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RESEARCH ARTICLE

From facilitative to competitive interactions between woody plants and plants with crassulacean acid metabolism (CAM): The role of hydraulic descent

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Abstract

Woody plants may facilitate the establishment of seedlings with crassulacean acid metabolism (CAM) by ameliorating the abiotic environment through an increase in soil water availability. Because of the low transpiration rate in shallow-rooted CAM plants and the consequently high soil water contents in the shallow soil, deep-rooted trees in tree-CAM associations could perform hydraulic descent transporting water from wetter shallow soil to drier deep soil in arid environments. It remains unclear, however, whether a high rate of hydraulic descent can turn the facilitation of CAM plants by woody plants into competition. In this study, we develop a mechanistic model to investigate the facilitation of shallow-rooted CAM plants by deep-rooted woody plants in the access to soil water resources along a rainfall gradient. The model results show that in the case of low-to-moderate root overlap woody plants could facilitate CAM plants in access to soil water; this effect is mainly induced by the reduction in evaporation from the soil surface due to shading. Both shading and hydraulic descent decrease (or hydraulic lift increases) along a rainfall gradient, thereby favoring facilitation. Investment in deep roots by woody plants is usually thought to increase niche differentiation with shallow-rooted plants, thereby reducing the competition and promoting species coexistence. This study indicates that deep root development could also favor competition through the mechanism of hydraulic descent, thereby changing our understanding of the role of root depth in niche differentiation between shallow and deep-rooted plants.

KEYWORDS

competition, crassulacean acid metabolism, facilitation, hydraulic descent, rainfall gradient, woody plants

1 | INTRODUCTION

While competitive interactions between coexisting species have long been considered major determinants of plant community structure and function (Tilman, 1982; Connell, 1983), studies in the past few decades have increasingly recognized the role of facilitation in plant community ecology (e.g., Callaway, 1995; Bruno, Stachowicz, & Bertness, 2003; Brooker et al., 2008), especially in stressful environments (e.g., Callaway et al., 2002; Maestre, Callaway, Valladares, & Lortie, 2009). An example of possible facilitation in dry and vegetation is associated with the ability of woody plants to facilitate seedling establishment in dryland species with crassulacean acid metabolism (CAM) (e.g., Withgott, 2000; Castillo-Landero & Valiente-Banuet, 2010; Cares, Muñoz, Medel, & Botto-Mahan, 2013). Mechanisms

often invoked to explain this facilitation involve an increase in soil water and/or nitrogen availability and/or refuge from extreme environmental stress (i.e., temperature and/or solar radiation) (e.g., Franco & Nobel, 1988, 1989; Drezner, 2007; Wang, D'Odorico, Manzoni, Porporato, & Macko, 2009; Cares et al., 2013).

Past studies indicate that facilitation of CAM plants by woody plants are species specific, that is, some plants are better facilitators than others (e.g., Withgott, 2000; Flores & Jurado, 2003; Castillo-Landero & Valiente-Banuet, 2010; Cares et al., 2013). However, it remains unclear what nurse plant characteristics determine such a difference in facilitation. Root depth and root density distribution affect water uptake and thus may determine the magnitude of facilitation. For example, Franco and Nobel (1988, 1989) showed that nurse plants (*Hilaria rigida*) with shallow roots strongly compete with CAM

plants for soil water resources and thus greatly reduce the growth of CAM seedlings. Density, cover, and/or leaf area index of nurse plants may also affect the magnitude of facilitation. Canopies with a higher plant density, cover, and/or leaf area index (LAI) may more effectively improve the microclimate (i.e., reduction of soil evaporation as a shade effect) (e.g., Ludwig, de Kroon, Berendse, & Prins, 2004; D'Odorico, Okin, & Bestelmeyer, 2012; Dohn et al., 2013; Moustakas, Kunin, Cameron, & Sankaran, 2013) and thus benefit CAM plants. However, Castillo-Landero and Valiente-Banuet (2010) observed that dense canopies of some nurse species had negative effects on the early fitness of the columnar cactus *Neobuxbaumia mezcalaensis*. Other studies also documented the inhibitory effects of dense canopies of some species on the establishment of CAM seedlings (e.g., De Viana, Sühling, & Manly, 2001).

Hydraulic redistribution translocating soil water in response to water potential gradients via plant root systems has important ecohydrological benefits (i.e., increase in nutrient uptake, transpiration, and photosynthesis) (e.g., Lee, Oliveira, Dawson, & Fung, 2005; Scott, Cable, & Hultine, 2008). The occurrence of this phenomenon has been documented within a range of different ecosystems (i.e., deserts, savannas, and forests) and plant species (i.e., trees/shrubs and grasses) (e.g., Brooks, Meinzer, Warren, Domec, & Coulombe, 2006; Neumann & Cardon, 2012; Prieto, Armas, & Pugnaire, 2012). Few studies, however, have evaluated the role of hydraulic redistribution in the facilitation of CAM seedlings by woody plants. Roots of deep-rooted plants can transport water from wetter deep soil layers to the drier shallow soil (hydraulic lift, HL) (e.g., Richards & Caldwell, 1987; Brooks et al., 2006). This process may contribute to the facilitation of shallow-rooted understory plants by deep-rooted plants (e.g., Flores & Jurado, 2003; Riginos, Grace, Augustine, & Young, 2009; Moustakas et al., 2013; Dohn et al., 2013). In contrast, hydraulic descent transporting water from wetter shallow soil to drier deep soil (e.g., Burgess, Adams, Turner, White, & Ong, 2001; Hultine, Scott, Cable, Goodrich, & Williams, 2004) is expected to favor deep-rooted plants and therefore enhance their competition with understory plants. A lower transpiration rate (root uptake) by CAM plants (Lüttge, 2004; Ogburn & Edwards, 2010) would increase water potential in the shallow soil layer, thus providing conditions favorable for hydraulic descent (Yu & D'Odorico, 2014a; Yu & Foster, 2016). It remains unclear, however, whether a high rate of hydraulic descent could turn CAM plant facilitation by woody plants into competition.

It is also unclear how such a facilitation changes along a rainfall gradient. The stress-gradient hypothesis suggests that facilitation becomes more important relative to competition along gradients of increasing abiotic stress (e.g., Bertness & Callaway, 1994; Callaway et al., 2002; Maestre et al., 2009). The stress-gradient hypothesis has been confirmed by some studies (e.g., Lortie & Callaway, 2006; Maestre et al., 2009), but other authors have found that facilitation tends to be prevalent under moderate water stress conditions (e.g., Maestre & Cortina, 2004; Michalet et al., 2006; McCluney et al., 2012). Under extreme stress nurse plants would be unable to mitigate stress conditions and ensure facilitation (e.g., Maestre & Cortina, 2004; Michalet et al., 2006). Shading increases with rainfall because the leaf area index increases (e.g., Dohn et al., 2013; Moustakas et al., 2013). Likewise, hydraulic descent reduces

(or hydraulic lift increases) along a rainfall gradient (e.g., Yu & D'Odorico, 2014a), thereby favoring shallow-rooted CAM plants. Can these processes induce an increase in CAM plant facilitation by woody plants along a rainfall gradient?

In this study, we develop a mechanistic model to investigate the facilitation of CAM plants by deep-rooted woody plants along a rainfall gradient. The specific goals of this research are (a) to identify the characteristics of deep-rooted (nurse) plants that affect the facilitation of CAM plants in access to soil water resources, (b) to evaluate whether a high rate of hydraulic descent can turn CAM plant facilitation by woody plants into competition, and (c) to investigate the mechanisms determining changes in facilitation along a rainfall gradient.

2 | METHODS

2.1 | Modeling framework

We develop a mechanistic model to investigate the facilitation of CAM plants by woody plants in the access to soil water resources along a rainfall gradient. The model quantifies transpiration ratio (ξ) of CAM plants between tree–CAM associations (T–C) and CAM alone (C) in the course of the growing season, defined as

$$\xi = \frac{T_{1c}(TC)}{T_{1c}(C)} \quad (1)$$

where $T_{1c}(TC)$ and $T_{1c}(C)$ are transpiration of CAM plants in tree–CAM associations and CAM alone, respectively. Therefore, a value of ξ greater than 1 indicates facilitation of CAM plants by woody plants while a value of ξ less than 1 indicates competition.

We use transpiration as an indicator of occurrence of facilitation or competition by woody plants on CAM plants because transpiration is linked to total CO₂ assimilation and plant productivity. To quantify the role of hydraulic redistribution in the facilitation of CAM plants by woody plants, the model accounts for soil moisture dynamics in two soil layers coupled by hydraulic redistribution by deep-rooted woody plants (e.g., Ryel, Caldwell, Yoder, Or, & Leffler, 2002; Lee et al., 2005; Yu & D'Odorico, 2014a). Roots of CAM plants are only present in the shallow soil layer (e.g., Franco & Nobel, 1988, 1989; Ogburn & Edwards, 2010) while woody plants occupy both the shallow and deep soil layers (e.g., Yu & D'Odorico, 2014a). CAM plants transpire at night (12 hr) (e.g., Lüttge, 2004; Ogburn & Edwards, 2010), while woody plants transpire in the daytime (12 hr) and perform hydraulic redistribution (HR) at night (12 hr) (e.g., Ryel et al., 2002; Lee et al., 2005; Yu & D'Odorico, 2014a). CAM plants typically have a non-negligible plant water capacitance (e.g., Lüttge, 2004; Ogburn & Edwards, 2010), and we account for the plant water capacitance by modeling the transient plant water storage dynamics (e.g., Schulte & Nobel, 1989; Lhomme, Rocheteau, Ourcival, & Rambal, 2001; Bartlett, Vico, & Porporato, 2014). In contrast, root uptake by trees and grasses are calculated at steady state neglecting the effects of plant water capacitance (e.g., Manzoni, Vico, Porporato, & Katul, 2013).

2.2 | Water balance

Soil moisture dynamics in the two soil layers for associations of woody plants and CAM plants ($T-C$) are modeled by two coupled equations

$$nZ_1 \frac{dS_1}{dt} = P - U_1 - E - D_1 + HR \quad (2)$$

and

$$nZ_2 \frac{dS_2}{dt} = D_1 - U_2 - D_2 - HR \quad (3)$$

where the subscripts 1 and 2 refer to the shallow and deep soil layer, respectively; n is the soil porosity, Z_1 and Z_2 are the soil layer thicknesses (mm), S_1 and S_2 are the relative soil moisture ($0 < S_1, S_2 \leq 1$), P is the rate of rainfall infiltration into the top soil layer (mm/day), U_1 and U_2 are the soil moisture losses from each soil layer due to root uptake (mm/day), E is the evaporation rate from the soil surface (mm/day), D_1 and D_2 are the drainage rates (mm/day), and HR is the hydraulic redistribution at the patch scale (mm/day). Positive values of HR indicate "hydraulic lift" (i.e., upward hydraulic redistribution), while negative values of HR indicate "hydraulic descent" (i.e., downward hydraulic redistribution). For CAM plants alone, only Equation 2 needs to be used to quantify soil moisture dynamics experienced by CAM plants, where HR is taken to be 0 mm/day and U_1 is root uptake by CAM plants. For tree-CAM associations, Equations 2 and 3 are used to determine soil moisture dynamics experienced by trees and CAM plants, where HR is a function of soil water potential gradient in the shallow and deep soil layers, U_1 is the sum of root uptake by CAM plants and trees in the shallow soil layer, and U_2 is root uptake by trees in the deep soil layer.

Precipitation is modeled as a sequence of intermittent rainfall events occurring as a marked Poisson process with average rainfall frequency, λ , (events per day). The depth (mm) of each storm is modeled as an exponentially distributed random variable with mean, h , (millimeter per event) (e.g., Rodriguez-Iturbe, D'odorico, Porporato, & Ridolfi, 1999). Runoff occurs when the surface layer is saturated (i.e., $S_1 = 1$). Drainage is assumed to be driven only by gravity and is expressed as $D = \frac{K_s}{\exp(\beta(1-S_c)) - 1} (\exp(\beta(S - S_c)) - 1)$, where K_s is the soil saturated hydraulic conductivity (mm/hr), β is the coefficient, S is the relative soil moisture, and S_c is the field capacity (Laio, Porporato, Ridolfi, & Rodriguez-Iturbe, 2001).

Uptake by woody plants is determined by the steady-state approach whereby uptake is equal to transpiration (e.g., Porporato, Laio, Ridolfi, Caylor, & Rodriguez-Iturbe, 2003; Manzoni et al., 2013). In the associations of woody plants and CAM plants, stomata of CAM plants close in the daytime (e.g., Lüttge, 2004; Ogburn & Edwards, 2010), and thus, the maximum total potential evapotranspiration in the daytime ($ET_{\max d} = 4.5$ mm/day) is partitioned into potential transpiration for woody plants ($T_{t \max d}$) and evaporation for soil surface ($E_{\max d}$). Potential evapotranspiration depends on available shortwave radiation and shortwave radiation exponentially decays through the plant canopy (Beer's law). Thus, following Caylor, Shugart, and Rodriguez-Iturbe (2005) and Yu and D'Odorico (2014a), Yu and D'Odorico (2014b), we have $T_{t \max d} = ET_{\max d} [1 - \exp(-k_s LAI_t)]$ and

$E_{\max d} = ET_{\max d} \exp(-k_s LAI_t)$, where k_s is the extinction coefficient of shortwave radiation, LAI_t is the leaf area index of woody plants (m^2/m^2). $T_{t \max d}$ is then partitioned into potential transpiration for the shallow soil layer ($T_{1td \max}$) and the deep soil layer ($T_{2td \max}$), respectively, by accounting for root depth and root density distribution, given by

$$T_{1td \max} = T_{td \max} \frac{Z_1 S_1}{Z_1 S_1 + Z_2 S_2} \quad (4)$$

$$T_{2td \max} = T_{td \max} \frac{Z_2 S_2}{Z_1 S_1 + Z_2 S_2} \quad (5)$$

(Yu & D'Odorico, 2014a). The actual transpiration is smaller than these maximum values because of the effect of soil moisture limitation, which is here expressed by the following function (e.g., Rodriguez-Iturbe et al., 1999),

$$t(S) = \begin{cases} 0, & S < S_w \\ \frac{S - S_w}{S^* - S_w}, & S < S^* \\ 1, & S \geq S^* \end{cases} \quad (6)$$

where S is the soil moisture, S^* is the vegetation-specific value of relative soil moisture above which transpiration is not limited by soil water availability, and S_w is the vegetation-specific wilting point at which point transpiration ceases. Therefore, the actual transpiration of woody plants in the shallow (T_{1tda}) and deep (T_{2tda}) soil layers are determined as

$$T_{1tda} = T_{1td \max} t(S_1) r_1 \quad (7)$$

$$T_{2tda} = T_{2td \max} t(S_2) r_2 \quad (8)$$

where r_1 and r_2 are cumulated (and normalized) tree root densities in the shallow and the deep soil layers, respectively ($r_1 + r_2 = 1$). As seen from Equations 4, 5, 7, and 8, high values of Z_1/Z_2 and r_1/r_2 indicate a high root overlap between woody plants and CAM plants and are expected to lead to a high T_{1tda} relative to T_{2tda} .

To model root uptake in CAM plants, we cannot make the steady-state assumption used for woody plants because of the ability of succulent CAM plants to store water. Therefore, we used the framework developed by Bartlett et al. (2014) to simulate the ecohydrologic controls on the physiology of CAM plants. The model simulates the functioning of CAM plants accounting for the effect of capacitances and resistances along the water flow pathway within the plant using an electric circuit analogy (Figure 1). Here, we summarize the main components of this framework and refer the reader to Bartlett et al. (2014) for more details on this model.

The leaf transpiration (T_{CAM}) per unit ground area is expressed by the following water balance equation whereby transpiration is balanced by the rates of water uptake, U_{CAM} , and the plant water capacitance (Q_w), that is,

$$T_{CAM} = U_{CAM} + Q_w \quad (9)$$

U_{CAM} and Q_w are a function of water potential gradients; thus, $U_{CAM} = g_{srp} (\Psi_{s1} - \Psi_x)$ and $Q_w = g_c LAI_c (\Psi_w - \Psi_x)$, where g_{srp} is the soil-root-plant conductance per unit ground area ($m \cdot s^{-1} \cdot MPa^{-1}$),

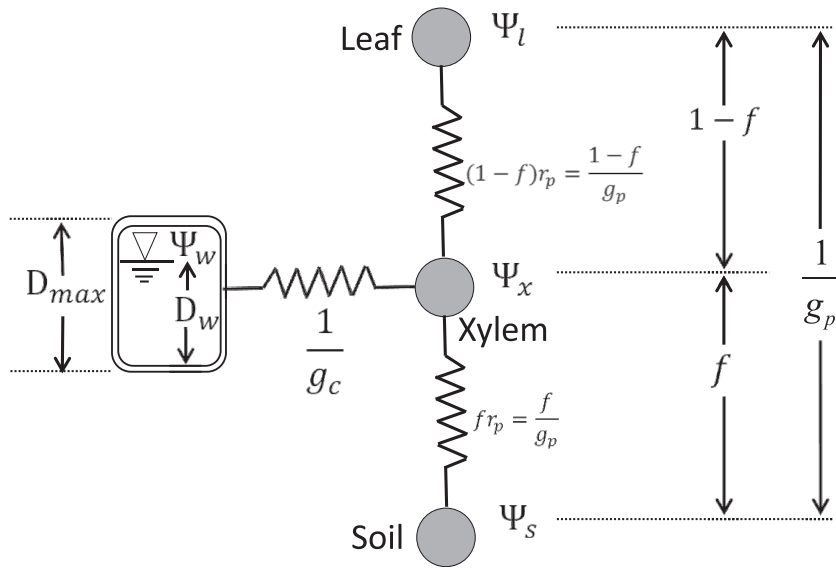


FIGURE 1 Schematic diagram of water flux within canopies of CAM plants. Ψ_l = leaf water potential; Ψ_s = soil water potential; Ψ_x = xylem water potential; Ψ_w = plant storage water potential; f = fraction of plant resistance below the storage branch connection; g_p = plant conductance per unit leaf area (r_p = plant resistance per unit leaf area); g_c = storage conductance per unit leaf area; D_{max} = maximum depth of water per unit leaf area; D_w = actual depth of water per unit leaf area. Adapted from Lhomme *et al.* (2001) and Bartlett *et al.* (2014)

$g_c LAI_c$ is the storage conductance per unit ground area ($m \cdot s^{-1} \cdot MPa^{-1}$) (g_c is the storage conductance per unit leaf area, and LAI_c is the leaf area index of CAM plants), Ψ_{s1} is the soil water potential in the shallow soil layer, Ψ_x is the water potential at the storage connection (MPa), and Ψ_w is the plant storage water potential (MPa). T_{CAM} is equal to the flux from the storage connection to the leaves, that is,

$$T_{CAM} = \frac{g_p LAI_c}{1-f} (\Psi_x - \Psi_l) \quad (10)$$

where g_p is plant conductance per unit leaf area, $\frac{g_p LAI_c}{1-f}$ is the plant conductance per unit ground area between the water potential at the storage connection node (Ψ_x) and leaf water potential (Ψ_l , MPa). The parameter f expresses the fraction of plant resistance below the storage branch connection (see Figure 1). The leaf transpiration (T_{CAM}) per unit ground area is also determined by the specific humidity gradient between the leaf mesophyll (q_l) and the atmosphere (q_a), that is,

$$T_{CAM} = l g_{msa} \frac{\rho_a}{\rho_w} (q_l - q_a) \quad (11)$$

where ρ_a is the air density (kg/m^3), ρ_w is the water density (kg/m^3), g_{msa} is the series of the mesophyll ($g_m LAI_c, m/s$), stomatal ($g_s LAI_c, m/s$), and atmospheric conductances ($g_a, m/s$) to water vapor per unit ground in well-watered conditions, respectively, that is, $g_{msa} = LAI_c g_m g_s \frac{g_a}{LAI_c g_m g_s + g_s g_a + g_m g_a}$, l is a coefficient limiting g_{msa} in dry conditions. In Equation 11, q_l is a function of Ψ_l and leaf temperature. Detailed calculations of the parameters g_{srp} , g_{msa} , l , q_l , Ψ_w , and other parameters can be found in Bartlett *et al.* (2014). The rate of CAM plant uptake is then calculated as in Bartlett *et al.* (2014), that is, combining Equations 9–11 with Equation 11 driven by atmospheric conditions.

Following Porporato *et al.* (2003) and Bartlett *et al.* (2014), soil evaporation is determined by accounting for soil water availability, given by

$$E = \begin{cases} 0, & 0 \leq S \leq S_h \\ E_{max} \frac{S - S_h}{1 - S_h}, & S_h < S < 1 \end{cases} \quad (12)$$

where S_h is the hygroscopic point below which surface soil evaporation ceases (Laio *et al.*, 2001) and E_{max} the potential evaporation during the day or at night ($E_{maxn} = 0.5$ mm/day). Note that for CAM plants alone the maximum total potential diurnal evapotranspiration ($ET_{maxd} = 4.5$ mm/day) is only contributed by potential evaporation at the soil surface ($E_{maxd} = 4.5$ mm/day) because the stomata of CAM plants are closed during the day (Lüttge, 2004; Ogburn & Edwards, 2010).

Hydraulic redistribution is determined as $HR = c C_{rmax} (\Psi_{s2} - \Psi_{s1}) \min(r_1, r_2)$ (e.g., Ryel *et al.*, 2002; Lee *et al.*, 2005; Yu & D'Odorico, 2014a), where C_{rmax} is the maximum root hydraulic conductance of the entire active root system ($mm \cdot MPa^{-1} \cdot hr^{-1}$), c a factor reducing root hydraulic conductance and accounting for soil water limitation, Ψ_{s2} and Ψ_{s1} the soil water potential (MPa) in the deep and shallow soil, respectively. Following Clapp and Hornberger (1978), Ψ is determined as $\Psi = \Psi_s \times S^{-d}$, where Ψ is the soil water potential, S is the soil moisture, while Ψ_s and d are experimentally derived parameters that have been determined for a variety of soils. The detailed calculations of c can be found in Yu and D'Odorico (2014a).

2.3 | Parameterization of the model

Crassulacean acid metabolism plants are predominant in arid and semiarid environments (Withgott, 2000; Ogburn & Edwards, 2010), and thus, we parameterize this model with respect to environmental conditions with low ($\lambda = 0.2/day$ and $h = 5$ mm) and moderate ($\lambda = 0.2/day$ and $h = 10$ mm) total rainfall amounts. Because this study investigates the facilitation or competition of CAM plants by woody plants, we assume that the growing seasons of trees and CAM plants coincide and last 210 days each year (e.g., Bhattachan *et al.*, 2012). CAM plants typically have very shallow roots (e.g., Franco & Nobel, 1988, 1989; Ogburn & Edwards, 2010), and thus, the root depth of CAM plants is taken to be constant ($Z_1 = 10$ cm) in all the simulations. The maximum root hydraulic conductance of the entire active root system (C_{rmax}) of woody plants is taken to be $C_{rmax} = 0.75 LAI_t mm \cdot MPa^{-1} \cdot hr^{-1}$ (e.g., Lee *et al.*, 2005; Yu & D'Odorico, 2014a). To investigate the characteristics of woody plants

leading to different facilitative effects on CAM plants, we vary the root depth (Z_2), the ratio between root density in the shallow and deep soil layers (r_1/r_2), and the leaf area index (LAI_t) of woody plants. When Z_2 is less than 40 cm, hydraulic descent performed by roots of woody plants is insignificant relative to situations of $Z_2 > 40$ cm (e.g., Caldwell, Dawson, & Richards, 1998; Espeleta, West, & Donovan, 2004). In this case, we can evaluate the extent to which deep-rooted woody plants facilitate CAM plants along a rainfall gradient without considering the effects of hydraulic descent. To investigate whether hydraulic descent can turn the facilitation of CAM plants by woody plants into competition, we increase the root depth (Z_2) and the leaf area index (LAI_t) of woody plants because these conditions can increase the rate of hydraulic descent (Yu & D'Odorico, 2014a). The soil type used in this study is sandy loam because soil texture with a high hydraulic conductivity (i.e., sand) is not favorable for the occurrence of hydraulic descent (e.g., Ryel et al., 2002; Yu & D'Odorico, 2014a). All the parameters used in this study can be found in Table 1.

3 | RESULTS

Modeling results show that woody plants having a low-to-moderate root overlap with CAM plants facilitate CAM plants access to soil water resources both in arid (Figure 2a) and semiarid environments (Figure 2b), as reflected by the fact that the ratio (ξ) between the transpiration rate of CAM plants in tree-CAM associations ($T-C$) and CAM plants alone (C) is greater than one ($\xi > 1$). Facilitation of CAM plants by woody plants decreases as the degree of root overlap increases and facilitation can turn into competition (i.e., $\xi < 1$) with high

degrees of root overlap; this transition to competition can occur both in arid (Figure 2a) and semiarid environments (Figure 2b).

With relatively high values of deep soil layer thickness (Z_2), trees in tree-CAM association can perform hydraulic redistribution. Modeling results show that in arid environments ($\lambda = 0.2/\text{day}$ and $h = 5$ mm) (Figure 3) trees in tree-CAM associations perform hydraulic descent in the case of a low-to-moderate range of deep-to-shallow root density ($\frac{r_2}{r_1} = 1$ or 3). By comparison, in semiarid environments ($\lambda = 0.2/\text{day}$ and $h = 10$ mm), trees in tree-CAM associations perform hydraulic lift in the case of a low value of $\frac{r_2}{r_1} = 1$ (Figure 3). With relatively low values of the $\frac{r_2}{r_1}$ ratio, woody plants facilitate CAM plants both in arid and semiarid environments even when the effects of hydraulic redistribution are accounted for (Figure 4). Hydraulic descent reduces the magnitude of facilitation of CAM plants by trees while hydraulic lift enhances facilitation (Figures 3 and 4). The facilitation of CAM plants by trees occurs because of the lower evaporation from the soil surface (E) (shade effect), and thus, the lower total evapotranspiration (ET_1) in the shallow soil layer in tree-CAM associations than with CAM plants alone; this effect is expected to occur both in arid and semiarid environments (Figure 5).

Next, we evaluate whether a high rate of hydraulic descent can turn the facilitation of CAM plants by woody plants into competition. Modeling results show that the transpiration ratio (ξ) (Equation 1) increases with Z_2 and the tree leaf area index (LAI_t) with the effect of inducing hydraulic descent, which is in contrast to the reduction of ξ with Z_2 and LAI_t in the absence of hydraulic descent (Figure 6a,b). In dry environment (Figure 6a), where there is a relatively strong hydraulic descent (Figure 7a), facilitation turns into competition. This is likely to occur when the leaf area index (i.e., $LAI_t = 2.5$ m²/m²)

TABLE 1 Parameters, parameter values, and reference sources used in this study

Parameter	Symbol	Value	Reference
Soil porosity	n	0.43	Laio et al. (2001)
Soil saturated hydraulic conductivity	K_s	33.33 mm/hr	Laio et al. (2001)
Soil coefficient affecting drainage	β	13.8	Laio et al. (2001)
Field capacity	S_{fc}	0.56	Laio et al. (2001)
Wilting point for woody plants	S_w	0.18	Laio et al. (2001)
Relative soil moisture for unstressed transpiration by woody plants	S^*	0.46	Laio et al. (2001)
Hygroscopic point	S_h	0.14	Laio et al. (2001)
Soil parameter relating soil water potential to relative soil moisture	ψ_s	-2.1×10^{-3} MPa	Laio et al. (2001)
Soil parameter relating soil water potential to relative soil moisture	d	4.9	Laio et al. (2001)
Extinction coefficient of shortwave radiation	k_s	0.35	Brutsaert (1982)
Storage conductance per unit leaf area	g_c	$0.002 \mu\text{m}\cdot\text{MPa}^{-1}\cdot\text{s}^{-1}$	Bartlett et al. (2014)
Leaf area index of CAM plants in arid environment	LAI_c	$1 \text{ m}^2/\text{m}^2$	This study
Leaf area index of CAM plants in semiarid environment	LAI_c	$2 \text{ m}^2/\text{m}^2$	This study
Plant conductance per unit leaf area	g_p	$0.0004 \mu\text{m}\cdot\text{MPa}^{-1}\cdot\text{s}^{-1}$	Bartlett et al. (2014)
Fraction of plant resistance below the storage branch connection	f	0.5	Bartlett et al. (2014)
Air density	ρ_a	$1.2 \text{ kg}/\text{m}^3$	Bartlett et al. (2014)
Specific humidity in the atmosphere in arid environment	q_a	$0.00359 \text{ kg}/\text{kg}$	This study
Specific humidity in the atmosphere in semiarid environment	q_a	$0.00504 \text{ kg}/\text{kg}$	This study
Factor reducing root hydraulic conductance ^a	c	$\frac{1}{1 + \frac{\max(\psi_{s2}, \psi_{s1})}{\psi_{s0}^b}}$	Ryel et al. (2002)

^a ψ_{s0} is the soil water potential where soil-root conductance is reduced by 50% and b is an empirical constant. $\psi_{s0} = -1$ MPa and $b = 3.22$ (Ryel et al., 2002).

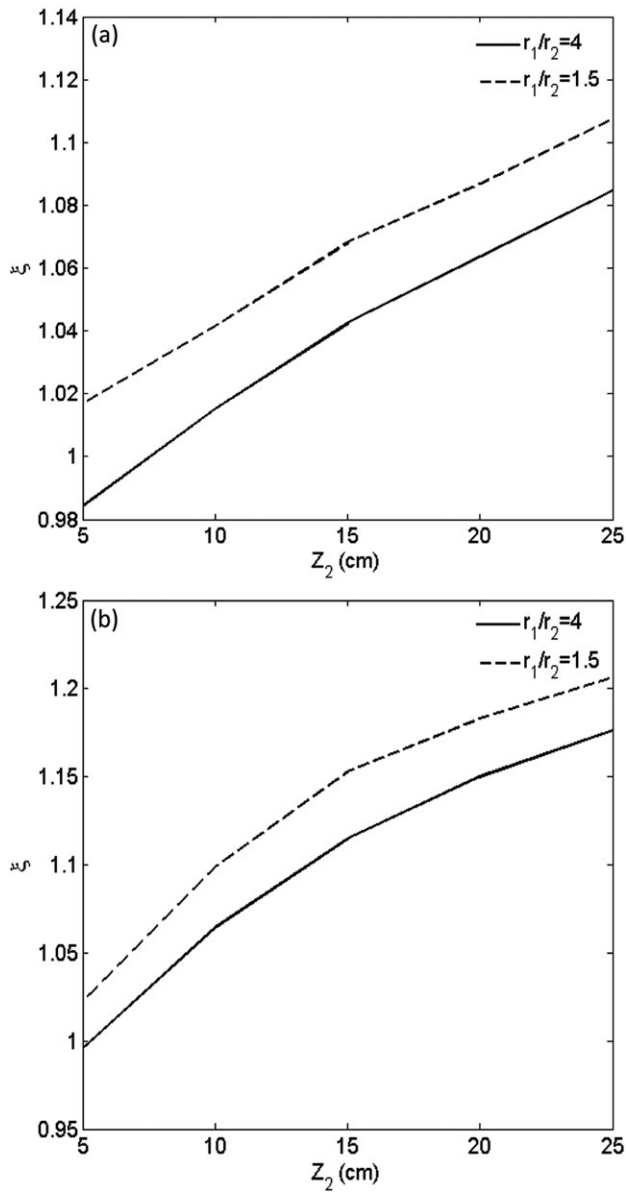


FIGURE 2 (a, b) Transpiration ratio (ξ) of CAM plants between tree-CAM associations (T-C) and CAM alone (C) as affected by the depth of deep soil layer (Z_2) and ratio (r_2/r_1) between root density in the deep and shallow soil layer in arid (a) and semiarid (b) environments, respectively. A low value of Z_2 and a high value of r_2/r_1 indicate a high root overlap between woody plants and CAM plants. Parameters: tree leaf area index ($LAI_t = 1.5 \text{ m}^2/\text{m}^2$) and $LAI_t = 3 \text{ m}^2/\text{m}^2$ in arid and semiarid environments, respectively

and root depth of trees are high (e.g., $Z_2 > 100$ cm). In fact, a higher value of LAI_t reduces the rate of soil evaporation because of the effect of shading. However, the increase in hydraulic descent with increasing LAI_t is greater than the reduction in soil evaporation (E) with LAI_t , and thus, the effects of hydraulic descent may outweigh the reduction in E both in arid and semiarid environments (Figure 7b). Likewise, modeling results show that the transpiration ratio (ξ) increases with r_2/r_1 when hydraulic descent is accounted for, which is in contrast to the reduction of ξ with r_2/r_1 without the effects of hydraulic descent in both arid (Figure 8a) and semiarid environments (Figure 8b). Overall, these results

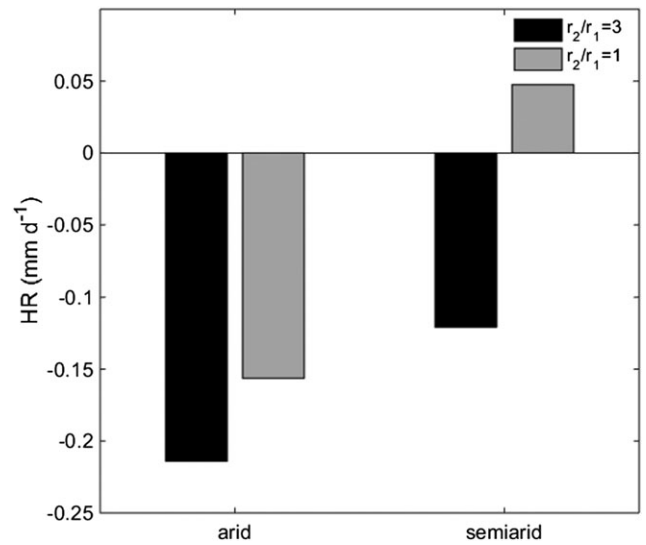


FIGURE 3 (a, b) Hydraulic redistribution (HR) by trees in tree-CAM associations in arid ($\lambda = 0.2/\text{day}$ and $h = 5$ mm) and semiarid ($\lambda = 0.2/\text{day}$ and $h = 10$ mm) environments, respectively. r_2/r_1 is the ratio between root density in the deep and shallow soil layer. Parameters: tree leaf area index ($LAI_t = 1.5 \text{ m}^2/\text{m}^2$) and $LAI_t = 3 \text{ m}^2/\text{m}^2$ in arid and semiarid environments, respectively; depth of the shallow soil layer ($Z_1 = 10$ cm); depth of the deep soil layer ($Z_2 = 40$ cm)

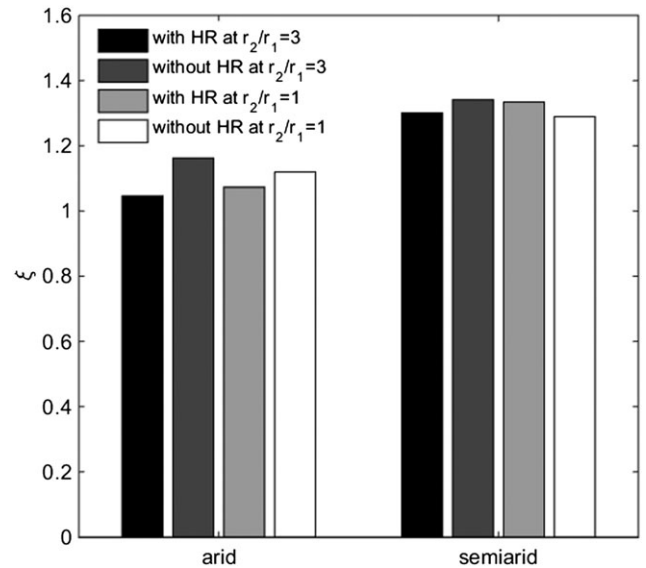


FIGURE 4 (a, b) Transpiration ratio (ξ) of CAM plants between tree-CAM associations (T-C) and CAM alone (C) in arid ($\lambda = 0.2/\text{day}$ and $h = 5$ mm) and semiarid ($\lambda = 0.2/\text{day}$ and $h = 10$ mm) environments, respectively. r_2/r_1 is the ratio between root density in the deep and shallow soil layer. Parameters: the same as Figure 3

indicates that a high value of hydraulic descent resulting from high values of LAI_t , Z_2 , and r_2/r_1 can turn CAM plant facilitation by woody plants into competition.

The facilitation of CAM plants by trees is greater in semiarid environment than that in arid environment (Figure 4). This can be explained by a greater reduction in E and, thus, in ET_1 and a reduction/increase in hydraulic descent/hydraulic lift in semiarid environments with respect to the case of arid environments (Figures 3 and 5).

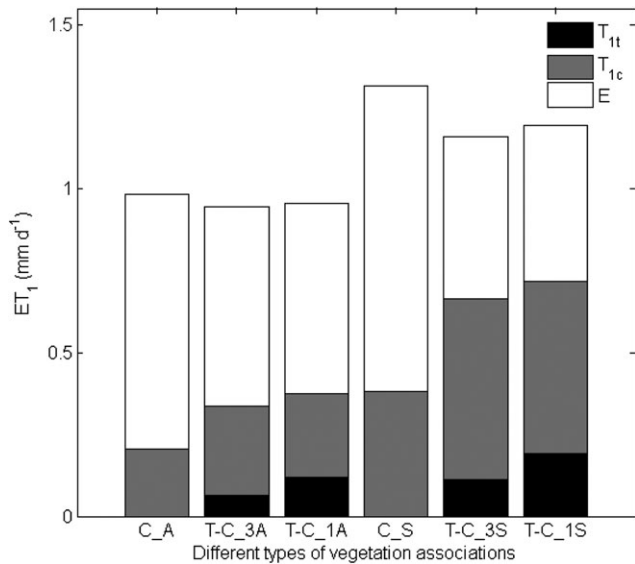


FIGURE 5 Actual evapotranspiration components in the shallow soil layer for CAM plants alone (C) and tree–CAM associations (T–C). T_{1t} refers to the transpiration by trees, T_{1c} refers to the transpiration by CAM plants, and E refers to evaporation at soil surface. The number “3” means $\frac{L_2}{r_1} = 3$ while the number “1” means $\frac{L_2}{r_1} = 1$. The label “a” means arid environment while label “S” means semiarid environment. Parameters: the same as Figure 4

4 | DISCUSSION

Plants with CAM are increasing their abundance in many dry lands worldwide (Borland, Griffiths, Hartwell, & Smith, 2009; Borland, Barrera Zambrano, Ceusters, & Shorrocks, 2011). This phenomenon could provide opportunities for CAM plant (i.e., *Agave* and *Opuntia ficus-indica*) cultivation and use as bioenergy crops with important implications for human adaptation to climate change in marginal lands (Davies, Dohleman, & Long, 2011; Cushman, Davis, Yang, & Borland, 2015). While other studies have attributed the increased abundance of CAM plants to changes in climate or increasing atmospheric CO₂ concentrations (e.g., Drennan & Nobel, 2000; Borland et al., 2009), this study investigates the role of interactions with other species; more specifically, we looked at the facilitation of CAM plants by deep-rooted woody plants along a rainfall gradient. To this end, we developed a mechanistic model to quantify the transpiration ratio (ξ) between CAM plant transpiration in tree–CAM associations (T–C) and CAM plants alone (C). The transpiration ratio was calculated at the growing season to yearly timescales. This model accounts for soil moisture dynamics in two soil layers coupled by hydraulic redistribution by deep-rooted woody plants (e.g., Ryel et al., 2002; Lee et al., 2005; Yu & D’Odorico, 2014a); therefore, the model allows us to evaluate the role of hydraulic redistribution.

The modeling results show that woody plants having a high degree of root overlap with CAM plants have competitive but not facilitative effects on CAM plants both in arid (Figure 2a) and semiarid environments (Figure 2b). Consistent with this result, the shallow-rooted nurse plants (*H. rigida*) was found to strongly compete with CAM plants for soil water resources and thus reduce seedling growth of CAM plants (Franco & Nobel, 1988, 1989). Similarly, other functional groups (i.e., *Pinus halepensis*, trees) have also been found to strongly compete

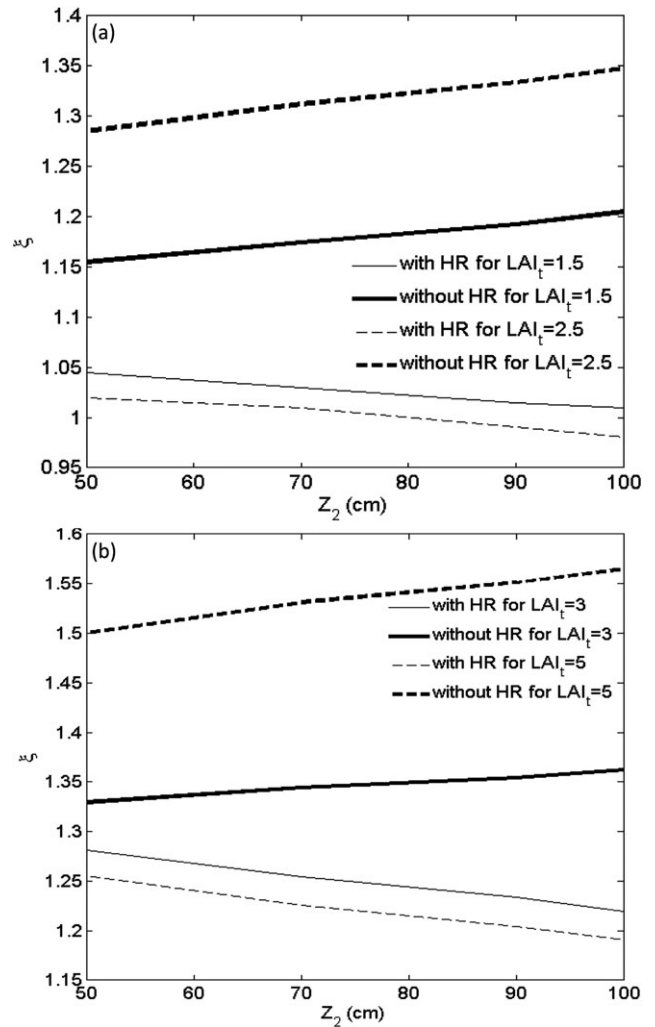


FIGURE 6 (a, b) Transpiration ratio (ξ) of CAM plants between tree–CAM associations (T–C) and CAM alone (C) as affected by the depth of deep soil layer (Z_2), tree leaf area index (LAI_t), and hydraulic redistribution (HR) in arid (a) and semiarid (b) environments, respectively

with understory plants (i.e., shrubs) for soil water resources because of a high root overlap (e.g., Maestre, Cortina, Bautista, & Bellot, 2003; Bellot, Maestre, Chirino, Hernandez, & de Urbina, 2004). By comparison, woody plants facilitate CAM plants in access to soil water resources in situations of a low-to-moderate root overlap (Figure 4); in these conditions, competition with CAM plants for soil water resource is weak and thus shading by woody plants predominates (Figure 5). This result is consistent with past studies that show that woody plant canopies reduce the incoming solar radiation and evapotranspiration and thus reduce water stress in understory plants (e.g., Ludwig et al., 2004; D’Odorico, Caylor, Okin, & Scanlon, 2007; Dohn et al., 2013; Moustakas et al., 2013).

Past studies have mostly focused on the role of hydraulic redistribution in interspecies interactions in ecosystems dominated by C₃ and/or C₄ species (Ludwig, Dawson, de Kroon, Berendse, & Prins, 2003; Zou, Barnes, Archer, & McMurtry, 2005; Brooks et al., 2006), while the effects of hydraulic descent in the facilitation of CAM plants by woody plants remain to be assessed (Yu & Foster, 2016). This study shows hydraulic descent reduces the magnitude of CAM plant facilitation by woody plants (Figure 4). In fact, hydraulic descent transports

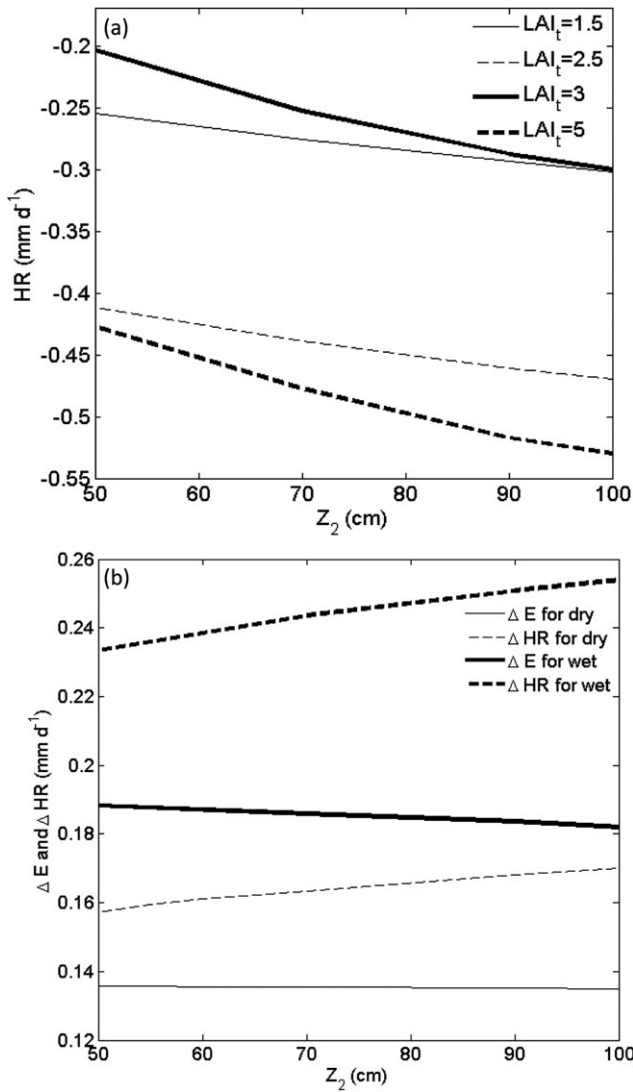


FIGURE 7 (a, b) Hydraulic redistribution (HR) as affected by the depth of deep soil layer (Z_2) and tree leaf index (LAI_t); (b) difference of soil evaporation from soil surface (ΔE) and hydraulic redistribution (ΔHR) between high leaf area index and low leaf area index as affected by the depth of deep soil layer (Z_2). Note that the tree leaf area index for arid environment is taken to be 1.5 and 2.5 m^2/m^2 while 3 and 5 m^2/m^2 for semiarid environment

water from shallow to deep soil layers and thus reduces water availability to CAM plants (e.g., Burgess et al., 2001; Hultine et al., 2004; Ryel, Leffler, Peek, Ivans, & Caldwell, 2004). Thus high rates of hydraulic descent can turn CAM plant facilitation by woody plants into competition (Figure 6a and 7a). Hydraulic descent in tree-CAM associations can be enhanced by an increase in tree leaf area index (LAI_t), tree root depth ($Z_1 + Z_2$), and the ratio (r_2/r_1) between root density in the deep and shallow soil layers (e.g., Yu & D'Odorico, 2014a). Consistent with these results, other studies have observed the inhibitory effects of dense tree canopies of some nurse species on the establishment of CAM plant seedlings in the field (e.g., De Viana et al., 2001; Castillo-Landero & Valiente-Banuet, 2010). While the introduction of woody plants could favor CAM plants restoration, this study highlights how this effect can depend both on the aboveground (i.e., LAI) and the belowground characteristics (i.e., root overlap with CAM plants) of woody plants.

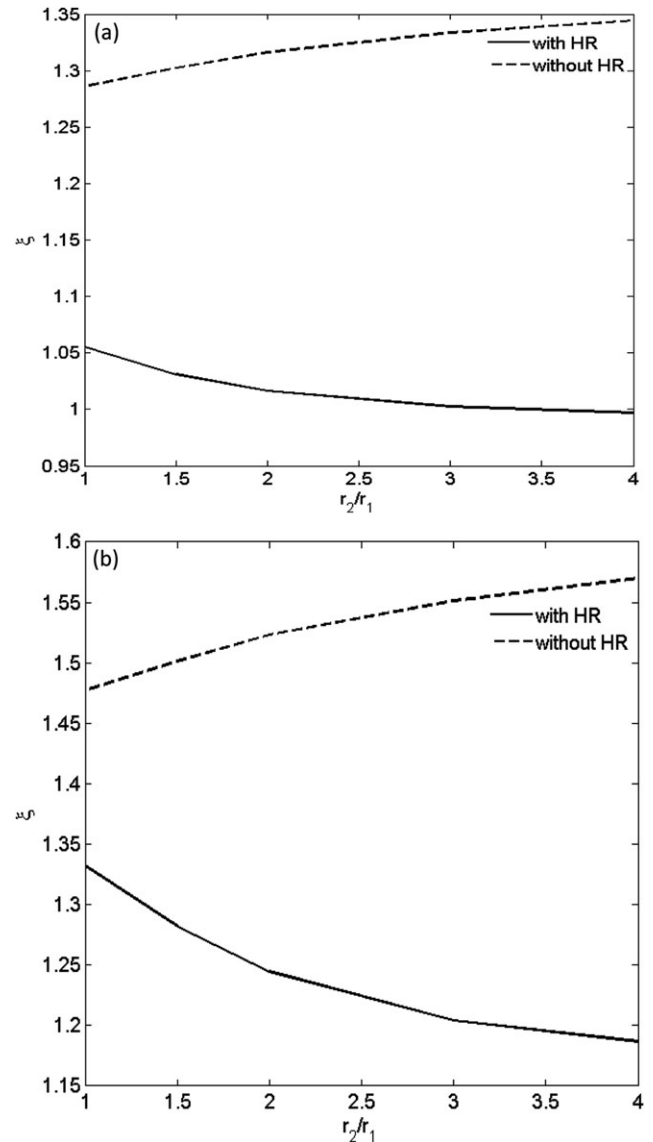


FIGURE 8 (a, b) Transpiration ratio (ξ) of CAM plants between tree-CAM associations (T-C) and CAM alone (C) as affected by ratio (r_2/r_1) between root density in the deep and shallow soil layer for arid (a) and semiarid environments (b), respectively. Parameters: depth of deep soil layer ($Z_2 = 90$ cm); $LAI_t = 2.5$ m^2/m^2 and $LAI_t = 5$ m^2/m^2 in arid (a) and semiarid environment (b), respectively

The ability of trees in tree-CAM associations to sustain high rates of hydraulic descent during the growing season is an important finding, in contrast to past studies at the timescale of rainfall/irrigation events (e.g., Schulze et al., 1998; Burgess et al., 2001) or during dormant season (e.g., Ryel et al., 2004; Hultine et al., 2004). In this study, CAM plants transpire at night but their transpiration rate is relatively low because of the low gradients in water vapor concentration existing during nighttime (Lüttge, 2004; Ogburn & Edwards, 2010). Moreover, CAM plants typically have a relatively low mesophyll conductance (e.g., Flexas et al., 2008; Nelson & Sage, 2008; Ripley, Abraham, Klak, & Cramer, 2013) and thus a low transpiration rate (Equation 11) because water storage restricts the gas space available for the diffusion of CO_2 into the photosynthetic tissue. These conditions favor the maintenance of relatively high soil moisture levels in the shallow soil and thus provide the conditions favorable for hydraulic descent (Yu & Foster, 2016).

In view of the ability of relatively high hydraulic descent rates to turn CAM plant facilitation into competition, this study may also improve our understating of traditional niche differentiation theory (e.g., Walter, 1971; Walker & Noy-Meir, 1982). In fact, a stronger allocation of woody plant roots into deeper soil layers (i.e., increase in niche differentiation with shallow-rooted plants) could still exert a competitive effect on shallow-rooted plants through the mechanism of hydraulic descent. Hydraulic descent could be an adaptive strategy trees take to invest in deep roots when soils have a relatively low hydraulic conductivity, thereby limiting the drainage rates (e.g., Burgess et al., 2001; Ryel et al., 2004). The rate of hydraulic descent increases as the root depth of woody plants increases (Figure 7a); in these conditions trees exert a competitive rather than a facilitative effect on CAM plants in access to soil water (Figure 6a). This study highlights the role of hydraulic descent in turning CAM plant facilitation by woody plants into competition. This may explain why, once adults, CAM plants (which benefit from the presence of trees during their establishment) are not strong enough to outcompete their nurse plants (i.e., trees), consistent with field observations (i.e., Reyes-Olivas, García-Moya, & López-Mata, 2002; Flores-Torres & Montana, 2015). The ability of woody plants to perform hydraulic redistribution (e.g., Neumann & Cardon, 2012; Prieto et al., 2012) may contribute to the explanation of tree–CAM association/coexistence that has been widely documented in different arid and semiarid regions including the Sonoran and Chihuahuan deserts (e.g., Hutto, McAuliffe, & Hogan, 1986; Drezner, 2007; Flores-Torres & Montana, 2015), the Zapotitlán de las Salinas or Tehuacan valley, central Mexico (e.g., Valiente-Banuet, Vite, & Zavala-Hurtado, 1991), coastal deserts in northern Sinaloa, Mexico (e.g., Reyes-Olivas et al., 2002), and Chilean arid and semiarid zones (e.g., Cares et al., 2013).

This study also evaluated how the facilitation of CAM plants by woody plants is expected to change along a rainfall gradient and tried to explain the underlying mechanisms. The modeling results show that the magnitude of CAM plant facilitation by woody plants increases along the rainfall gradient (Figures 2 and 4). Consistent with this result, other studies indicate that facilitation is more prevalent under moderate conditions (i.e., water availability) (e.g., McCluney et al., 2012); in fact, nurse plants may not sufficiently mitigate stressful conditions at high water stress level (e.g., Maestre, Cortina, & Bautista, 2004; Michalet et al., 2006). The factors driving the increase in facilitation along a rainfall gradient include shading and reduction of hydraulic descent (or increase in hydraulic lift). We note that this study does not account for the effects of other environmental factors/indicators (i.e., temperature and/or solar radiation). In fact, in arid environments, the environmental stress could be high not only because of limited soil water availability but also because of high temperature and/or solar radiation. Thus, facilitation of CAM plants by trees could be even stronger in harsh arid environments (e.g., Bertness & Callaway, 1994; Callaway et al., 2002; Maestre et al., 2009), where trees provide refuge for CAM plants also from other forms of extreme environmental stress (i.e., temperature and/or solar radiation) (Franco & Nobel, 1988, 1989; Withgott, 2000). Consistent with this idea, Reyes-Olivas (2002) found the occurrence of competitive effects of woody plants on CAM plants in access to soil water in coastal deserts of Mexico, where temperature tends to be less extreme.

5 | CONCLUSION

This study developed a mechanistic model to investigate the facilitation of CAM plants by woody plants along a rainfall gradient. The modeling results show that both the aboveground characteristics (i.e., LAI) and the belowground characteristics (i.e., root overlap with CAM plants) of woody plants could account for changes in the strength of CAM plant facilitation. In situations with a high root overlap between CAM plants and trees or with a high rate of hydraulic descent (i.e., the cases with a deeper tree roots, higher leaf area index, and higher root density ratio between the deep and shallow soil layer), trees exert a competitive rather than facilitative effects on CAM plants in arid environment. Facilitation increases along a rainfall gradient because of the increase in shading and the decrease/increase in hydraulic descent/lift. Overall, this study may improve traditional niche differentiation theory in dryland vegetation because more investment in deeper roots by trees—which was traditionally thought to increase niche differentiation with shallow-rooted plants and thus reduce competition—could still favor a competitive effect on shallow-rooted plants through the mechanism of hydraulic descent.

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