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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-Ladero & Valiente-Banuet, 2010; Cares, Muñoz, Medel, & Botto-Mahan, 2013). Mechanisms often invoked to explain this facilitation involve an increase in soil water availability 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-Ladero & 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-Landro and Valiente-Banuet (2010) observed that dense canopies of some nurse species had negative effects on the early fitness of the columnar cactus *Neobuxbaumia megalosperma*. Other studies also documented the inhibitory effects of dense canopies of some species on the establishment of CAM seedlings (e.g., De Viana, Sühring, & 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; Rigosín, 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 (\(\xi\)) of CAM plants between tree-CAM associations (T-C) and CAM alone (C) in the course of the growing season, defined as

\[
\xi = \frac{T_{1C}(TC)}{T_{1C}(C)}
\]

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 \(\xi\) greater than 1 indicates facilitation of CAM plants by woody plants while a value of \(\xi\) 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 CO\(_2\) 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 wooden 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

\[
\frac{dS_1}{dt} = P - U_1 - E - D_1 + HR
\]

and

\[
\frac{dS_2}{dt} = D_1 - U_2 - D_2 - HR
\]

where the subscripts 1 and 2 refer to the shallow and deep soil layer, respectively; \(n\) is the soil porosity, \(S_1\) and \(S_2\) are the soil layer thicknesses (mm), \(D_1\) 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, \(\lambda\) (events per day). The depth (mm) of each storm is modeled as an exponentially distributed random variable with mean, \(\frac{1}{\lambda}\). 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 \(D = K_s \beta (S - S_p) - 1\), where \(K_s\) is the soil saturated hydraulic conductivity (mm/hr), \(\beta\) is the coefficient, \(S\) is the relative soil moisture, and \(S_p\) 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., Portoraro, 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., Lütte, 2004; Ogburn & Edwards, 2010), and thus, the maximum total potential evapotranspiration in the daytime (\(ET_{max} = 4.5 \text{ mm/day}\)) is partitioned into potential transpiration for woody plants (\(T_{max,d}\)) and evaporation for soil surface (\(E_{max}\)). 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 \(T_{max,d} = ET_{max}[1 - \exp(-k_s LAI_c)]\) and \(E_{max} = ET_{max} \exp(-k_s LAI_c)\), where \(k_s\) is the extinction coefficient of shortwave radiation, \(LAI_c\) is the leaf area index of woody plants (m$^2$/m$^2$), \(T_{max,d}\) is then partitioned into potential transpiration for the shallow soil layer (\(T_{1dmax}\)) and the deep soil layer (\(T_{2dmax}\)), respectively, by accounting for root depth and root density distribution, given by

\[
T_{1dmax} = \frac{T_{dmax}}{Z_1 S_1}{Z_1 S_1 + Z_2 S_2}
\]

\[
T_{2dmax} = \frac{T_{dmax}}{Z_2 S_2}{Z_1 S_1 + Z_2 S_2}
\]

(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),

\[
t(S) = \begin{cases} 0, & S < S_w \\ \frac{S - S_w}{S' - S_w}, & S_w < S < S' \\ 1, & S \geq S'
\end{cases}
\]

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 (\(T_{1d}\)) and deep (\(T_{2d}\)) soil layers are determined as

\[
T_{1d} = T_{1dmax} \cdot t(S) \cdot r_1
\]

\[
T_{2d} = T_{2dmax} \cdot t(S) \cdot r_2
\]

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 \(T_{1d}\) relative to \(T_{2d}\).

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,

\[
T_{CAM} = U_{CAM} + Q_w
\]

\(U_{CAM}\) and \(Q_w\) are a function of water potential gradients; thus, \(U_{CAM} = \gamma_{sw} (\Psi_{wd} - \Psi_s)\) and \(Q_w = \gamma_{sw} LAI_c (\Psi_w - \Psi_s)\), where \(\gamma_{sw}\) is the soil-root-plant conductance per unit ground area (m$^{-1}$ MPa$^{-1}$).
where \( g_c \) is the leaf stomatal conductance per unit ground area (m\( \cdot \)s\(^{-1}\)·MPa\(^{-1}\)) and \( g_m \) is the leaf mesophyll conductance per unit area (m\( \cdot \)s\(^{-1}\)·MPa\(^{-1}\)). The parameter \( f \) expresses the fraction of plant resistance below the storage branch connection (see Figure 1). The leaf transpiration \( T_{\text{CAM}} \) per unit ground area is also determined by the specific humidity gradient between the leaf mesophyll \( (q_l) \) and the atmosphere \( (q_a) \), where

\[
T_{\text{CAM}} = g_m \frac{\rho_a}{\rho_w} (q_l - q_a) \tag{11}
\]

where \( \rho_a \) is the air density (kg/m\(^3\)), \( \rho_w \) is the water density (kg/m\(^3\)), \( g_m \) is the series of the mesophyll conductance \( (g_m L A I_c \text{m/s}) \), stomatal conductance \( (g_s \text{m/s}) \), and atmospheric conductances \( (g_a \text{m/s}) \) to water vapor per unit ground area in well-watered conditions, respectively, that is, \( g_m = L A I_c \frac{g_m}{g_m + g_s + g_a} \). The parameter \( I \) is a coefficient limiting \( g_m \) in dry conditions. In Equation 11, \( q_l \) is a function of \( \Psi_l \) and leaf temperature.

Detailed calculations of the parameters \( g_{\text{top}}, g_{\text{root}}, \Psi_{\text{top}}, \Psi_{\text{root}}, \Psi_{\text{water}}, \) 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

\[
E = \begin{cases} 
0, & 0 \leq S \leq S_h \\
\frac{S - S_h}{S_{\text{max}} - S_h}, & S_h < S < 1 \end{cases} \tag{12}
\]

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

Hydraulic redistribution is determined as

\[
HR = c (\Psi_{12} - \Psi_{s1}) \min(r_1, r_2) \tag{e.g., Ryel et al., 2002; Lee et al., 2005; Yu & D’Odorico, 2014a),
\]

where \( c \) is the maximum root hydraulic conductance of the entire active root system \((\text{mm} \cdot \text{MPa}^{-1} \cdot \text{hr}^{-1})\), a factor reducing root hydraulic conductance and accounting for soil water limitation, \( \Psi_{s2} \) and \( \Psi_{s1} \) the soil water potential \((\text{MPa})\) in the deep and shallow soil, respectively. Following Clapp and Hornberger (1978), \( \Psi \) is determined as \( \Psi = \Psi_{s2} + S^d \), where \( S \) is the soil water potential, \( S^d \) is the soil moisture, and \( \Psi_{s2} \) 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 \( (\lambda = 0.2/\text{day} \text{ and } h = 5 \text{ mm}) \) and moderate \( (\lambda = 0.2/\text{day} \text{ and } h = 10 \text{ mm}) \) 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., Bhatthan 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 \((Z_r = 10 \text{ cm})\) in all the simulations. The maximum root hydraulic conductance of the entire active root system \((c_{\text{max}})\) of woody plants is taken to be \( c_{\text{max}} = 0.75 \text{ LAI}_i \text{ m} \cdot \text{MPa}^{-1} \cdot \text{hr}^{-1} \) (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) 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) 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 (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 ($\xi$) 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 ($\lambda = 0.2$/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 ($\frac{r_1}{r_2}$ = 1 or 3). By comparison, in semiarid environments ($\lambda = 0.2$/day and $h = 10$ mm), trees in tree–CAM associations perform hydraulic lift in the case of a low value of $\frac{r_1}{r_2}$ = 1 (Figure 3). With relatively low values of the $\frac{r_1}{r_2}$ 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 evaportranspiration ($ET_{1}$) 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 ($\xi$) (Equation 1) increases with $Z_2$ and the tree leaf area index (LAI) with the effect of inducing hydraulic descent, which is in contrast to the reduction of $\xi$ with $Z_2$ and LAI 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., $LAI = 2.5$ m²/m²).

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

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Symbol</th>
<th>Value</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil porosity</td>
<td>$n$</td>
<td>0.43</td>
<td>Laio et al. (2001)</td>
</tr>
<tr>
<td>Soil saturated hydraulic conductivity</td>
<td>$K_s$</td>
<td>33.33 mm/hr</td>
<td>Laio et al. (2001)</td>
</tr>
<tr>
<td>Soil coefficient affecting drainage</td>
<td>$\beta$</td>
<td>13.8</td>
<td>Laio et al. (2001)</td>
</tr>
<tr>
<td>Field capacity</td>
<td>$S_f$</td>
<td>0.56</td>
<td>Laio et al. (2001)</td>
</tr>
<tr>
<td>Wilting point for woody plants</td>
<td>$S_w$</td>
<td>0.18</td>
<td>Laio et al. (2001)</td>
</tr>
<tr>
<td>Relative soil moisture for unstressed transpiration by woody plants</td>
<td>$S'$</td>
<td>0.46</td>
<td>Laio et al. (2001)</td>
</tr>
<tr>
<td>Hygroscopic point</td>
<td>$S_h$</td>
<td>0.14</td>
<td>Laio et al. (2001)</td>
</tr>
<tr>
<td>Soil parameter relating soil water potential to relative soil moisture</td>
<td>$\Psi_s$</td>
<td>$-2.1 \times 10^{-3}$ MPa</td>
<td>Laio et al. (2001)</td>
</tr>
<tr>
<td>Soil parameter relating soil water potential to relative soil moisture</td>
<td>$d$</td>
<td>4.9</td>
<td>Laio et al. (2001)</td>
</tr>
<tr>
<td>Extinction coefficient of shortwave radiation</td>
<td>$k_s$</td>
<td>0.35</td>
<td>Brutsaert (1982)</td>
</tr>
<tr>
<td>Storage conductance per unit leaf area</td>
<td>$g_c$</td>
<td>0.002 $\mu$-MPa⁻¹-s⁻¹</td>
<td>Bartlett et al. (2014)</td>
</tr>
<tr>
<td>Leaf area index of CAM plants in arid environment</td>
<td>$LAI_c$</td>
<td>1 m²/m²</td>
<td>This study</td>
</tr>
<tr>
<td>Leaf area index of CAM plants in semiarid environment</td>
<td>$LAI_s$</td>
<td>2 m²/m²</td>
<td>This study</td>
</tr>
<tr>
<td>Plant conductance per unit leaf area</td>
<td>$g_p$</td>
<td>0.0004 $\mu$-MPa⁻¹-s⁻¹</td>
<td>Bartlett et al. (2014)</td>
</tr>
<tr>
<td>Fraction of plant resistance below the storage branch connection</td>
<td>$f$</td>
<td>0.5</td>
<td>Bartlett et al. (2014)</td>
</tr>
<tr>
<td>Air density</td>
<td>$p_o$</td>
<td>1.2 kg/m³</td>
<td>Bartlett et al. (2014)</td>
</tr>
<tr>
<td>Specific humidity in the atmosphere in arid environment</td>
<td>$q_a$</td>
<td>0.00359 kg/kg</td>
<td>This study</td>
</tr>
<tr>
<td>Specific humidity in the atmosphere in semiarid environment</td>
<td>$q_a$</td>
<td>0.00504 kg/kg</td>
<td>This study</td>
</tr>
<tr>
<td>Factor reducing root hydraulic conductance</td>
<td>$c$</td>
<td>$\frac{1}{1 + \frac{1}{\mu} \left(\frac{R_c}{R_s}\right)^{1/3}}$</td>
<td>Ryel et al. (2002)</td>
</tr>
</tbody>
</table>

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$\Psi_{50}$ is the soil water potential where soil–root conductance is reduced by 50% and $b$ is an empirical constant. $\Psi_{50} = -1$ MPa and $b=3.22$ (Ryel et al., 2002).
and root depth of trees are high (e.g., $Z_2 > 100$ cm). In fact, a higher value of $LA_{It}$ reduces the rate of soil evaporation because of the effect of shading. However, the increase in hydraulic descent with increasing $LA_{It}$ is greater than the reduction in soil evaporation ($E$) with $LA_{Ic}$, 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 ($\xi$) increases with $r_{2}/r_{1}$ when hydraulic descent is accounted for, which is in contrast to the reduction of $\xi$ with $r_{2}/r_{1}$ without the effects of hydraulic descent in both arid (Figure 8a) and semiarid environments (Figure 8b). Overall, these results indicate that a high value of hydraulic descent resulting from high values of $LA_{It}$, $Z_2$, 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 $ET_2$ and a reduction/increase in hydraulic descent/hydraulic lift in semiarid environments with respect to the case of arid environments (Figures 3 and 5).
Plants with CAM are increasing their abundance in many dry lands worldwide (Borland, Griffiths, Hartwell, & Smith, 2009, Borland, Barrera Zambrano, Ceusters, & Shorrock, 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 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.

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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\text{t}), tree root depth (Z\text{1} + Z\text{2}), and the ratio (r\text{2}/r\text{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\text{2} = 90 cm); LAI\text{t} = 2.5 m\text{2}/m\text{2} and LAI\text{t} = 5 m\text{2}/m\text{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\text{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, Garcia-Moya, & Lopez-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., Caries 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 costal 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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