Title

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Direct and Indirect Facilitation of Plants with Crassulacean Acid Metabolism (CAM)

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ABSTRACT

Plants with crassulacean acid metabolism (CAM) are increasing their cover in many dryland regions around the world. Their increased dominance has been related to climate warming and atmospheric CO_2 fertilization, while the effects of interspecies interactions and the role of CAM plant facilitation by trees and grasses remain poorly understood. Woody plants are known for their ability to directly facilitate CAM plants through amelioration of the abiotic environment. Mechanisms of indirect facilitation of trees on CAM plants in tree–grass–CAM associations, however, have received less attention. It is also unclear whether grasses might facilitate CAM plants in mixed tree–grass–CAM communities. For instance, the inclusion of grasses in tree–CAM associations could enhance hydraulic lift and facilitate CAM plants in their access to shallow soil moisture at the expenses of deep-rooted trees. If this effect outweighs the competitive effects of grasses on CAM plants, grasses could overall facilitate CAM plants through hydraulic lift. Here we develop a process-based ecohydrological model to investigate the direct and indirect facilitation in tree–CAM–grass associations; the model quantifies transpiration of CAM plants when isolated as well as in associations with trees and/or grasses. It is found that woody plants having a high root overlap with CAM plants indirectly facilitate CAM plants by significantly reducing grass transpiration in shaded conditions. For situations of a low-to-moderate root overlap, facilitation may occur both directly and indirectly. Conversely, grasses are unable to indirectly facilitate CAM plants through the mechanism of hydraulic lift because the competitive effects of grasses on CAM plants outweigh the facilitation induced by hydraulic lift.

Key words: direct facilitation; indirect facilitation; woody plants; crassulacean acid metabolism (CAM); grasses; transpiration; hydraulic lift.

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INTRODUCTION

Plants with crassulacean acid metabolism (CAM) are increasing their abundance in many dryland regions around the world (Borland and others 2009, 2011). This effect is typically related to changes in climate or increasing atmospheric CO_2 concentrations (for example, Drennan and Nobel 2000; Borland and others 2009), whereas the role of interactions with other species and the relationship with other ongoing changes in plant

community composition (for example, woody plant encroachment and grass invasions) remain not completely understood. The role of facilitation or positive interactions has been increasingly emphasized in plant community studies in the past few decades (Bruno and others 2003; Brooker and others 2008), especially under high levels of environmental stress (Callaway and others 2002; Maestre and others 2009). A common example of facilitation that has been widely documented is the nurse effect of woody plants on CAM plants in dryland regions (Withgott 2000; Castillo and Valiente-Banuet 2010; Cares and others 2013). Studies of CAM plants engender scientific interest because their photosynthetic plasticity can buffer fluctuations in environmental conditions (Borland and others 2009, 2011). Renewed interest in CAM plants is further contributed by their suitability as feedstock for bioenergy production in dryland regions (Borland and others 2009; Davis and others 2011).

Past studies have largely focused on the direct facilitation of woody plants on CAM plants, whereby woody plants increase the establishment rate of CAM plants by increasing soil resource availability (water and/or nitrogen) and/or providing refuge from physical stress under extreme environmental conditions (temperature and/or solar radiation) (Withgott 2000; Castillo and Valiente-Banuet 2010; Cares and others 2013). Indirect facilitation of woody plants on CAM plants, however, remains poorly investigated. Indirect facilitation involves three interacting species in which competitive species A suppresses species B and thus reduces the competitive effect of species B over species C (Levine 1999; Kunstler and others 2006; Brooker and others 2008). Studies suggest that indirect facilitation tends to occur in a system where pairs of plants (A–B, B–C) compete for different resources (Levine 1999; Pagès and others 2003; Callaway 2007; Brooker and others 2008). For example, woody plants suppress the growth of herbaceous vegetation through light competition (A–B) and thus lead to competitive release of soil nutrients (water and/or nitrogen) which favors a third species (B–C) (Levine 1999; Siemann and Rogers 2003; Kunstler and others 2006).

Experimental evidence of indirect facilitation among species of different trophic levels has been extensive (for example, Rousset and Lepart 2000; Corcket and others 2003; Boulant and others 2008; Anthelme and Michalet 2009); fewer studies have investigated indirect facilitation among species within the same trophic level, especially in arid and semiarid systems (Brooker and others 2008; Cuesta

and others 2010). This is presumably due to the simultaneous occurrence of direct facilitation (Miller 1994; Siemann and Rogers 2003) and the difficulty in interpreting the results of experiments in which more than one species is manipulated (Callaway 2007). In fact, species A can also compete with species C and thus indirect facilitation requires that the indirect facilitative effect through suppression of a shared competitor outweighs the direct competitive effect (Levine 1999; Brooker and others 2008). For instance, Pagès and others (2003) and Pagès and Michalet (2003) found that the direct negative effect of species A on species C through light reduction outweighs the indirect positive effect of competitive release. Some models have explored the indirect facilitation among species within the same trophic level (for example, Lawlor 1979; Vandermeer 1990; Stone and Roberts 1991), but their approach has been mostly theoretical with no reference to specific functional groups. Here we develop a process-based model to investigate the emergence of indirect facilitation within dryland plant communities with three functional groups: C_3 woody plants, C_4 grasses, and CAM plants.

C_4 grasses sustain a high additional metabolic cost for photosynthesis in hot and/or dry environments, and thus tend to be shade intolerant (for example, Siemann and Rogers 2003; Sage and McKown 2006; Borland and others 2009). In contrast, the photosynthetic plasticity of CAM plants and their acclimation to shade allows them to be shade tolerant (Medina and others 1986; Fetene and others 1990; Ceusters and others 2011). Grasses and CAM plants are typically shallow rooted (Ogburn and Edwards 2010; Nippert and others 2012), and thus they compete for soil water resources. Thus, in tree–CAM–grass associations, it may be straightforward to expect that trees can suppress grasses through light reduction (for example, Siemann and Rogers 2003; Kunstler and others 2006) and thus indirectly facilitate CAM plants (Figure 1A, B). This may imply that the widely documented phenomenon of woody plant encroachment (Van Auken 2000; D'Odorico and others 2012) can directly and/or indirectly exert a positive net effect on CAM plant productivity in dryland regions.

What remains unclear is how tree–CAM associations respond to increase in grass density (grass invasions). Grasses will compete with CAM plants, but increase in grass transpiration and root uptake from the shallow soil layer are expected to promote the occurrence of hydraulic lift (for example, Yu and D'Odorico 2014a). Hydraulic lift transports
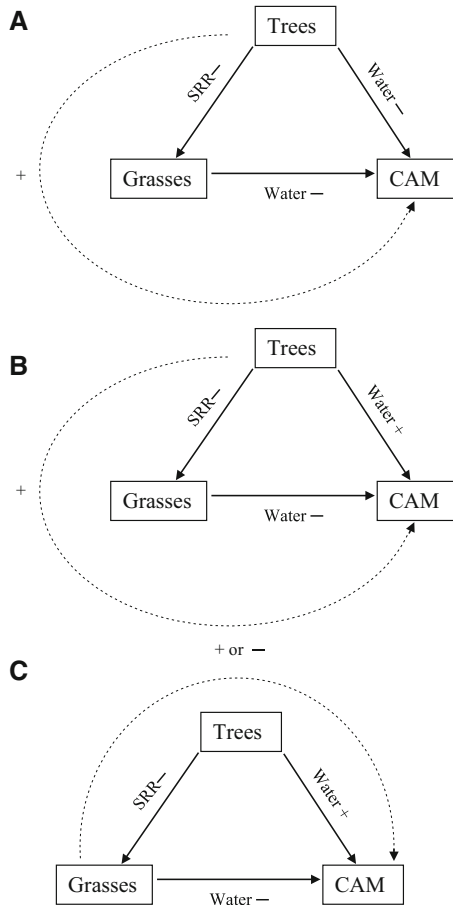
Figure 1. Schematic diagram of indirect (*dotted line*) and direct (*solid line*) interactions among C_3 trees, C_4 grasses, and CAM plants. **A**, **B** Trees suppress grass transpiration through solar radiation reduction (SRR) and reduce the competitive effect of grasses on CAM plants in access to soil water resources, thus indirectly facilitating CAM plants. **A** Trees and CAM plants compete for soil water resources because of a high degree of root overlap; **B** trees directly facilitate CAM plants in situations of a low-to-moderate root overlap. **C** Inclusion of grasses in tree–CAM associations increases hydraulic lift suppressing trees and thus may indirectly facilitate CAM plants.

water from the wetter deep soil to the drier shallow soil through plant roots (Richards and Caldwell 1987; Ludwig and others 2003). Shallow-rooted plants have been found to be capable of scavenging the lifted water (Richards and Caldwell 1987; Zou and others 2005; Brooks and others 2006). Thus, it has been suggested that hydraulic lift contributes to facilitation of deep-rooted plants on shallow-rooted plants (Riginos and others 2009; Moustakas and others 2013; Dohn and others 2013) at the expense of deep-rooted plants (Yu and D'Odorico 2014a). However, can the benefit to CAM plants associated

with hydraulic lift induced by grass invasions out-weigh the competitive effect? In other words, can the introduction of grasses into tree–CAM associations indirectly facilitate CAM plants through the mechanism of hydraulic lift (Figure 1C)?

In this study, we develop a model to investigate the occurrences of direct and indirect facilitation in tree–CAM–grass associations along a rainfall gradient. We quantify CAM plant transpiration—here used as an indicator of water availability—in CAM plants alone, CAM–grass, tree–CAM, and tree–CAM–grass associations, at seasonal-to-annual timescales. By clarifying the roles of direct and indirect facilitation in the tree–CAM–grass associations, our study contributes to the understanding of dynamics of CAM plants in response to important global environmental change phenomena, such as woody plant encroachment and/or grass invasions.

METHODS

We develop a model to investigate the direct and indirect facilitation in tree–CAM–grass associations along a rainfall gradient. The model simulates soil moisture dynamics in two soil layers and accounts for flows between them due to drainage and hydraulic redistribution (HR) (Ryel and others 2002; Lee and others 2005; Yu and D'Odorico 2014a). It quantifies transpiration of CAM plants in CAM plants alone (C), CAM–grass (C–G), tree–CAM (T–C), and tree–CAM–grass (T–C–G) associations, at seasonal-to-annual timescales (Table 1). Transpiration can be linked to total CO_2 assimilation and hence to plant fitness. A lower transpiration of CAM plants in CAM–grass (C–G) and tree–CAM (T–C) associations than in CAM plants alone (C) indicates the competitive effects of grasses and trees on CAM plants and vice versa. A comparison of transpiration of CAM plants in tree–CAM–grass (T–C–G) and CAM–grass (C–G) associations can explain whether trees directly or indirectly facilitate CAM plants. A comparison of CAM plant transpiration rates in tree–CAM–grass (T–C–G) and tree–CAM (T–C) associations will indicate whether grasses indirectly facilitate CAM plants through the mechanism of hydraulic lift. To this end, in the following subsections, we define the CAM transpiration ratios (see below for details). We focus on the case in which roots of CAM plants and grasses grow only in the shallow soil layer (Ogburn and Edwards 2010; Nippert and others 2012), while roots of woody plants (trees) are present in both the shallow and deep soil layers (Yu and D'Odorico 2014a). Woody plants and grasses transpire in the

Table 1. A Summary of Vegetation Associations in This Study

Vegetation associations	Deep-rooted plants	Shallow-rooted plants	Plants performing HR at night
CAM		CAM	
CAM–grass		CAM; grass	
Tree–CAM	Tree	CAM	Tree
Tree–CAM–grass	Tree	CAM; grass	Tree

daytime (12 h) and woody plants perform HR at night (12 h) (Ryel and others 2002; Lee and others 2005; Yu and D'Odorico 2014a), while CAM plants are assumed to transpire only at night (12 h) (Lüttge 2004; Ogburn and Edwards 2010). Some facultative CAM plants can actually perform regular C_3 photosynthesis and thus also transpire during daytime (for example, Borland and others 2011). This effect can be easily accounted for by varying the duration of transpiration in facultative CAM plants. In this study, however, we will focus on the case of obligated CAM plants. To account for the non-negligible plant water capacitance of CAM plants (Lüttge 2004; Ogburn and Edwards 2010), we account for changes in water storage in CAM plants (for example, Lhomme and others 2001; Bartlett and others 2014).

Water Balance

Soil moisture dynamics in the two soil layers for tree–CAM (T–C) and tree–CAM–grass (T–C–G) associations are modeled by two coupled equations:

$$nZ_1 \frac{dS_1}{dt} = P - U_1 - E - D_1 + HR, \qquad (1)$$

and

$$nZ_2 \frac{dS_2}{dt} = D_1 - U_2 - D_2 - HR, \qquad (2)$$

where the subscripts 1 and 2 refer to the shallow and deep soil layers, 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 d^{-1}); U_1 and U_2 are the soil moisture losses from each soil layer due to root uptake (mm d^{-1}); E is the evaporation rate from the soil surface (mm d^{-1}); D_1 and D_2 are the drainage rates (mm d^{-1}); and HR is the hydraulic redistribution at the patch scale (mm d^{-1}). Positive values of HR indicate ''hydraulic lift'' (that is, upward hydraulic redistribution), while negative values of HR indicate ''hydraulic descent'' (that is, downward hydraulic redistribution). For CAM plants alone (C) and CAM–grass associations (C–G), only equation (1) needs to be used to quantify

soil moisture dynamics, where HR is taken to be 0 mm d^{-1}, because in these two cases, there are no deep-rooted plants to perform HR.

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 (mm per event) (Rodriguez-Iturbe and others 1999). Runoff occurs when the surface layer is saturated (that is, $S_1 = 1$). Drainage is assumed to be driven only by gravity and is expressed as $D = \frac{K_s[\exp(\beta(S-S_{fc})-1]}{\exp[\beta(1-S_{fc})-1]}$, where K_s is the soil saturated hydraulic conductivity (mm h^{-1}), β is a coefficient, S is the relative soil moisture, and S_{fc} is the field capacity (Laio and others 2001).

Uptakes by woody plants and grasses are determined assuming that steady-state exists within the soil–plant–atmosphere continuum, and therefore uptake is taken being equal to transpiration (Porporato and others 2003; Manzoni and others 2013). The maximum total potential evapotranspiration in the daytime is assumed to be constant (Table 2). Transpiration of CAM plants does not occur during daytime (Lüttge 2004; Ogburn and Edwards 2010). Therefore, for CAM plants alone (C), the maximum total potential evapotranspiration in the daytime (ET_{maxd}) is contributed only by the potential evaporation at the soil surface (E_{maxd}). For the CAM–grass associations (C–G), ET_{maxd} is partitioned into potential transpiration for grasses (T_{gmaxd}) and potential evaporation at the soil surface (E_{maxd}), where T_{gmaxd} depends on grass cover (f_g), as

$$T_{gmaxd} = ET_{maxd} f_g, \qquad (3)$$

For the tree–CAM associations, ET_{maxd} is partitioned into potential transpiration for trees (T_{tmaxd}) and potential evaporation from the soil surface (E_{maxd}). For the tree–CAM–grass associations, ET_{maxd} is partitioned into potential transpiration for trees (T_{tmaxd}) and grasses (T_{gmaxd}), and potential evaporation from the soil surface (E_{maxd}). To account for the solar radiation reduction by trees, the incident shortwave radiation is assumed to vertically irradiate the plant and soil surfaces (Caylor

Table 2. Parameters, Parameter Values, and Reference Sources Used in the Study

Parameter	Symbol	Value	References
Maximum total potential evapotranspiration in the daytime	ET_{maxd}	4.5 mm d^{-1}	This study
Total potential evaporation at soil surface at night	E_{maxn}	0.5 mm d^{-1}	This study
Extinction coefficient of shortwave radiation	k_s	0.35	Brutsaert (1982)
Leaf area index of woody plants in arid environment	LAI_t	1.5 m^2 m^{-2}	This study
Leaf area index of woody plants in semiarid environment	LAI_t	3 m^2 m^{-2}	This study
Storage conductance per unit leaf area	g_c	0.002 μm MPa^{-1} s^{-1}	Bartlett and others (2014)
Leaf area index of CAM plants in arid environment	LAI_c	1 m^2 m^{-2}	This study
Leaf area index of CAM plants in semiarid environment	LAI_c	2 m^2 m^{-2}	This study
Plant conductance per unit leaf area	g_p	0.0004 μm MPa^{-1} s^{-1}	Calkin and Nobel (1986)
Fraction of plant resistance below the storage branch connection	f	0.5	Bartlett and others (2014)
Air density	ρ_a	1.2 kg m^{-3}	Bartlett and others (2014)
Specific humidity in the atmosphere in arid environment	q_a	0.00359 kg kg^{-1}	This study
Specific humidity in the atmosphere in semiarid environment	q_a	0.00504 kg kg^{-1}	This study
Factor reducing root hydraulic conductance[1]	c	$\frac{1}{1+\frac{\max(\Psi_{s2},\Psi_{s1})^b}{\Psi_{50}}}$	Ryel and others (2002)

[1]Ψ_{50} is the soil water potential where soil–root conductance is reduced by 50% and b an empirical constant. $\Psi_{50} = -1$ MPa and b = 3.22 (Ryel and others 2002)

and others 2005; Yu and D'Odorico 2014a, b). Potential evapotranspiration depends on the available shortwave radiation, which exponentially decays through the tree canopy according to Beer's law. Therefore, following Caylor and others (2005) and Yu and D'Odorico (2014a, b), for the tree–CAM associations, we have $T_{tmaxd} = ET_{maxd}[1 - \exp(-k_s LAI_t)]$ and $E_{maxd} = ET_{maxd} \exp(-k_s LAI_t)$, where k_s is the extinction coefficient of shortwave radiation, and LAI_t is the leaf area index of woody plants (m^2 m^{-2}). Likewise, for the tree–CAM–grass associations (T–C–G), we have

$$T_{tmaxd} = ET_{maxd}[1 - \exp(-k_s LAI_t)], \qquad (4)$$

$$T_{gmaxd} = ET_{maxd} \exp(-k_s LAI_t)f_g, \qquad (5)$$

$$E_{maxd} = ET_{maxd} \exp(-k_s LAI_t)(1 - f_g), \qquad (6)$$

A comparison between equations (3) and (5) shows that trees reduce shortwave radiation and thus decrease the grass transpiration rate even when the grass cover remains the same as in the case with no trees.

Potential transpiration for trees (T_{tmaxd}) is contributed by the shallow soil layer (T_{1tdmax}) and the deep soil layer (T_{2tdmax}); these two fractions are assumed to be proportional to the water volume available in each layer (Yu and D'Odorico 2014a):

$$T_{1tdmax} = T_{tdmax} \frac{Z_1 S_1}{Z_1 S_1 + Z_2 S_2}, \qquad (7)$$

$$T_{2tdmax} = T_{tdmax} \frac{Z_2 S_2}{Z_1 S_1 + Z_2 S_2}, \qquad (8)$$

The actual transpiration by plants depends on the soil water availability (Rodriguez-Iturbe and others 1999); we express the limitation of transpiration by soil water availability as

$$\tau(S) = \begin{cases} 0, & S < S_w \\ \dfrac{S - S_w}{S^* - S_w}, & S < S^* \\ 1, & S \geq S^* \end{cases},$$

where $\tau(S)$ expresses soil moisture limitations on evapotranspiration, 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 transpiration ceases. Trees and grasses are assumed to have the same S^* and S_w. Therefore, the actual transpiration rates of woody plants in the shallow (T_{1tda}) and deep (T_{2tda}) soil layers are determined as

$$T_{1tda} = T_{1tdmax}\tau(S_1)r_1, \qquad (9)$$

$$T_{2tda} = T_{2tdmax}\tau(S_2)r_2, \qquad (10)$$

where r_1 and r_2 are the cumulated (and normalized) tree root densities in the shallow and the deep soil layers, respectively ($r_1 + r_2 = 1$). The actual transpiration by grasses (T_{1gda}) is determined as $T_{1gda} = T_{gmaxd} \times \tau(S_1)$. As seen from equations (7) through (10), a high degree of overlap between the roots of trees and CAM plants are characterized by high values of Z_1/Z_2 and r_1/r_2 and is expected to lead to the competitive effects of trees on CAM plants.

Uptake by CAM plants is determined using a non-steady-state approach. Following other studies (for example, Lhomme and others 2001; Bartlett and others 2014), we model the non-steady-state plant water storage by incorporating capacitances and resistances into the water flow pathway similar to the case of electric circuits (Figure 2). In this method, the rates of water uptake (U_{CAM}) and the plant water capacitance (Q_w) balance the leaf transpiration (T_{CAM}) per unit ground area. Therefore, we have

$$T_{CAM} = U_{CAM} + Q_w, \qquad (11)$$

Following Bartlett and others (2014), U_{CAM} and Q_w are controlled by water potential gradients, with $U_{CAM} = g_{srp}(\Psi_{s1} - \Psi_x)$ 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 s^{-1} MPa^{-1}), $g_c LAI_c$ is the storage conductance per unit ground area (m s^{-1} MPa^{-1}) (g_c is storage conductance per unit leaf area and LAI_c is leaf area index of CAM plants), Ψ_{s1} is the soil water potential in the shallow soil layer, and Ψ_x is the xylem water potential (MPa), Ψ_w is the plant storage water potential (MPa). T_{CAM} is the flux from the xylem to the leaves, which can be expressed as

$$T_{CAM} = \frac{g_p LAI_c}{1 - f}(\Psi_x - \Psi_l), \qquad (12)$$

where g_p is the plant conductance per unit leaf area, f is the fraction of plant resistance below the storage branch connection (Figure 2), and $\frac{g_p LAI_c}{1-f}$ is

the plant conductance per unit ground area between the storage connection node (with water potential, Ψ_x, MPa) and leaf (with water potential, Ψ_l, MPa).

The leaf transpiration (T_{CAM}) per unit ground area can be also calculated (for example, Bartlett and others 2014) as a function of the specific humidity gradient between the leaf mesophyll (q_l) and the atmosphere (q_a), that is,

$$T_{CAM} = l g_{msa} \frac{\rho_a}{\rho_w}(q_l - q_a), \qquad (13)$$

where ρ_a is the density of air (kg m^{-3}), ρ_w is the density of water (1 kg m^{-3}), and g_{msa} are the series of the mesophyll, stomatal, and atmospheric conductances (m s^{-1}) to water vapor per unit ground under well-watered conditions (that is, $g_m LAI_c$, $g_s LAI_c$, and g_a, respectively); thus, g_{msa} can be expressed as $g_{msa} = LAI_c g_m g_s \frac{g_a}{LAI_c g_m g_s + g_s g_a + g_m g_a}$. In equation (13), l is a coefficient limiting g_{msa} in dry conditions, while q_l is a function of Ψ_l and leaf temperature. Detailed calculations of parameters g_{srp}, Ψ_w, g_{msa}, l, q_l, and other parameters can be found in Bartlett and others (2014). The rate of CAM plant uptake is then calculated combing equations (11)–(13) as in Bartlett and others (2014) with equation (13) driven by atmospheric conditions.

Actual evaporation from soil surface (E) also depends on soil water availability. Consistent with Porporato and others (2003) and Bartlett and others (2014), we have
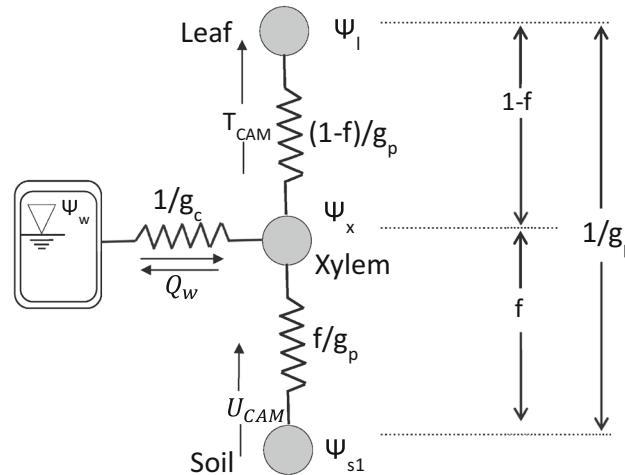

Figure 2. Schematic diagram of water flux within canopies of CAM plants. Ψ_l, leaf water potential; Ψ_{s1}, soil water potential in the shallow soil layer; Ψ_x, xylem water potential; Ψ_w, plant storage water potential; f, fraction of plant resistance below the storage branch connection; g_p, plant conductance per unit leaf area; g_c, storage conductance per unit leaf area; U_{CAM}, uptake rate of CAM plants; T_{CAM}, transpiration rate of CAM plants; Q_w, water capacitance of CAM plants. Adapted from Lhomme and others (2001) and Bartlett and others (2014).

$$E = \begin{cases} 0, & 0 \leq S \leq S_h \\ E_{max} \dfrac{S - S_h}{1 - S_h}, & S_h < S < 1 \end{cases}, \qquad (14)$$

where S_h is the hygroscopic point below which evaporation at the soil surface ceases (Laio and others 2001), and E_{max} is the potential evaporation during the daytime or at night. The daytime potential evaporation is calculated with equation (6), whereas the total potential evaporation from the soil surface at night (E_{maxn}) is assumed to be constant (Table 2).

Consistent with other studies (Ryel and others 2002; Lee and others 2005; Yu and D'Odorico 2014a), hydraulic redistribution is determined as $HR = c C_{rmax}(\Psi_{s2} - \Psi_{s1}) \min(r_1, r_2)$, where C_{rmax} is the maximum root hydraulic conductance of the entire active root system (mm MPa^{-1} h^{-1}); c is a factor reducing root hydraulic conductance and a function of soil water potential (Table 2); and Ψ_{s2} and Ψ_{s1} are the soil water potentials (MPa) in the deep and the shallow soil layers, respectively. 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 the experimentally derived parameters that have been determined for a variety of soils (Table 2) (Clapp and Hornberger 1978). The detailed calculations of c can be found in Yu and D'Odorico (2014a).

CAM Plants' Transpiration Ratios

To compare the different levels of water stress in CAM plants in different associations with other functional types, we define the transpiration ratios as $\xi = \frac{T_{1C}(Cas)}{T_{1C}(C)}$, where $T_{1C}(Cas)$ and $T_{1C}(C)$ are the transpiration rates of CAM plants in CAM associations (with trees, grasses, or both) and CAM plants alone, respectively. Likewise, to evaluate whether grasses indirectly facilitate CAM plants, we define the transpiration ratio (ξ) between tree–CAM–grass associations (T–C–G) and tree–CAM associations (T–C) as $\xi = \frac{T_{1C}(TCG)}{T_{1C}(TC)}$, where $T_{1C}(TCG)$ and $T_{1C}(TC)$ are the transpiration rates of CAM plants in tree–CAM–grass association and tree–CAM associations, respectively.

Parameterization of the Model

The model is mainly parameterized with respect to environmental conditions with two rainfall regimes corresponding to arid ($\lambda = 0.2$ d^{-1} and $h = 5$ mm) and semiarid ($\lambda = 0.2$ d^{-1} and $h = 10$ mm) environments. Soil moisture dynamics are simulated with a time step of half an hour for 10 years. The transpiration rates of CAM plants in CAM associations and CAM alone are averaged over 10 years and then used to calculate the transpiration ratios defined above. Other variables such as evapotranspiration and hydraulic redistribution are also reported as average values over 10 years. The growing seasons of trees, grasses, and CAM plants are assumed to coincide and last 210 days each year (Bhattachan and others 2012). The root depths of CAM plants and grasses are assumed to be the same and constant ($Z_1 = 10$ cm) in all the simulations (Ogburn and Edwards 2010; Nippert and others 2012). To investigate whether a high degree of root overlap leads to the competitive effects of trees on CAM plants (Figure 1A), low values of deep soil layer thickness ($Z_2 = 10$ cm) and root allocation to the deep soil ($r_2/r_1 = 0.2$) are used, thus precluding the occurrence of hydraulic distribution (Caldwell and others 1998; Espeleta and others 2004). Conversely (Figure 1B, C), woody plants with deeper roots (that is, $Z_2 = 30$ cm) can perform hydraulic redistribution; these conditions allow us to evaluate the role played by hydraulic redistribution in the direct and/or indirect facilitation in tree–CAM–grass associations. This model is mainly implemented in loamy sand, and the results of sensitivity analysis of sandy loam are provided in Supplementary Material. Parameters describing various soil characteristics used in this study can be found in Table 3. The maximum root hydraulic conductance of woody plants for the entire active root system (C_{rmax}) is taken to be $C_{rmax} = 0.75$-LAI$_t$ mm MPa^{-1} h^{-1}, following Lee and others (2005) and Yu and D'Odorico (2014a). Other parameters required in this study can be found in Table 2. This study does not explicitly account for the effects of canopy interception in the soil moisture balance. Canopy interception in CAM asso-

Table 3. Parameters Describing Various Soil Characteristics Used in This Study

Soil types	Ψ_s (MPa)	d	K_s (mm h^{-1})	n	β	S_h	S_w	$S*$	S_{fc}
Sandy loam	-2.1×10^{-3}	4.9	33.33	0.43	13.8	0.14	0.18	0.46	0.56
Loamy sand	-0.88×10^{-3}	4.38	50	0.42	12.76	0.08	0.11	0.33	0.35

The values of these parameters are from Laio and others (2001). Following Laio and others (2001), β is calculated as $\beta = 2 \times d + 4$.

ciations could be higher than that in CAM plants alone. To account for the effect of canopy interception, we rerun the model in which rainfall in excess of canopy interception is available for infiltration in the soil moisture balance. By this way, we calculated the canopy interception (CI) as CI = 0.2 × LAI (Yu and others 2012), where LAI is leaf area index of canopies. Grass cover is taken to be 70% both in arid and semiarid environments in this study, and the LAI of grasses is taken to be 2.5 m^2 m^{-2}. The LAIs of trees and CAM plants can be found in Table 2. Some grasses have deeper roots (that is, 20–40 cm) than CAM plants. To evaluate the effect of deeper grass root zones, we allow the root depth of grasses to differ from that of CAM plants (that is, Z_1) and investigate the model's sensitivity to changes in this parameter. The sensitivity of this model with respect to changes of rainfall regime is also evaluated. The results of this sensitivity analysis, which are detailed in Supplementary Material, are generally consistent with those presented in the main text.

RESULTS

We first focus on the case of a plant community with a high degree of root overlap between trees and CAM plants; under these conditions, trees with very shallow roots (that is, 20 cm) cannot perform hydraulic redistribution. A high degree of root overlap leads to a relatively strong competition for soil water resources between trees and CAM plants both in arid (Figure 3A) ($\lambda = 0.2$ d^{-1} and $h = 5$ mm) and semiarid environments (Figure 3B) ($\lambda = 0.2$ d^{-1} and $h = 10$ mm); this fact is evidenced by a lower transpiration of CAM plants in tree–CAM (T–C) associations than by themselves. This result can be explained by the high rate of water uptake from the shallow soil layer by trees and thus the high water losses (ET_1) from the shallow soil and the lower soil water availability (Figure 4A, B). Likewise, grasses exert a higher competition on CAM plants than trees in both arid (Figure 3A) and semiarid environments (Figure 3B). Interestingly, transpiration rate of CAM plants in the tree–CAM–grass associations (T–C–G) is higher than that in the CAM–grass associations both in arid (Figure 3A) and semiarid environments (Figure 3B), which indicates that trees facilitate CAM plants. This facilitation of trees on CAM plants in tree–CAM–grass associations results from a substantial reduction in grass transpiration (Figure 4A, B). Overall, these results indicate that trees indirectly facilitate CAM plants by significantly reducing grass transpiration.
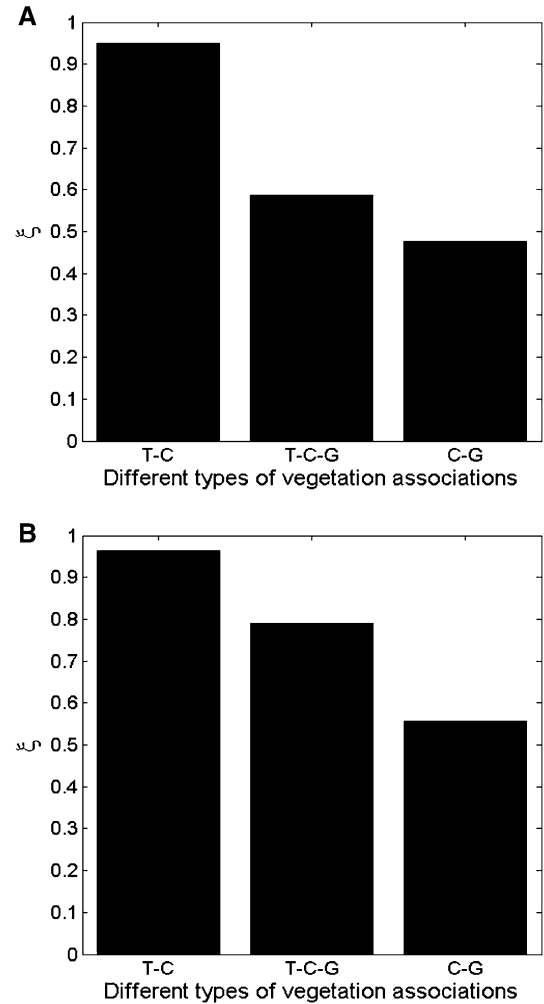

Figure 3. **A**, **B** Transpiration ratios (ξ) of CAM plants between CAM associations and CAM alone for arid ($\lambda = 0.2$ d^{-1} and $h = 5$ mm) (**A**) and semiarid ($\lambda = 0.2$ d^{-1} and $h = 10$ mm) (**B**) environments in loamy sand in the case of a high degree of root overlap between trees and CAM plants. Parameters: the depth of shallow soil layer, $Z_1 = 10$ cm; the depth of deep soil layer, $Z_2 = 10$ cm; grass cover in arid and semiarid environments, $f_g = 70$ %; and root allocation into the deep soil layer, $s_{r_1}^{r_2} = 0.2$.

We now focus on the case in which woody plants have deeper roots and can thus perform hydraulic redistribution. In arid environments ($\lambda = 0.2$ d^{-1} and $h = 5$ mm), drainage (D_1) from the shallow to the deep soil layer is overall small, and therefore the deep soil layer is often drier than the shallow soil. Thus, hydraulic redistribution is often in the form of hydraulic descent (that is, downward) performed by trees (Figure 5A). In contrast, trees perform hydraulic lift in semiarid environments ($\lambda = 0.2$ d^{-1} and $h = 10$ mm), where drainage intensity is sufficient to maintain higher levels of soil
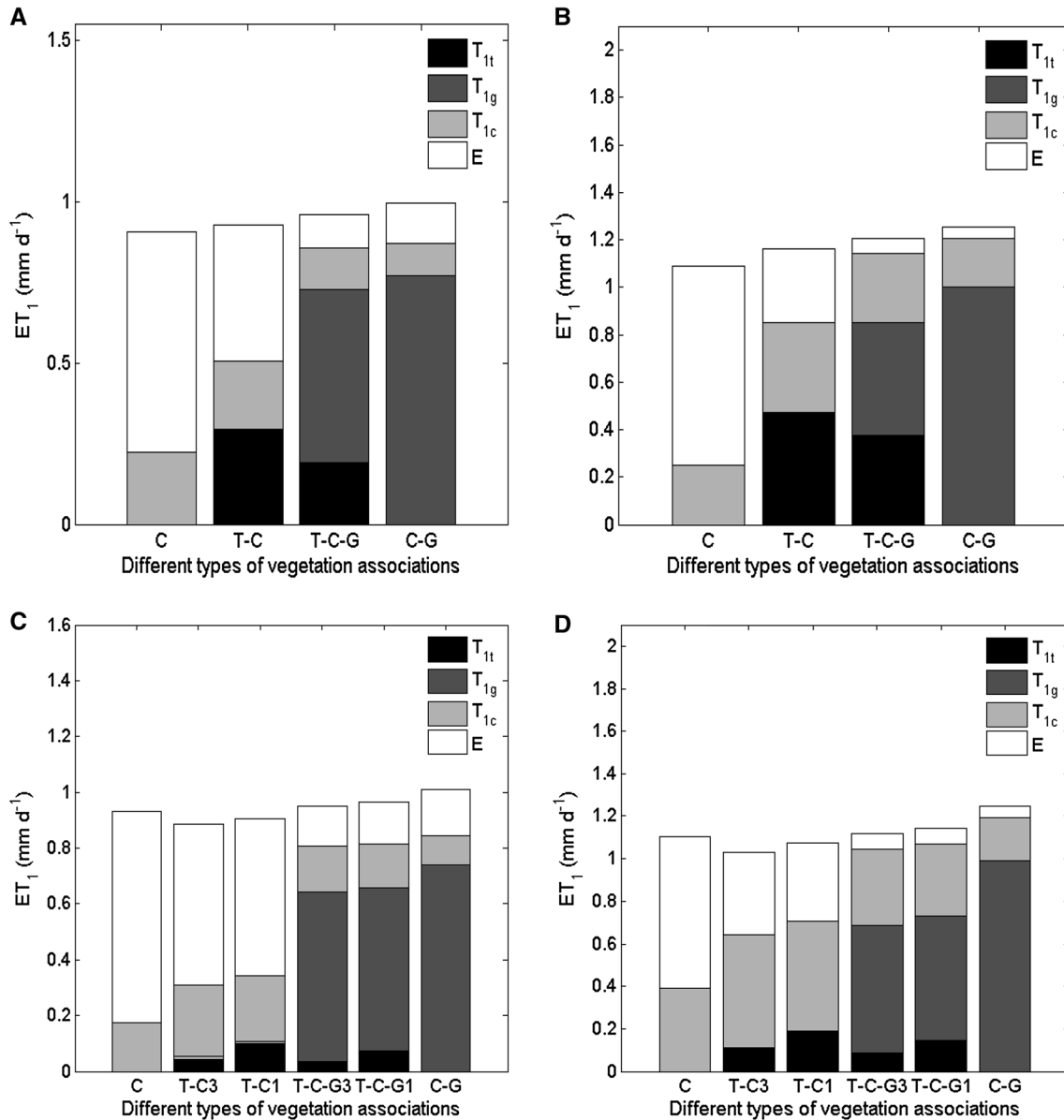
Figure 4. **A**, **B** Actual evapotranspiration components in the shallow soil layer for CAM plants alone (**C**), tree–CAM (T–C), tree–CAM–grass (T–C–G), and CAM–grass (C–G) associations for arid ($\lambda = 0.2$ d^{-1} and $h = 5$ mm) (**A**) and semiarid ($\lambda = 0.2$ d^{-1} and $h = 10$ mm) (**B**) environments in loamy sand in the case of a high degree of root overlap between trees and CAM plants. T_{1t} refers to the transpiration by trees, T_{1g} refers to the transpiration by grasses, T_{1c} refers to the transpiration by CAM plants, and E refers to evaporation from the soil surface. Parameters: the same as Figure 3A, B. **C**, **D** Actual evapotranspiration components in the shallow soil layer for CAM plants alone (C), tree–CAM (T–C), tree–CAM–grass (T–C–G), and CAM–grass (C–G) associations for arid ($\lambda = 0.2$ d^{-1} and $h = 5$ mm) (**C**) and semiarid ($\lambda = 0.2$ d^{-1} and $h = 10$ mm) (**D**) environments, in loamy sand in the case of a low-to-moderate root overlap between trees and CAM plants. $\frac{r_2}{r_1}$, root allocation into the deep soil layer. The number "3" means $\frac{r_2}{r_1} = 3$, while the number "1" means $\frac{r_2}{r_1} = 1$. Parameters: depth of shallow soil layer, $Z_1 = 10$ cm; depth of deep soil layer, $Z_2 = 30$ cm; grass cover in arid and semiarid environments, $f_g = 70$ %.

moisture in the deep than in the shallow soil (Figure 5B); a low allocation of roots to the deep soil layer (that is, high r_1/r_2) increases water usage in the shallow soil and thus enhances hydraulic lift (Figure 5B). Reduction of rainfall frequency (the same total amount of rainfall) reduces the hydraulic descent performed by trees in arid environment (Supplementary Figure S5A) and increases hydraulic lift in semiarid environment (Supplementary Figure S5B). Inclusion of grasses
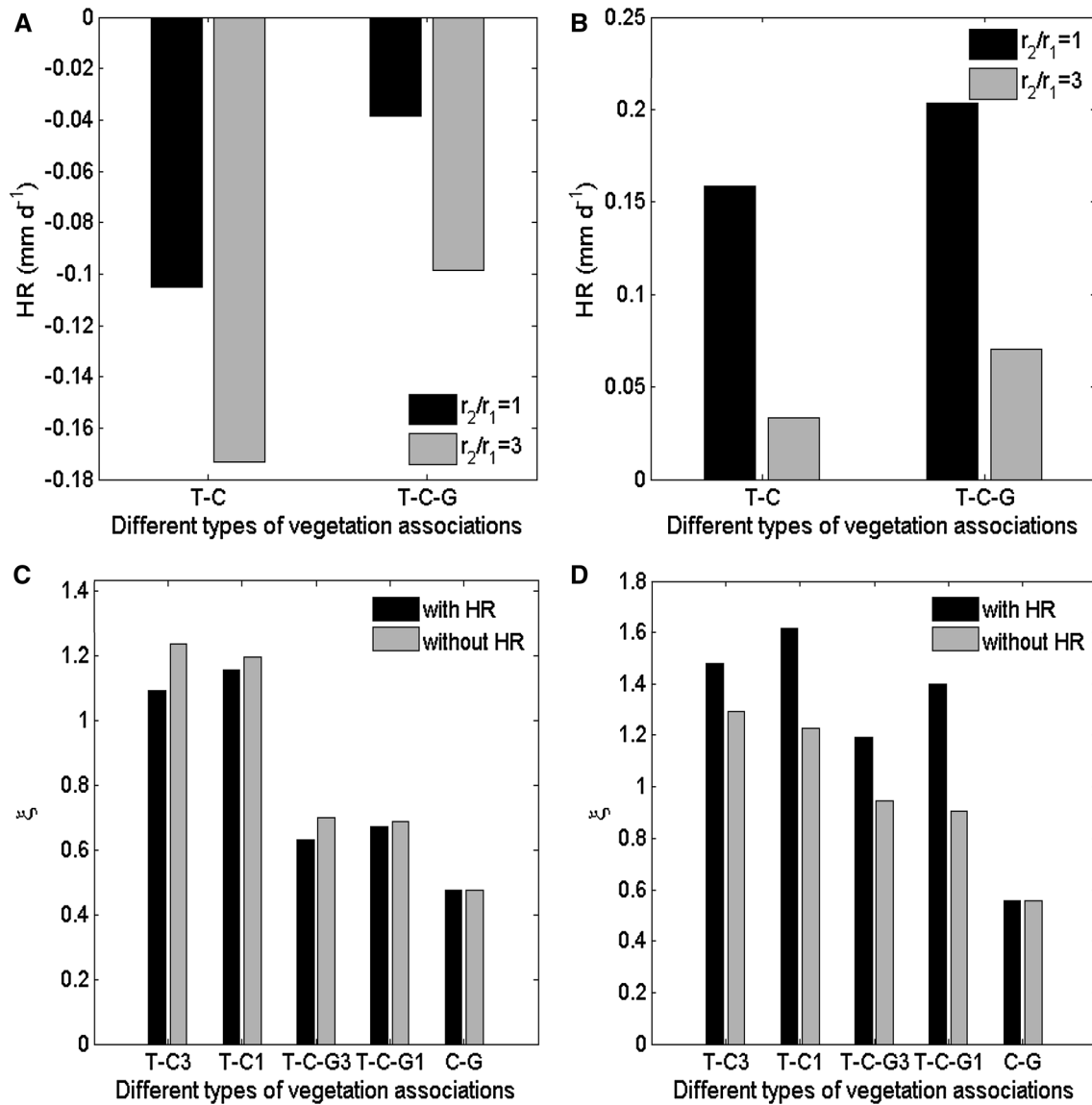
Figure 5. **A**, **B** Hydraulic redistribution (HR) by trees in tree–CAM (T–C) and tree–CAM–grass (T–C–G) associations for arid ($\lambda = 0.2$ d^{-1} and $h = 5$ mm) (**A**) and semiarid ($\lambda = 0.2$ d^{-1} and $h = 10$ mm) (**B**) environments. **C**, **D** Transpiration ratio (ξ) of CAM plants between CAM associations and CAM alone for arid ($\lambda = 0.2$ d^{-1} and $h = 5$ mm) (**C**) and semiarid ($\lambda = 0.2$ d^{-1} and $h = 10$ mm) (**D**) environments. All panels refer to the case of loamy sand and low-to-moderate root overlap between trees and CAM plants. Parameters: the same as Figure 4C, D.

into tree–CAM associations also increases water usage in the shallow soil, thus reducing hydraulic descent in arid environments (Figure 5A) and increasing hydraulic lift in semiarid environments (Figure 5B). Regardless of the effects of hydraulic redistribution, direct facilitation of trees on CAM plants occurs in situations of a low-to-moderate root overlap between trees and CAM plants, and this effect is weaker in arid (Figure 5C) than in semiarid environments (Figure 5D). Hydraulic descent reduces (Figure 5A, C) whereas hydraulic lift increases the direct facilitation of CAM plants by

trees (Figure 5B, D). Interestingly, a high rate of hydraulic lift can lead to a higher transpiration of CAM plants in tree–CAM–grass associations (T–C–G) with respect to the case of CAM plants alone (C) (Figure 5D), which indicates that CAM plants may prefer to establish themselves under canopies of trees even in the presence of grass competition. The indirect facilitation of trees on CAM plants occurs because trees substantially reduce grass transpiration in tree–CAM–grass associations (T–C–G) compared to CAM–grass associations (C–G), especially in semiarid environments (Figure 4C, D). Overall,
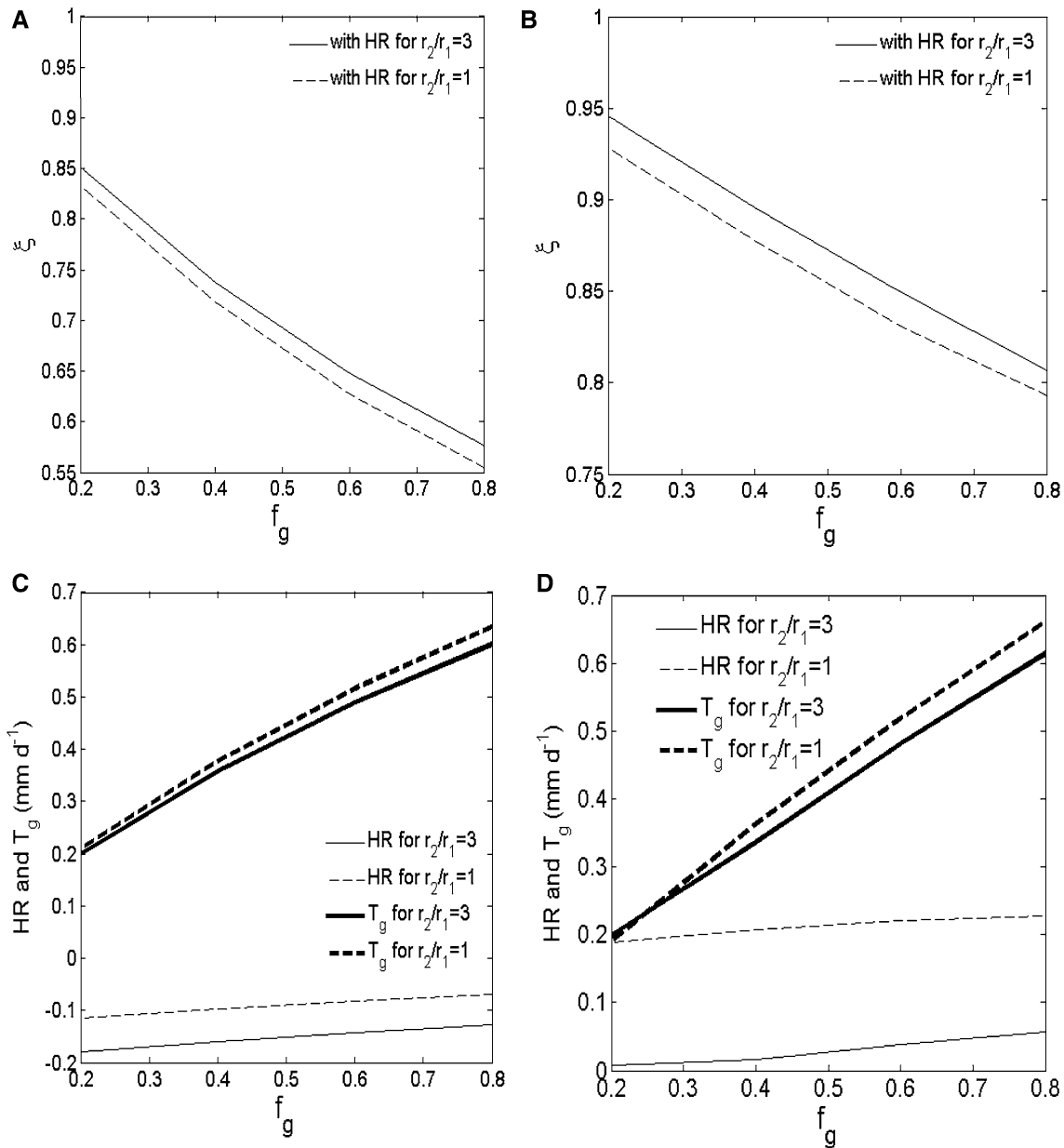
Figure 6. A, B Transpiration ratio (ξ) of CAM plants between tree–CAM–grass association (T–C–G) and tree–CAM association (T–C) for arid ($\lambda = 0.2$ d^{-1} and $h = 5$ mm) (**A**) and semiarid ($\lambda = 0.2$ d^{-1} and $h = 5$ mm) (**B**) environments in loamy sand as affected by grass cover (f_g). **C, D** Hydraulic redistribution (HR) and grass transpiration (T_g) in tree–CAM–grass (T–C–G) association in loamy sand as affected by grass cover (f_g) for arid (**C**) and semiarid (**D**) environments. Parameters: the depth of shallow soil layer, $Z_1 = 10$ cm; the depth of deep soil layer, $Z_2 = 30$ cm.

this leads to a higher transpiration of CAM plants when they are in tree–CAM–grass associations (T–C–G) than in CAM–grass associations (C–G) (Figure 5C, D). Thus, we conclude that direct facilitation of CAM plants by trees occurs simultaneously with the indirect effect in situations of a low-to-moderate root overlap between trees and CAM plants.

Transpiration of CAM plants in tree–CAM–grass associations (T–C–G) is lower than that in tree–CAM associations (T–C) in both arid (Figures 5C, 6A) and semiarid environments (Figures 5D, 6B) regardless of the effects of hydraulic redistribution. A higher rate of hydraulic lift by trees in tree–CAM–grass associations reduces the competitive effects of grasses on CAM plants, as indicated by an

increase of transpiration ratio of CAM plants between tree–CAM–grass associations (T–C–G) and CAM–grass (C–G) (Figure 5D). However, reduction in hydraulic descent and the increase in hydraulic lift cannot outweigh the increase of shallow soil moisture depletion by grass transpiration (competitive effect of grasses) (Figure 6C, D). This explains why an increase in grass cover reduces transpiration ratio of CAM plants between tree–CAM–grass associations (T–C–G) and tree–CAM associations (T–C) (Figure 6A, B). Overall, these results indicate that the introduction of grasses in tree–CAM associations still exerts a competitive effect on CAM plants in presence of a relatively high hydraulic lift rate. In other words, the addition of grasses cannot indirectly facilitate CAM plants through the mechanism of hydraulic lift.

DISCUSSION

Our study evaluates conditions that could lead to indirect facilitation in dryland vegetation. Particularly, we focus on the case of CAM plants whose direct facilitation by woody plants has been widely documented (Withgott 2000; Castillo and Valiente-Banuet 2010; Cares and others 2013). We developed a model to quantify transpiration of CAM plants in CAM plants alone (C), CAM–grass (C–G), tree–CAM (T–C), and tree–CAM–grass (T–C–G) associations, at seasonal-to-annual timescales. A comparison of transpiration of CAM plants in these communities allows us to investigate the direct and indirect facilitation in tree–CAM–grass (T–C–G) associations. The role of hydraulic redistribution is accounted for by coupling soil moisture dynamics in a shallow soil layer and the underlying soil (Ryel and others 2002; Lee and others 2005; Yu and D'Odorico 2014a).

Our study shows that woody plants having a high degree of root overlap with CAM plants indirectly facilitate CAM plants in the access to soil water resources (Figures 1A, 3A, B). The indirect facilitation occurs because woody plants significantly reduce grass transpiration through solar radiation reduction (Figure 4A, B) and thus reduce the competition of grasses on CAM plants in the access to soil water resources (Levine 1999; Brooker and others 2008). These results are consistent with other studies. For example, Siemann and Rogers (2003) found that canopies of alien Chinese tallow tree (*Sapium sebiferum*) reduce the competitive interaction of grasses and thus indirectly facilitate the growth of tree seedlings in shaded conditions. Kunstler and others (2006) indicated that shade from shrub canopies indirectly

facilitates *Fagus* survival by limiting herb competition for access to soil water resources. Other possible mechanisms of grass suppression by trees include allelopathy (Knipe and Herbel 1966; Callaway 2007; Ehlers and others 2014). In contrast, other studies indicate that the indirect positive effect can be outweighed by the direct negative effect (Pagès and others 2003; Pagès and Michalet 2003), thus precluding the occurrence of indirect facilitation (Levine 1999; Brooker and others 2008). In our study, CAM plants are thought to be shade tolerant because of their photosynthetic plasticity and acclimation to shade, as confirmed by experimental evidence (Medina and others 1986; Fetene and others 1990; Ceusters and others 2011).

Our study also shows that woody plants having a low-to-moderate root overlap with CAM plants have a direct facilitation effect on CAM plants along with an indirect facilitation effect (Figures 1B, 5C, D). The direct facilitation effect results from a substantial reduction of evaporation from the soil surface (shade effect) (Figure 4C, D), consistent with other studies (Ludwig and others 2004; D'Odorico and others 2007; Dohn and others 2013; Moustakas and others 2013). Experimental evidences confirming the direct facilitation effects of woody plants on CAM plants are extensive (Withgott 2000; Castillo and Valiente-Banuet 2010; Cares and others 2013). The simultaneous occurrence of direct and indirect facilitation was also suggested by other studies. Miller (1994) found that indirect effect is often confounded by the simultaneous occurrence of direct effect. Siemann and Rogers (2003) documented the occurrence of direct facilitation via nitrogen and indirect facilitation via light reduction in tree–tree seedling–grass associations in Texas, USA.

Woody plants with relatively deep roots and a low-to-moderate root overlap with CAM plants can perform hydraulic redistribution (Figure 5A, B), which may play a role in the direct and indirect facilitation in the tree–CAM–grass (T–C–G) associations. Past studies suggest that hydraulic lift can contribute to the facilitation of understory plants by trees (Riginos and others 2009; Dohn and others 2013; Moustakas and others 2013). Our study confirms the weakening of direct facilitation of CAM plants by trees with hydraulic descent (Figure 5C), and the enhancement of direct facilitation when hydraulic lift occurs (Figure 5D). Moreover, we found that hydraulic lift increases transpiration of CAM plants in tree–CAM–grass (T–C–G) associations with respect to the case with CAM plants alone, in contrast to the situation without hydraulic lift (Figure 5D). Therefore, hydraulic lift

may contribute to explain the preference of CAM plants to establish and grow under tree canopies even in presence of grass competition rather than bare soils. Unlike the case of direct facilitation, hydraulic lift may reduce the indirect facilitation of CAM plants by trees because it favors grasses at the expense of trees (Richards and Caldwell 1987; Zou and others 2005; Brooks and others 2006; Yu and D'Odorico 2014a), thereby increasing the competitive effects of grasses on CAM plants. This effect depends on how CAM plants and grasses compete for the access to hydraulically lifted water. CAM plants transpire and photosynthesize at night when trees perform hydraulic lift, although neither trees nor grasses transpire for photosynthesis (Lüttge 2004; Ogburn and Edwards 2010). Thus, it has been suggested that CAM plants should benefit more than grasses from hydraulic lift (Yoder and Nowak 1999). By comparison, hydraulic descent suppressing grass growth increases the indirect facilitation of trees on CAM plants (Burgess and others 2001; Hultine and others 2004).

Past studies have largely ignored whether inclusion of grasses in tree–CAM associations can indirectly facilitate CAM plants through the mechanism of hydraulic lift (Figure 1C). Yu and D'Odorico (2014a) found that a high rate of transpiration by grasses in the shallow soil layer can promote the occurrence of hydraulic lift. Thus, the indirect facilitation of CAM plants by grasses will occur if the benefits from hydraulic lift outweigh the competitive effects of grasses on CAM plants (Levine 1999; Brooker and others 2008). Our study shows that the competitive effects of grasses on CAM plants outweigh the hydraulic lift effect (Figure 6D), thereby leading to a lower transpiration of CAM plants in tree–CAM–grass associations (T–C–G) than that occurs without grasses (that is, T–C) (Figure 5D). Therefore, transpiration ratio of CAM plants between tree–CAM–grass association (T–C–G) and tree–CAM association (T–C) decreases with the increasing grass cover even in cases with relatively high rates of hydraulic lift (Figure 6B). In fact, conditions that maximize hydraulic lift (high hydraulic conductivity, relatively small leaf area index, and high tree root allocation in the shallow soil layer) are associated with strong grass competition with CAM plants. However, the ability of CAM plants to benefit from hydraulic lift cannot be ignored because of their preferential access to hydraulically lifted water (Yoder and Nowak 1999; Lüttge 2004; Ogburn and Edwards 2010). Overall, this model-based study provides the first analysis of the direct and indirect facilitation in the tree–CAM–grass (T–C–G) associations. More experimental evidence is needed to further support these results.

CONCLUSIONS

We found that a high degree of root overlap favors competition between trees and CAM plants for soil water resources, but trees indirectly facilitate CAM plants by significantly reducing grass transpiration in shaded conditions. Under conditions with a low-to-moderate root overlap, the indirect effect is confounded by the simultaneous occurrence of the direct effect. The increase of hydraulic lift with inclusion of grasses in tree–CAM association is not sufficient to outweigh the competitive effects of grasses on CAM plants, thus precluding the indirect facilitation of grasses on CAM plants through hydraulic lift.

ACKNOWLEDGMENTS

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