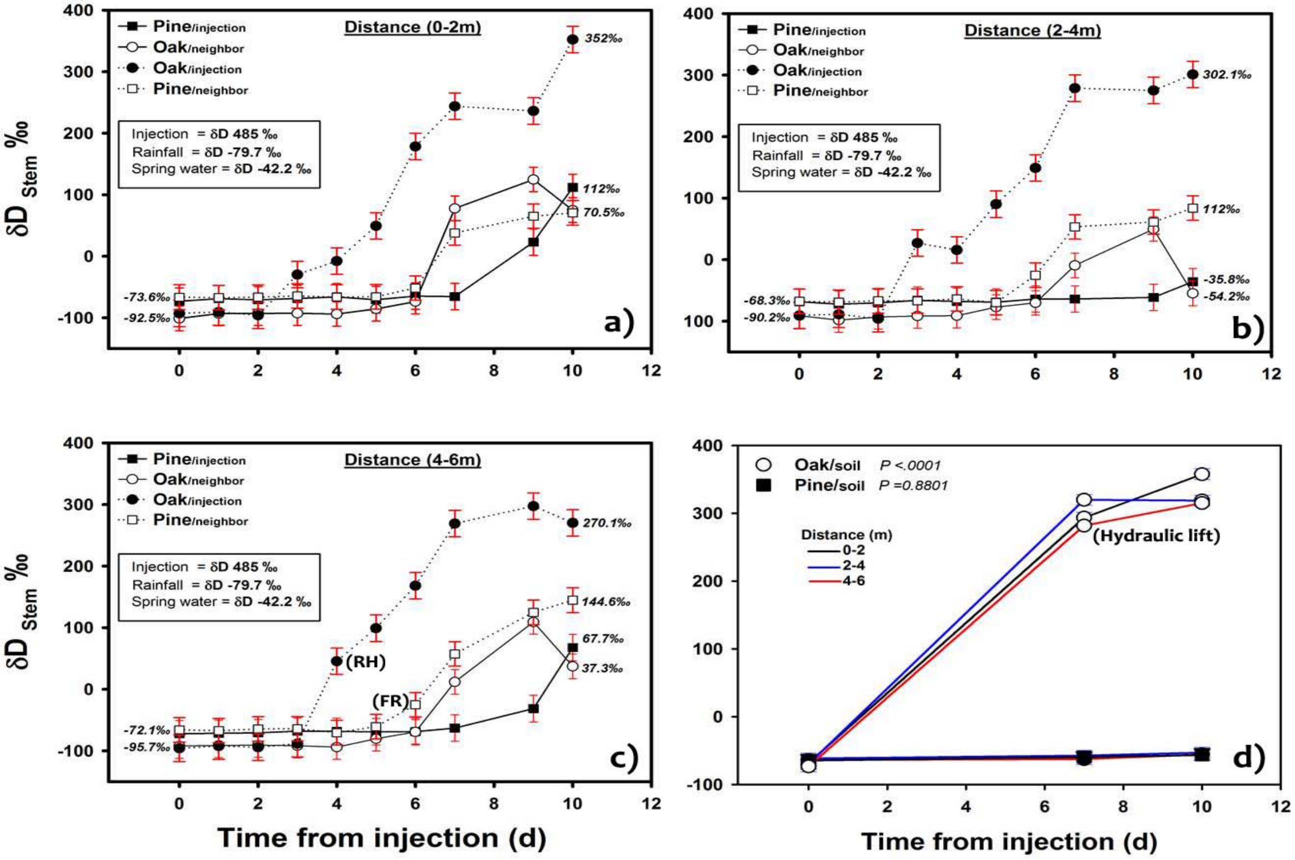
δD Stem ‰
Distance (0-2m)
Pine/injection
Oak/neighbor
Oak/injection
Pine/neighbor
Injection = δD 485 ‰
Rainfall = δD -79.7 ‰
Spring water = δD -42.2 ‰
352‰
112‰
70.5‰
-73.6‰
-92.5‰
a)
Distance (2-4m)
302.1‰
112‰
-35.8‰
-54.2‰
-68.3‰
-90.2‰
b)
Distance (4-6m)
270.1‰
144.6‰
67.7‰
37.3‰
(RH)
(FR)
-72.1‰
-95.7‰
c)
Time from injection (d)
Oak/soil P <.0001
Pine/soil P =0.8801
Distance (m)
0-2
2-4
4-6
(Hydraulic lift)
d)
400
300
200
100
0
-100
0
2
4
6
8
10
12

Fig. 4.8

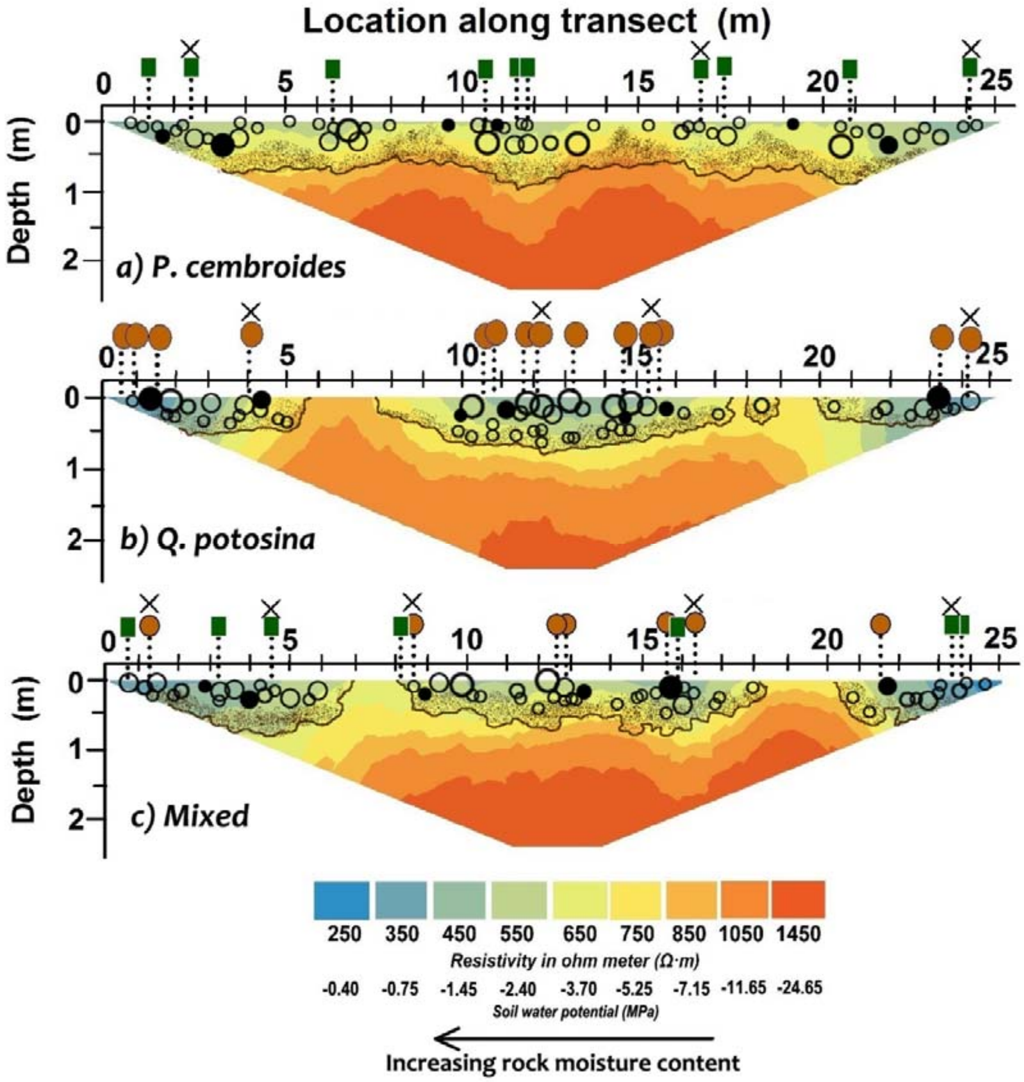
Location along transect (m)
0
5
10
15
20
25
Depth (m)
0
1
2
a) P. cembroides
b) Q. potosina
c) Mixed
250
350
450
550
650
750
850
1050
1450
Resistivity in ohm meter (Ω·m)
-0.40
-0.75
-1.45
-2.40
-3.70
-5.25
-7.15
-11.65
-24.65
Soil water potential (MPa)
Increasing rock moisture content

Fig. 4.9

4.5. Supporting Information

4.5.1. Materials and methods

Study site and geology

The study was conducted at Sierra San Miguelito Volcanic Complex (SSMVC) in a tropical semiarid mixed forest of in the physiographic province Mesa Central in central Mexico (Orozco et al. 2002), where pine and oak trees are distributed in monospecific and mixed stands (2350 m.a.s.l.; latitude 22.25° and longitude -101.12°). This volcanic complex is affected by punctual fracturing at small scale where the pine-oak forest is established. Due to presence of very shallow and rocky soils (<25 cm), trees have used weathered rocks to get support. Lithological profiles show a high density of vertical roots distributed into the fractures and soil pockets (U. Rodriguez Robles et al., unpublished). According to the World Reference Base for Soil Resources (WRB) classification system, soil at this site correspond to lithic–paralithic Leptosols (LPlip) (FAO 2006). Organic matter content is very high (60%) in these soils (Perez et al. 2009).

The SSMVC originated in the Oligocene age (31 a 26 My), is located mostly in the southwest corner of the state of San Luis Potosí, and represents one of the most voluminous rhyolitic volcanic events on Earth (McDowell & Keizer 1977). The Oligocene sequence consists in widely distributed accumulation of lava and ignimbrites. At the beginning of the SSMVC volcanic activity this formed the complex by lava spills of Rhyolitic composition (Portezuelo Latite and San Miguelito Rhyolite), that formed exogenous domes (Orozco et al. 2002; Tristán et al. 2009). Between 27 and 28 My ago, there was a punctual volcanic activity of basic composition that followed the main faults that were sectioning Sierra San Miguelito (SSM) with NW-SE orientation (Labarthe & Jiménez 1992). The entire sequence of the SSM was affected by a large number of normal faults (Shunshan et al. 2005). However, fractured volcanic rocks that constitute SSM are sealed by minerals of hydrothermal origin, turning SSM of geologic low permeability, limiting water recharge to the deep aquifer in the state capital (Ramos et al. 2007). SSM is not considered as recharge zone, therefore rain that falls in the mountain is mostly superficially drained, with a small proportion moving through hypodermic flow (subsurface flow).

Experimental plots and study species

We established 12 experimental plots (4*stand type) of 25 m diameter. In each plot monospecific they selected 10 individuals and in mixed plots 12 individuals (6*specie) with a total of 128 trees to which is applied different treatments. 12 trees (3*specie*stand type, randomly selected trees) of the 128 trees, were excluded surface roots. Soil depth was determined by GPR and ERT geophysical techniques and calibrated technique with coring from the soil surface to the rock matrix. Three soil corings were carried out for each plot (n = 48).

Mexican pinion (*Pinus cembroides* Zucc., 1832) and potosina oak (*Quercus potosina* Trel., 1924) are the two dominant tree species in the tropical semiarid pine–oak forest ecosystem in central-northwest Mexico. *Q. potosina* and *P. cembroides* occur either in islands of pure stands or in mixtures; *Q. potosina* grows generally on rocky shallow soils sites (< 25cm) unlike *P. cembroides* with deeper soils (> 50 cm). *P. cembroides* is a small tree (average 4.2 m) with evergreen needles with 2, 3 or 4 needles per fascicle, while *Q. potosina* is a short statured (average 3 m) with clusters of 4-6 leaves semideciduous broadleaf tree. Oak 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 (Pérez et al. 2014).

Rainfall partitioning

The climate is semiarid, with summer precipitation lasting from June to September and with small winter rains between December and January accounting for 5% of total annual rainfall, for the last 65 years annual average rainfall accounts for 408 mm (Weather station “La Purisima”, 22° 5' 22.4", 101°

12' 28.9" and observational data on site), where 64% of the years are below average and only 12% over 500 mm of rainfall (Figure S4.1).

We have collected over a period of 36 months (3 years), moisture ingress of meteorological events from tropical storms of the Pacific ocean basins (18 events) and the Gulf of Mexico (16 events); cold fronts (12 events); and water-rock interaction (6 events). To this end, five rain collectors installed with mineral oil between different stand types.

To this end, rain collectors installed five with mineral oil between different types of stand. After the income of each meteorological event, supported by forecasts from; The National Meteorological Service of Mexico (http://smn.cna.gob.mx/), The Weather Network INIFAP (http://clima.inifap.gob.mx/), The Weather Channel (http://weather.com/) and The Tropical Weather Center (http://wx.hamweather.com/tropical/). Samples were collected in glass vials with screw caps and transported in coolers to prevent isotopic fractionation to the laboratory for analysis. With the analysis of the 52 meteorological events was possible to draw a sketch map of Local Meteoric Water Line (LMWL).

Isotope hydrology techniques

Tree water sources

Samples for tree water sources were collected in January 2012 (early winter), to December 2015 (late autumn), a total 36 months. Comparing twig water isotopic signatures to the potential sources of rainfall, surface soil water and groundwater is possible using the natural abundance of hydrogen isotopes ($^{2}H/H$) and oxygen isotopes ($^{18}O/^{16}O$). For each sampling date (total = 72 samples), we collected a stem fully covered with periderm from each of 16 (four*specie*stand; pine/pure, oak/pure, pine/mixed and oak/mixed) randomly selected adult trees (n = 16 stem samples per sampling date, total = 1152 stems). Trees that they are excluded roots were sampled monthly (Oct 2012 – Dec 2013, total = 15 samples) we collected a stem from each tree (n = four stem samples per sampling date, total = 60 stems). The bark of each stem was peeled off and the stem stored in 30-mL glass vials sealed with parafilm-lined caps.

Tracing D2O in xylem tissues

To examine dynamics of water transport and storage in into the two species, we implemented a procedure similar to that described by James et al. (2003) and Meinzer et al. (2006) used to inject deuterium oxide (99.9 atom % D_2O) into the transpiration stream through holes spaced at regular intervals around the circumference of the trunk. The holes were filled with D_2O and was refilled periodically. The D_2O was injected simultaneously through four holes spaced 90° apart in each of the trees. The dosage was kept constant at ≈0.7 g D_2O per cm of sapwood circumference. This assay is performed in two treatments; one drought (spring 2013) and the other, after winter rain events (winter 2014). In spring 2013, the injections (δD = 366‰, enriched 5.6 times compared to natural abundance of deuterium) began on May 28 at 11:00 h and were completed by 13:30 h (total = eight injected trees, four pine/pure and four pine/mixed). In winter 2014 the injections (δD = 503‰, enriched 17.1 times compared to natural abundance of deuterium) began on February 21 at 10:00 h and were completed by 14:00 h (total = 16 injected trees, four pine/pure, four pine/mixed, four oak/pure and four oak/mixed). Presence of the D_2O tracer in stem water was detected by periodically collecting twigs from the different regions of the upper crown and immediately sealing them in borosilicate (VWR®) and then wrapped with Parafilm to prevent evaporation. Stem samples were collected prior to D_2O injections to establish baseline hydrogen isotope ratios. After the injection of D_2O (day 0), during the next 10 days, were performed periodic collections of branches at 12:00 hours.

D_2O injection in fractured rock and tracing D2O in soil and xylem tissues

To examine species root foraging into the two identified niches, we implemented an essay using labeled water (δD = -88.2‰, $\delta^{18}O$ = -11.8‰, natural abundance). We choose either oak or pine (monospecific stands) as targets, selecting a tree that was neighboring a tree from the other species (oak → pine, pine→oak) at three ranges (0-2, 2-4 and 4-6 m). Within 30-50 cm of the target tree we located a rock fracture where we installed a 1.5 cm diameter hose down to 30 cm. Labeled water (δD = 485.1‰, enriched 6.5 times compared to natural abundance of deuterium) was slowly applied with a syringe

(500 ml) into the hose, to avoid spreading labeled water on the soil surface. Presence of the D_2O tracer was detected by collecting seven branches from different regions of the crown. After the injection of D_2O (day 0), we collected every other day branches, wood cores from the target plant and its closest neighbor tree and soil during the next 10 days. In all cases, branches were collected at 12:00 hours.

Lab analysis

Water extraction of soils and stems for isotope analysis was carried out by cryogenic vacuum distillation in a extraction line of 5 ports (West et al., 2006). δD and $\delta^{18}O$ values of the stem, soil, precipitation and water-rock interaction was measured using a isotope ratio mass spectrometer (Picarro L1102-i water isotope analyzer, PICARRO, INC) at the Institute for Scientific and Technological Research of San Luis Potosi, IPICYT. Results are reported in d values, representing deviations in per mil (‰) from the Vienna Standard Mean Ocean Water (V-SMOW). Overall analytical precision of the spectrometer was ±0.1& for $\delta^{18}O$ and ±0.6 & for δD.

Diameter at Breast Height and Wood Moisture Content

We have indirectly estimated the Diameter at Breast Height of trees (DBH, favor of slope) with a tape measure. A mark to 1.30 m high in favor of slope, was placed around the trunks (4*space*plot, total = 64 trees) and measurements were made periodically to the trees (five ecohydrological periods). The value was divided by PI (3.1416...) to estimate the diameter.

16 trees (1*species*plot), was extracted 2 cylinders wooden with measures 1"x1" the end of each ecohydrological period (Depletion: February 2013 and April 2014; Recovery: May 2013; Wet: October 2013 and 2014) to which it was determined the wood moisture content. The Wood Moisture Content (WMC) was calculated from the weight of the fresh samples (Wfresh) and the weight of the dried samples (Wdry):

$$WMC = (W_{fresh} - W_{dry}) / W_{dry} \times 100\%$$

Water potential

We measured midday soil and leaf water potential (Ψ_{soil} and Ψ_{leaf}, respectively) from 11 to 14 hrs at biweekly intervals from September 2012 to December 2014. We used psychrometric techniques and a dewpoint microvoltimeter HR-33 (Wescor Inc., South Logan, UT, USA) to determine soil (TSP-55; Wescor Inc.) and Ψ_{leaf} (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 (four*space*plot, total = 64) at 12 cm depth within 100 cm from the tree trunk.

Anatomy

Eight healthy pine and oak trees were selected from the mixed stands. Three samples of the stem of each tree with a perforating punch collected; one to 0.20, 1.30 and 3.00 m above ground level, respectively. In each of the trees, they were cut four fine roots three millimeters in diameter. Samples included wood and vascular cambium; and were fixed immediately in FAA (Berlyn & Miksche 1976). In the laboratory, samples were washed and stored in GAA (glycerin-95% ethanol-water, 1:1:1).

Transverse and radial sections 30-40 mm thick including wood and vascular cambium were obtained with a sliding microtome. For each sample unbleached sections (Ruzin 1999) were stained with safranin-fast green (Johansen 1940) and mounted with synthetic resin. Macerations were prepared using Jeffrey’s solution (Berlyn & Miksche 1976). Temporary slides were prepared to gather data on vessel element, fibre lengths and tracheids.

Measurements were performed using an image analyzer BIO7 1.6 (Eclipse Public License) adapted to a video camera (Hitachi KP-D51) and a microscope (Olympus BX-50). The terminology used for wood description follows the recommendations of the International Association of Wood Anatomists (IAWA Comittee 1989).

Geophysical images

ERT is a method to generate images on the variation of electrical resistivity in either two or three dimensions below a line or grid of electrodes placed on the soil surface. Data consist in measurements of voltage differences between electrode pairs in response to current injection between additional electrode pairs (Kirsch & Yaramanci 2009). Measurements were performed using the SYSCAL KID SWITCH-24 (IRIS instruments) with a 24-multi-electrode switch box.

GPR is an impulse radar system designed for shallow and subsurface investigations. An electromagnetic pulse from a transmitting antenna on the ground penetrates the soil and reflects the boundary layer of objects with different physical values (Blindow 2009). It is known that most of soils and rocks have very low conductivity (about < 10-2 S/m), thus the electromagnetic waves propagation is mainly affected by electrical dielectric constants of soils and rocks (Parsekian et al. 2015). GPR profiles were performed using a MALÅ RAMAC system with 500 and 800 MHz antennas. Thus, the 500 MHz antenna allowed us to estimate the size, position and depth of roots within 2 to 6 cm diameter range, while the 800 MHz antenna served to differentiate the exfoliated rock base from potential roots (0.6 to 4 cm diameter) present underneath the rock.

For data processing and filtering radargrams, we applied the routine proposed by *U. Rodriguez Robles et al., unpublished.*

Calculations and statistical analyses

To compare differences in the isotopic composition of the xylem sap and ecophysiological water relation variables used a multifactorial repeated-measures ANOVA. The mixed model for isotopic composition of the xylem sap included, species with two levels (*Q. potosina* and *P. cembroides*, fixed effect), stand with two levels (monospecific and mixed, fixed effect), distance with three levels (0-2, 2-4, 4-6 m, fixed effect) and time (sampling dates, random effect) for fractures water injection treatment; for water variables included, as classification factors, species with two levels (*Q. potosina* and *P. cembroides*, fixed effect), stand with two levels (monospecific and mixed, fixed effect) and time (sampling dates, random effect) with 56 levels (biweekly dates) and 30 levels (biweekly dates) for root exclusion treatment; Differences of diameter breast height and wood moisture content included, species with two levels and ecohydrological periods with five levels (Depletion 2013, Recovery 2013, Wet 2013, Depletion

2014 and Wet 2014). Regarding the water transport treatment in P. cembroides trunks by stand type were analyzed using a one-way ANOVA followed by a Tukey's post hoc mean comparison test. All statistical analyses were run in SAS University Edition (Free Statistical Software) using a mixed model (PROC MIXED) for the repeated-measures analysis and a generalized linear model (PROC GLM) for the univariate analysis.

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4.4.2. Figures

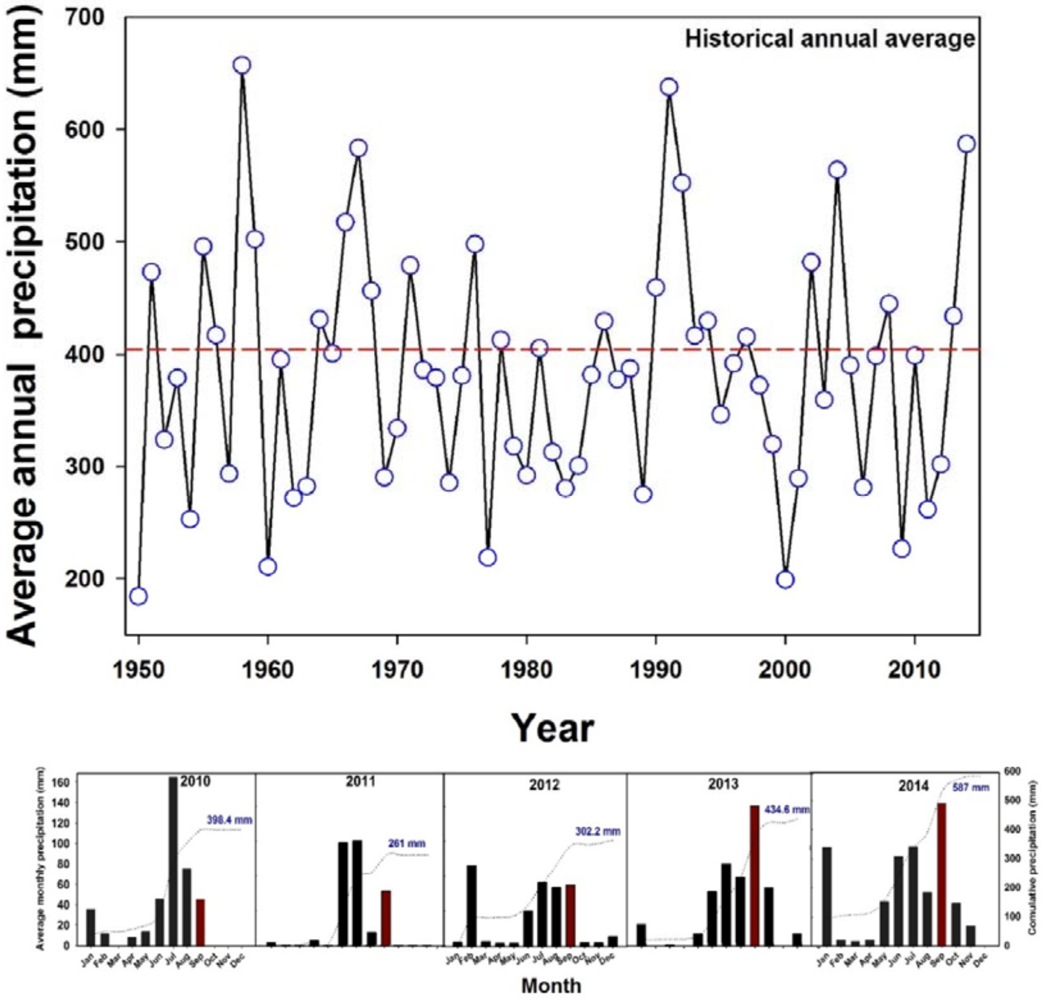

Figure S4.1. Historical mean annual precipitation for a period of 65 years in the SSM. Dashed line indicates the historical annual precipitation (top). Monthly rainfall in the last five years of the study (bottom).

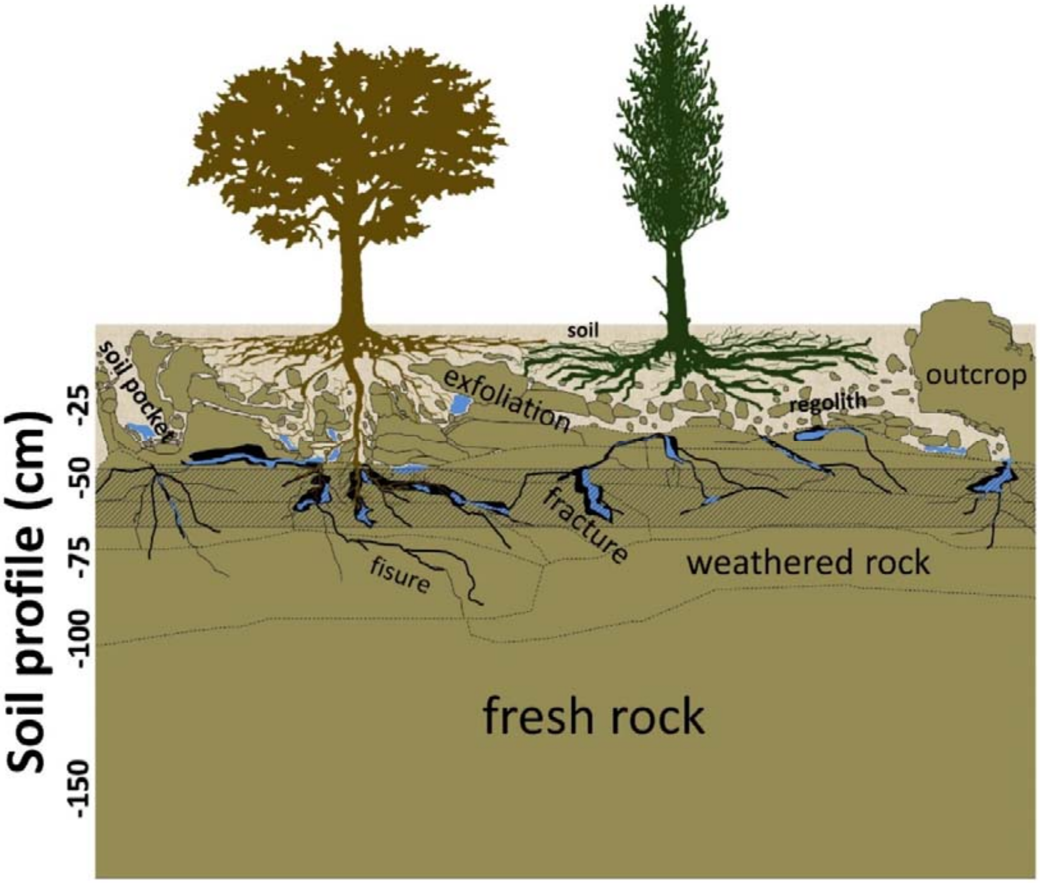

Figure S4.2. Shallow rocky soil profile of tropical semiarid mixed forest in ‘Sierra San Miguelito, a volcanic mountain range in Central North Mexico. Fracturing and fissuring (-35 to -75 cm depth), exfoliated rock (-45 to 0 cm), soil pockets and regolith (-5 to -38 cm) and a very thin layer of soil (<25 cm).

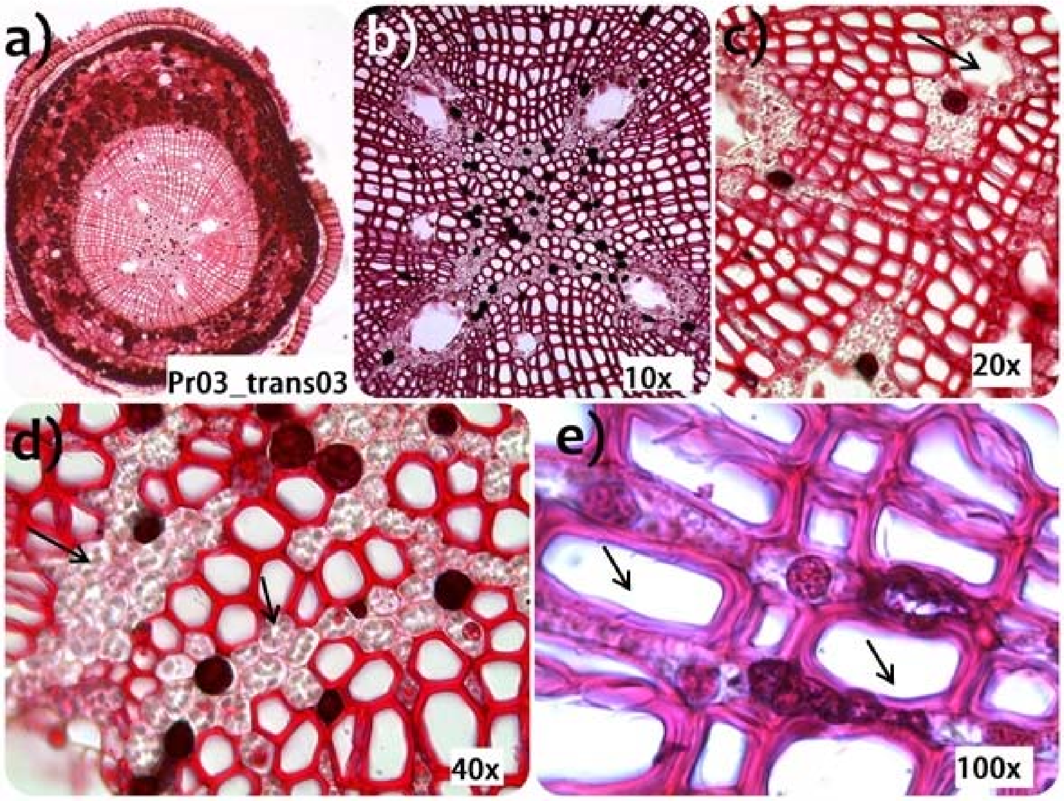

Figure S4.3. Histological cross sections in pine roots: **(a)** roots of 2 mm, **(b)** pith, intercellular spaces between tracheids; **(c)** axial intercellular (resin) canals, **(d)** organic deposits (resin plugs) in heartwood tracheids, **(e)** latewood tracheids thick-walled; axial parenchyma present**.**

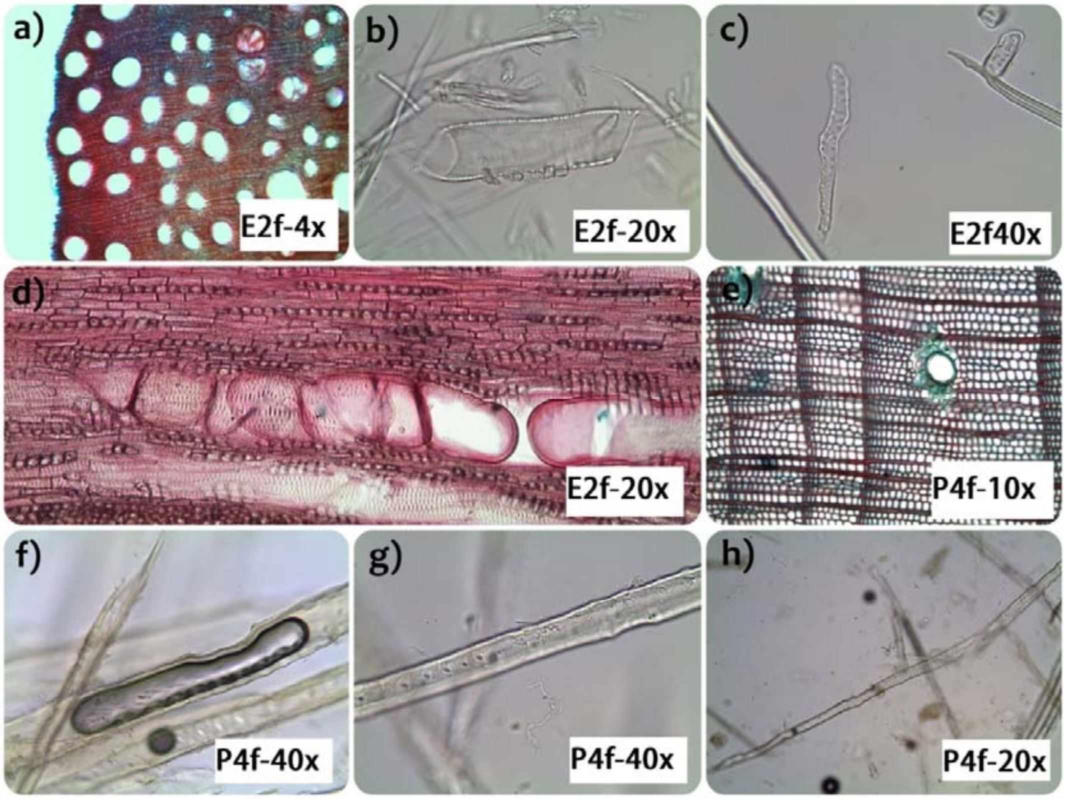

Figure S4. Histological transversal and tangential sections in pine and oak stems: **(a)** solitary vessel of distinct sizes**; v**essels with sclerotic tyloses **(b)** body of vessel element, **(c)** body of fibre-tracheids, **(d)** vessel elements flanked by fibre-tracheids**;** cavitated vessel **(e)** growth rings; transition from early wood to latewood abrupt **(f)** tracheid with air bubble**, (g)** tracheid pitting, **(h)** longitudinal tracheid.

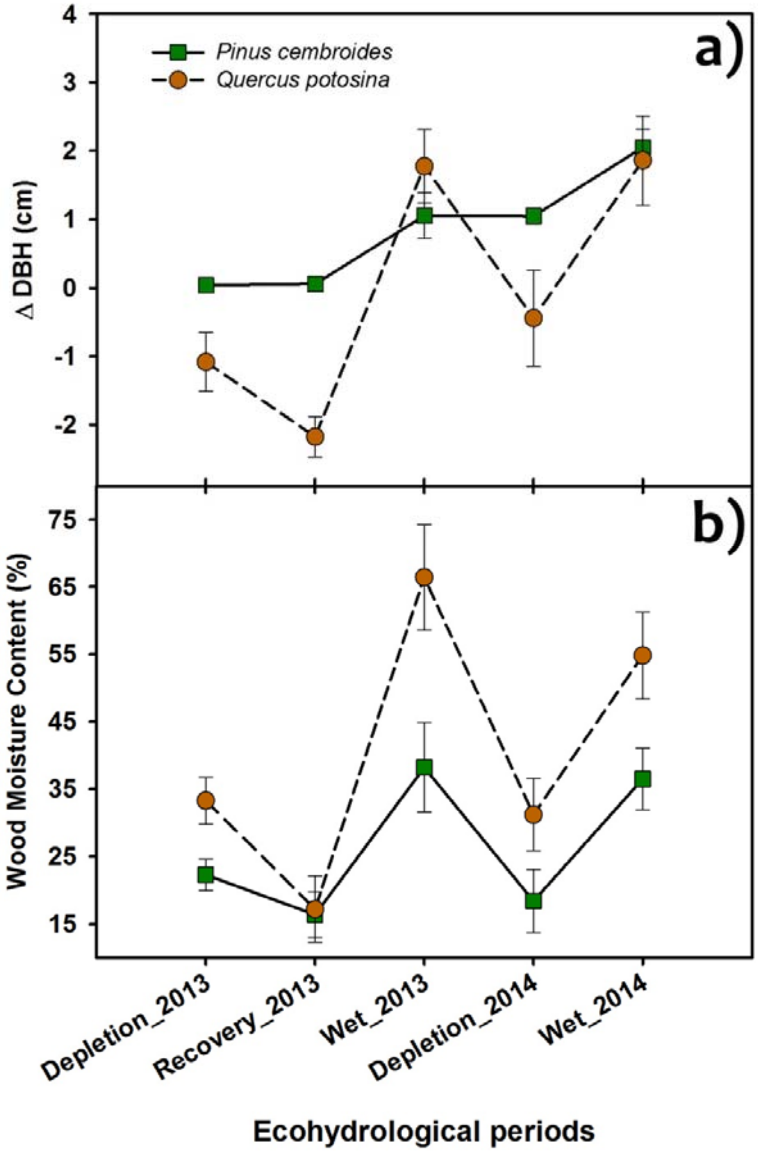

Figure S4.5. (a) Diameter at breast height and **(b)** wood moisture content of trees of *Pinus cembroides* and *Quercus potosina* corresponding to the end of ecohydrological periods.

GENERAL CONCLUTIONS

Although the underlying mechanisms require further research, our results provide the first evidence in support of the role of weathered rock water as a source in arid regions. Here, we demonstrated that rocky soils also include a high degree of water content variability and large offsets in the physiological status of trees. Incorporating geospatial niches as a major aspect of ecosystem structure may clarify some of the apparent paradoxes of forest growing on rock-dominated landscapes, such as variability in the spatial patterns of tree mortality under drought conditions.

Quercus potosina showed the opportunistic strategies to capture water during periods of low water availability, keeping stable its water potential. The variation in their water potential along the sampling period and its maximum drop (~ 5.5 MPa) indicates that *Pinus cembroides* and *Q. potosina* presented an risky water deficit. However, it was observed that both species are adapted to water deficit exhibiting however, very different strategies to cope with drought (e.g., root distribution in different soil profiles, hydraulic redistribution, anatomical structures, etc). For instance, *Q. potosina* used different water sources throughout the year, including water from the fractured rock, which through hydraulic redistribution make available to *P. cembroides* when growing in coexistence. The observed positive interaction between oak and pine shed doubts on the long-term capacity of P. cembroides to succeed in monocultures under increasingly limiting geohydrometeorological conditions, and provided evidence of the importance of Q. potosina to maintain the structure and functioning in this water-limited biome

Perspectives and future work

Our results have important implications for functional ecology, the study of life under extreme conditions and arid land reclamation and use. *Quercus potosina* can be preferably used for reforestation programs in areas with predominantly rocky soil profiles. This species is optimal for reforestation in xeric sites with shallow soils. These benefits need to be evaluated in the context of management and ecological restoration programs of arid and semiarid regions. This study gives strength from scientific perspective the importance of decreeing Sierra de San Miguelito as a protected natural area.

Climate change is expected to exacerbate regional mortality events. To forecast their impact, studies needed include; forest carbon balance, insect resistance, carbon starvation and hydraulic failure regarding drought survival and mortality. To do this, it is needed an inter-multidisciplinary group.

ANEXOS

List of publications

1. Rodriguez-Robles U., Arredondo J.T., Huber-Sannwald E. & Vargas R. (2015). Geoecohydrological mechanisms couple soil and leaf water dynamics and facilitate species coexistence in shallow soils of a tropical semiarid mixed forest. New Phytol, 207, 59-69.

2. Rodriguez-Robles U., Arredondo J.T., Huber-Sannwald E., Ramos-Leal J.A. & Yepez E.; Geophysical tools for tree root studies: a case study of a semiarid forest on shallow rocky soils. In preparation.

3. Rodriguez-Robles U., Arredondo J.T., Huber-Sannwald E. &Yepez E. Ramos-Leal.; Geoecohydrological niches facilitate tree species coexistence in water-limited environments. In preparation.

4. Rodriguez-Robles U., Arredondo J.T., Huber-Sannwald E &Yepez E. Ramos-Leal.; Multidimensionality niche in species coexistence: crossing boundaries between disciplines and scales. In preparation.