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Vegetation Controls on Dryland Salinity

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Key Points:

- The effects of salinity on evapotranspiration and the soil water budget depend on salt tolerance and can significantly vary across species
- Salt-tolerant plants are shown to exert major feedback on soil salinization through transpiration and by reducing leaching occurrence
- Plant salt tolerance is a crucial factor in controlling and limiting dryland salinization across natural ecosystems and rain-fed farmlands

Supporting Information:

- Supporting Information S1
- Figure S1
- Figure S2
- Figure S3
- Figure S4

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Abstract In salt-affected soils, salt stress causes a drastic reduction of plant transpiration. The extent of this reduction is a function of vegetation salt tolerance and can result in highly species-specific controls on soil water budget and salinization levels. Despite their crucial role in regulating the hydrology of saline soils, the effects of salt tolerance on transpiration remain mostly unexplored. Here we propose a minimalist stochastic model of primary salinization which reproduces the hitherto overlooked feedback of salinity on the soil water balance and the active role of plant salt tolerance in modulating such an effect. We show that vegetation can exert significant control on leaching occurrence and soil salinization, thus imposing a species-specific upper limit, C_{\max} , to the concentration of soluble salts in the soil. Since C_{\max} increases with plant salt tolerance, salt-resilient species have the potential to sustain more saline conditions in the soil, eventually creating a favorable environment for their ecological success.

Plain Language Summary In arid regions, thousands of hectares of arable land are lost daily to soil salinization as a result of both natural processes and human-induced modifications of the local hydrological regime. Salt-tolerant species (*halophytes*) have been proposed as an economically viable alternative to traditional salt-sensitive crops (*glycophytes*) to reclaim saline soils and even contrast dryland degradation. Under saline conditions, however, halophytes use water more efficiently—and transpire comparatively more—than conventional crops, raising the question of whether their ability to tolerate salinity can have an impact on the long-term soil water balance and future salinization trends. To better understand the relation between vegetation, salinity, and soil water dynamics, we propose here a simple parameterization of the effects of salt tolerance on evapotranspiration in salt-affected ecosystems. Using a minimalist stochastic model of natural salinization, we then show that different levels of plant salt tolerance correspond to distinct transpiration, soil moisture, and salinization trajectories. Halophytes, in particular, tend to maintain higher levels of salinity in the soil compared with glycophytes, eventually re-engineering the habitat in their favor. These results suggest that the long-term effects of plant salt tolerance on salinization should be carefully considered in planning large-scale transitions to halophytic agriculture.

1. Introduction

Salt-affected soils amount to approximately ~ 1.1 Gha worldwide, corresponding to nearly 10% of the total land surface of our planet (FAO, 2015; Fischer et al., 2008; Massoud, 1981; Ruan et al., 2010; Wicke et al., 2011). Of these, more than 0.8 Gha are already classified as *saline* (i.e., moderately to severely salt-affected, showing a conductivity of the saturation extract, EC_e , of 4 dS/m and above; Chhabra, 2005; Richards, 1954) or *saline-sodic* (a condition in which severe sodicity accompanies salinity; Ghassemi et al., 1995) and are substantially lost to crop production. Conventional crops are, in fact, predominantly salt-sensitive, and their yield is already dramatically reduced at EC_e 's as low as 1–2 dS/m (Maas & Grattan, 1999).

Salinization is particularly widespread in arid and semiarid parts of the world (Figure 1a; De Pascale & Barbieri, 1997; D'Odorico & Porporato, 2006; FAO et al., 2012; Fischer et al., 2008; Lombardini, 2006; Rohades et al., 1992), where it represents a major threat for subsistence agriculture and food security (Casey, 1972; Godfray et al., 2010; Goodin et al., 1990; Raheja, 1966). Additionally, climate change, land use modifications, groundwater overabstraction, and erroneous irrigation practices are expected to further exacerbate the problem in the next decades (Jesus et al., 2015; Pankova & Konyushkova, 2014; Pitman & Läuchli, 2002; Qadir et al., 2014).

Salt-tolerant species (halophytes) possess the ability to maintain elevated levels of productivity in salt-affected soils, and they have been proposed as an alternative to traditional salt-sensitive crops (glycophytes) to ameliorate and reclaim marginal saline soils (Glenn et al., 1999; Goodin et al., 1990; Qadir et al., 2000; Roy et al., 2014; Rozema & Flowers, 2008; Yamaguchi & Blumwald, 2005). Many studies have investigated the use of halophytes for phytoremediation (Ammari et al., 2008; Cheeseman, 2016; Glenn et al., 2013; Hamidov et al., 2007; Qadir et al., 2000), biosaline agriculture (Brown et al., 2018; Choukr-Allah et al., 2016; Glenn et al., 1999; Nikalje et al., 2017; Rohades et al., 1992), and silviculture (Hbirkou et al., 2011; Khamzina et al., 2009; Qureshi & Ismail, 2017), showing extremely encouraging results at the small/medium-plot scale and a broad potential for future upscaling. A recent assessment has further suggested that salt-affected soils potentially available to rain-fed biosaline forestry (i.e., biomass production from silviculture in saline soils; Arora et al., 2013; Wicke et al., 2011) may account for as much as 0.97 Gha worldwide, resulting in a global economic potential for bioenergy production of about 21 EJ/year, equivalent to 4% of current global energy consumption (Wicke et al., 2011).

However, the sustainable transition to intensive biosaline agriculture, saline soils reclamation, and more in general, the management of salinization in natural ecosystems all calls for a better understanding of the interactions and feedbacks between vegetation, hydrological regime, and salinization (Perri et al., 2017, 2018). Under saline conditions, halophytes can attain water use efficiency substantially higher than salt-sensitive species, leading to higher rates of transpiration and a lower occurrence of leaching events (Flowers & Colmer, 2008; Wendelberger & Richards, 2017). Their ability to better exploit water in salt-affected soils should be therefore assessed in light of the possible feedback on soil water balance, salinization trends, land-atmosphere interactions, and ecosystem dynamics.

Here we explore the effects of salt tolerance on soil water budget and primary salinization—also known as dryland or natural salinity. The coupled dynamics of relative soil moisture, s , and salt mass in the root zone, m , is investigated through a minimalist stochastic model explicitly accounting for the dependence of evapotranspiration, ET , on salinity, and for the species-specific nature of this forcing. This simple modeling framework is then used to infer long-term salinization trajectories (here represented in terms of concentration of soluble salts in the soil, C) as a function of hydroclimatic variability, initial level of soil salinization, and vegetation characteristics.

2. Methods

Suweis et al. (2010) previously investigated the coupled dynamics of s and m in the absence of species-specific salinity controls on evapotranspiration. To introduce the effects of vegetation and salt tolerance, we start from a similar standpoint, considering soil moisture and the salt mass at a point under seasonally fixed conditions and null salt inputs from irrigation or groundwater up-flows. This is equivalent to neglect secondary salinization effects, which are dominant in irrigated agricultural areas (Nosetto et al., 2009; Runyan & D'Odorico, 2010), but less important in natural saline soils, accounting for the vast majority of salt-affected lands (approximately 95% of the total; Figure 1a; Qadir et al., 2014).

The soil is described as a spatially uniform reservoir, characterized by vertically averaged soil porosity n , rooting depth Z_r , relative soil moisture s , salt mass m , and salt concentration $C = \frac{m}{nZ_r s}$. Under such assumptions, the water balance of salt-affected soils can be written as (Porporato et al., 2004; Rodríguez-Iturbe & Porporato, 2007; Rodríguez-Iturbe et al., 1999):

$$nZ_r \frac{ds}{dt} = R(t) - ET[s(t), C(t)] - L[s(t), t], \quad (1)$$

where $R(t)$ represents the rate of infiltration from precipitation, $ET[s(t), C(t)]$ the evapotranspiration rate, and $L[s(t), t]$ the deep infiltration rate. Soil water dynamics in equation (1) is driven by the stochastic input of precipitation $R(t)$. This is modeled as an instantaneous random pulse, with frequency of occurrence λ and exponentially distributed rainfall depth of mean $\alpha = nZ_r s_1 / \gamma$, where s_1 represents the effective field capacity and γ is a dimensionless scale parameter (Laio et al., 2001; Porporato et al., 2004; Rodríguez-Iturbe et al., 1999, 2001; Suweis et al., 2010). The strength and form of the dependence of ET on salt concentration C is determined by the level of plant salt tolerance (as described in section 2.2).

Given the longer time scales of salt-mass dynamics, the salt-mass balance is obtained considering: (a) a constant-rate input from precipitation (and for fixed rain salt concentration C_R) and dry deposition \mathcal{M}_d (Hillel,

2000), (b) a plant salt uptake directly proportional to m through the uptake rate β_{UP} (Manzoni et al., 2011), and (c) instantaneous leaching events of frequency λ_L and normalized mean depth μ (Calabrese et al., 2017; Mau et al., 2014; Suweis et al., 2010):

$$\frac{dm}{dt} = C_R R(t) + \mathcal{M}_d - \beta_{UP} m(t) - C(t)L[s(t), t]. \quad (2)$$

The uptake rate β_{UP} is here assumed to be >0 only for highly tolerant species (Parida & Jha, 2010; Qadir et al., 2000). This reflects the ability of halophytes to cope with excess salinity by both intracellular compartmentalization (*salt accumulators*) and leaf excretion (*salt secretors*) and the fact that these adaptations allow them to uptake salt from the soil (Parida & Jha, 2010; Waisel, 1972). A more general formulation of (2) may include the salt input from irrigation and groundwater up-flows, thus allowing for secondary salinization effects.

Equations (1) and (2) represent a bidirectionally coupled stochastic system (Porporato et al., 2015). In absence of salinity feedback on the soil water budget (i.e., for ET not depending on C) and assuming null salt uptake from vegetation, system (1) and (2) reduces to the one analyzed by Suweis et al. (2010), where the dynamics of soil moisture drives salt-mass accumulation through leaching events, but it is not affected by the level of salinization. In this case, the associated master equations can be separately solved at steady state considering s as an independent, fast-evolving stochastic variable (Mau et al., 2014; Suweis et al., 2010, 2011). When species-specific salinity controls are introduced, however, s cannot be treated anymore as independent of m , and some approximations are required to allow for the analytical tractability of the coupled system Gardiner, 2004; Van Kampen, 2011). In particular, the frequency of the leaching events, λ_L , becomes a function of s , m , and salt tolerance, resulting in a state-dependent forcing on the salt-mass dynamics.

2.1. Salinity Controls on Evapotranspiration

The mechanism through which salinity affects plant transpiration and growth includes two distinct phases: (a) a fast-acting osmotic-stress phase caused by the presence of soluble salts in the root zone, and (b) an ionic-stress phase caused by the accumulation over time of toxic ions within the plant (Munns & Tester, 2008). During the osmotic phase, dissolved salts increase the energy with which water is held in the soil, thus reducing the total water potential and causing abiotic stress (De Oliveira et al., 2013; Munns, 2002). Ionic stress, in contrast, takes place over longer time scales and is characterized by ion cytotoxicity, ultimately causing metabolic imbalances, oxidative stress (Tuteja et al., 2012), and accelerating the senescence of mature leaves (Greenway & Munns, 1980; Munns & Tester, 2008).

The extent to which transpiration is reduced in response to osmotic and ionic stress is mainly a function of plant salt tolerance and can vary significantly across species—resulting in highly species-specific salinity controls on the soil water budget (Parida & Jha, 2010). In spite of this, it is a common hydrological practice to assume the effects of osmotic stress as dominant (as well as *species-independent*; Bras & Seo, 1987; Shah et al., 2011; Vermue et al., 2013) and implicitly account for the limiting effects of salinity on ET by introducing a non-negligible soil osmotic potential based on the Van't Hoff law, $\pi(C) = \kappa C$, where $\kappa = i_v RT/M$, i_v is the Van't Hoff's constant of the solute, T the soil water temperature, R the universal gas constant, and M the salt molecular weight (see Bras & Seo, 1987; Shah et al., 2011; Wadleigh & Ayers, 1945). Accordingly, one can define a virtual, or equivalent, moisture content \tilde{s} (Bras & Seo, 1987; Shah et al., 2011), which depends on both the actual soil water content, s , and the concentration of soluble salts in the soil, C , in the form:

$$\tilde{s} = s_s \psi_s^b \left[\psi_s \left(\frac{s}{s_s} \right)^{-\frac{1}{b}} + \kappa C \right]^{-b}. \quad (3)$$

Here b is a parameter related to soil connectivity and tortuosity, ψ_s the soil matric potential at saturation, and s_s the relative soil moisture at saturation ($s_s = 1$). However, the sole osmotic effects accounted for in equation (3) (prevalently *physical*) cannot explain the diversity of adaptations and plant transpiration patterns exhibited by different species in response to salt stress (Ahmad et al., 2013; Munns & Tester, 2008; Parida & Das, 2005), and a more species-specific approach is required to model salinity controls on the soil water budget.

2.2. Species-Dependent ET as a Function of Salinity

To account for the species-specific nature of vegetation response to salt stress, we propose a simple parameterization of the relation between ET and root-zone salt concentration, C , based on the proportionality between crop yield and transpiration (Homaei et al., 2002; Shani et al., 2007) and incorporating the cumulative effect of the different morphological, physiological, and biochemical mechanisms determining salt

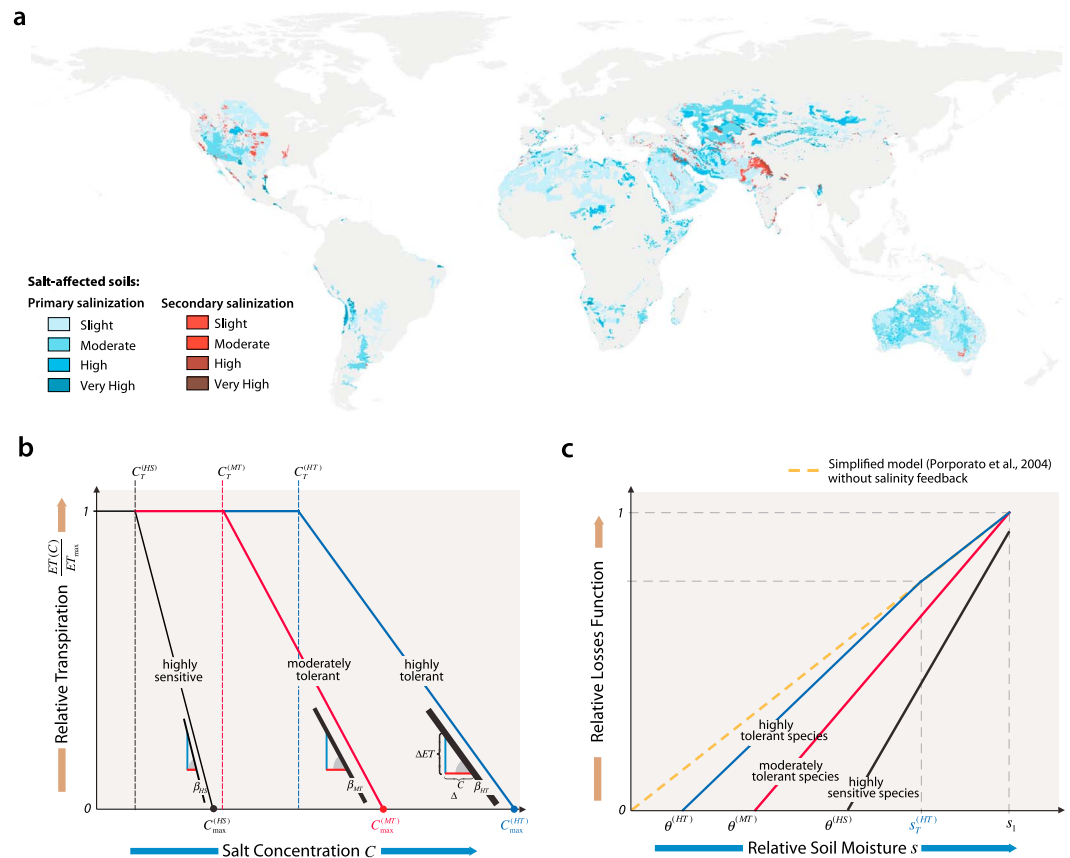


Figure 1. (a) Global distribution of saline soils from FAO Harmonized World Soil Database, v1.2 (FAO et al., 2012; Fischer et al., 2008). The blue color scale refers to the intensity of salinization in rain-fed or naturally saline soils, while the red scale indicates the salinization level in soils affected by secondary salinization, here defined as salt-affected croplands with an irrigated area $\geq 15\%$. Soil salinization is ranked as *slight* if the electric conductivity of the saturated soil paste (EC_e) lies in between 2 and 4 dS/m, *moderate* for $4 < EC_e < 8$ dS/m, *high* for $8 < EC_e < 16$ dS/m, and *very high* for EC_e above 16 dS/m (Fischer et al., 2008; Rohades et al., 1992). Intensity of salinity is obtained here as a weighted average of EC_e in the top and subsoil (see section S1 and Wicke et al., 2011). (b) Typical transpiration patterns for *highly salt-sensitive* (black line), *moderately tolerant* (red line), and *highly tolerant* (blue line) species (modified from Maas & Hoffman, 1977). (c) Salinity tolerance-dependent loss function for highly sensitive, moderately tolerant, and highly tolerant plants, as compared with salinity independent losses (orange-dashed line) with null wilting point from Porporato et al. (2004). Colors as in (b).

tolerance (Greenway & Munns, 1980; Hillel, 2000; Munns, 2002; Munns & Termaat, 1986; Munns & Tester, 2008). Experimental data of ET as a function of salinity are available only for a limited number of species (see Perri et al., 2017, 2018, and references therein). However, a large bulk of work has been devoted to the experimental investigation of the effects of salinity on crop yield (Ball, 1988; Bernstein, 1975; Homae et al., 2002; Maas & Hoffman, 1977; Maas, 1986), of which transpiration represents a robust proxy (Katul et al., 2000; Shani et al., 2007).

These experimental studies have shown that above their specific salt-endurance threshold, all species display an approximately linear decline of relative crop yield, Y_r (i.e., the ratio of the actual to the potential yield) in response to increasing C (Feinerman et al., 1982; Hanks, 1983; Hanson et al., 2006; Hasanuzzaman et al., 2014; Homae et al., 2002; Maas, 1986; Maas & Hoffman, 1977; Munns & Tester, 2008). Since over long salt-exposure times (weeks to months), ET and plant growth tend to be linearly related (Ben-Gal et al., 2003; De Oliveira et al., 2013; Skaggs et al., 2014), it is reasonable to assume (Ben-Gal et al., 2003; De Wit, 1958; Hanks, 1974; Shani & Dudley, 2001; Shani et al., 2007):

$$Y_r \simeq ET/ET_{\max} \simeq ET_r, \quad (4)$$

and describe the relation between ET and C as a piecewise linear function (Figure 1b), with salt-stress threshold C_T and rate of transpiration decline above C_T , β :

$$ET(C) = \begin{cases} ET_{\max} [1 - \beta(C - C_T)] & C \geq C_T, \\ ET_{\max} & C < C_T \end{cases} \quad (5)$$

Note that equation (5) simply reproduces the observed relation between ET and C . Depending on their level of salt tolerance, plants start to experience salt stress for different values of the salt-stress threshold C_T (Figure 1b). Above C_T , transpiration gradually declines with increasing salt concentration at rate β .

The main advantage of this simple formulation is that C_T and β can be directly estimated from $Y_r - C$ experimental data, widely available in the literature. We consider here three main categories of plant salt tolerance (Maas & Hoffman, 1977): (i) *high tolerance* (characterized by an elevated salt-stress limit, C_T , usually greater than 5 g/L and low β , < 0.075 L/g), (ii) *moderate tolerance* ($2 < C_T < 5$ g/L and $0.075 < \beta < 0.1$ L/g), and (iii) *high sensitivity* ($C_T < 2$ g/L and $\beta > 0.1$ L/g). Higher is plant salt tolerance, wider is the range of concentrations between the onset of salt stress at C_T and the complete inhibition of transpiration—taking place at $C_{\max} = \frac{1}{\beta} + C_T = \frac{\chi}{\beta}$ with $\chi = 1 + \beta C_T$. Remarkably, C_{\max} depends on salt tolerance only and represents the concentration for which the ability of plants to uptake water from the soil becomes completely impaired (i.e., C_{\max} is higher for halophytes given their ability to better exploit water in the soil). At C_{\max} , evaporation becomes dominant, although other processes like salt-crust formation can occur at this stage, leading to a substantial lowering of evaporative rates or even evaporation suppression (Eloukabi et al., 2013; Fujimaki et al., 2006; Nachshon et al., 2018).

2.3. Water Losses for Given Salinity and Salt Tolerance

Following Milly (2001), we assume the water losses, $\rho(s)$, to be a linear function of s between the wilting point, s_w (here set equal to 0), and well-watered conditions ($s = s_1$). Rainfall exceeding s_1 is instantaneously lost via deep percolation at $s = s_1$ (Porporato et al., 2004; Suweis et al., 2010). Then, substituting equation (5) in the losses function described above, one can obtain an expression for the salinity-dependent water losses as a function of relative soil moisture s , soil salt mass m , and for given vegetation salt tolerance $\{C_T, \beta\}$:

$$\rho(s, m) = \begin{cases} \eta \chi (s - \theta) & \theta \leq s \leq s_T \quad (a) \\ \eta s & s_T < s \leq s_1 \quad (b) \end{cases} \quad (6)$$

Here $\eta = \frac{ET_{\max}}{nZs_1}$ is the normalized evapotranspiration loss under well-watered conditions, while the dependence of ρ on m and salt tolerance is embedded in $\theta = C_{\text{sat}} \frac{\beta}{\chi} = \frac{C_{\text{sat}}}{C_{\max}}$ (with $C_{\text{sat}} = \frac{m}{nZ_r}$ the concentration at saturation) and $s_T = \frac{C_{\text{sat}}}{C_T}$, which, respectively, represent the minimum relative water content of the soil and the value of soil moisture at which salt stress first occurs, for given salinization and salt-tolerance level (Figure 1c). The minimum relative soil moisture, θ , represents a *virtual wilting point*, corresponding to the water that is unavailable to root uptake and transpiration, due to the cumulative effect of osmotic and ionic stress.

The value of θ increases with the level of salinization (the higher the salinity, the more water becomes unavailable to vegetation) and decreases with the strength of salt tolerance (salt-tolerant species are able to extract water from the soil more efficiently against low potentials and phytotoxic effects, thus lowering θ). The piecewise expression in equations (6a) and (6b) represents the water losses of highly tolerant species, for which salt stress starts to occur only at high values of C (i.e., for any given salinization level m , at $s_T \ll s_1$). For moderately tolerant ($s_T \cong s_1$) and highly sensitive ($s_T \gg s_1$) species, the losses function reduces to equation (6a) with $s_T \geq s_1$, accounting for the fact that these species are experiencing salt stress across the entire range of exploitable soil moisture $[\theta(m, C_T, \theta), s_1]$ (see Figure 1c, also showing the losses in absence of salinity feedback, $\rho(s)$; orange-dashed line).

3. Results

The “short-term” effects of salt tolerance on the soil water balance and salt accumulation are highlighted in Figures 2a–2d, which show a 1-year long numerical simulation of precipitation (a), relative soil moisture (b), salt mass (c), and salt concentration (d) from the coupled system in equations (1) and (2), under moderately saline conditions. The simulations are set to reproduce (i) the salt-tolerance-mediated feedback of salinity on ET of equation (5) (for intermediate salt tolerance; red solid line), (ii) the species-independent relation between transpiration and C based on equation (3) (that we indicate in the following as Van’t Hoff approximation; turquoise solid line), and (iii) null salinity feedback (black-dashed line), for arid climatic conditions. In absence of salinity feedback, soil moisture s can reach extremely low values despite the energetic limit imposed by the

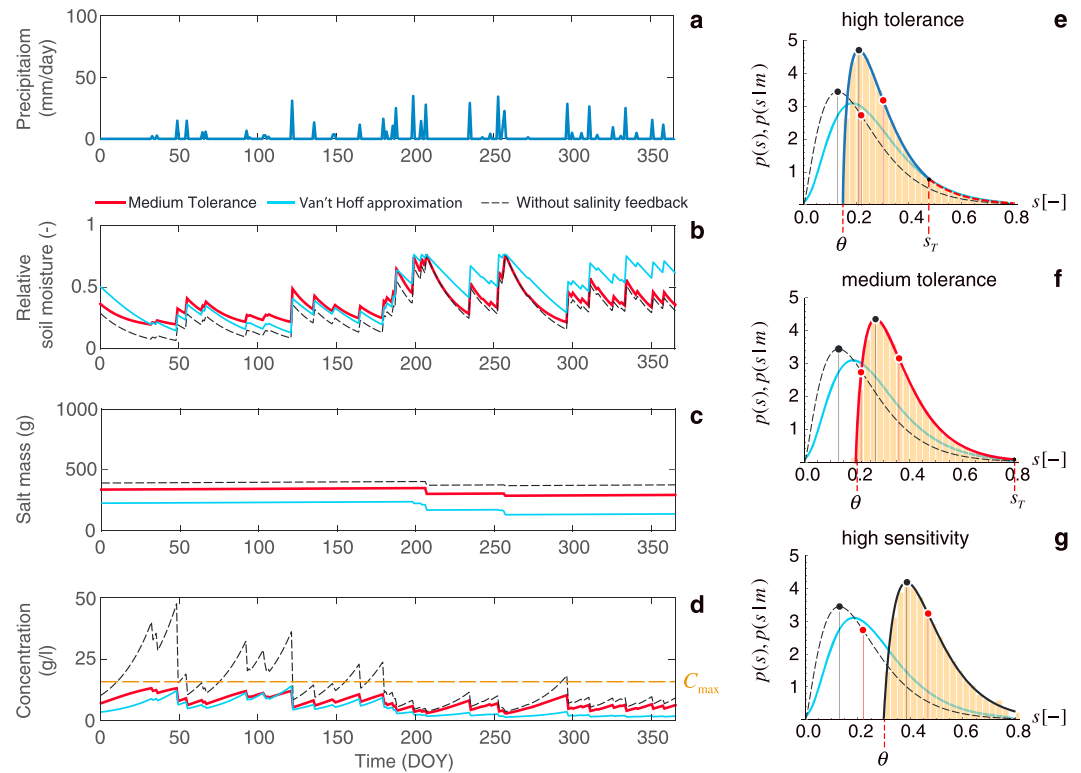


Figure 2. (a–d) Numerical simulations from the simplified physical model of coupled soil moisture–salt–mass dynamics in equations (1) and (2), with and without salinity feedback on ET . The effects of salinity on transpiration are explicitly included as a function of plant tolerance (red solid line), accounted for only in terms of osmotic effects in the soil (Van’t Hoff approximation, turquoise solid line) or completely inhibited (black-dashed line). Simulations are forced by the same random input of precipitation (a) and set to reproduce hydrologic conditions representative of arid climates ($\lambda = 0.1/\text{day}$, $\alpha = 10 \text{ mm}$). The relative soil moisture (b), salt mass (c), and salt concentration (d) for the case of explicit feedback of soil salinity on ET are obtained for a moderately tolerant species ($\beta = 0.084 \text{ L/g}$, $C_T = 3.84 \text{ g/L}$). The yellow-dashed line in (d) represents the maximum possible concentration (C_{max}) that the coupled system can reach for the said level of salt tolerance. Parameters used in the simulations are $ET_{max} = 4.5 \text{ mm/day}$, $n = 0.45$, $s_1 = 0.8$, $s_w = 0$, and $Z_r = 30 \text{ cm}$. (e–g) Soil moisture conditional probability density function for (e) high tolerance (blue solid line for $s \leq s_T$ and blue-dashed line for $s > s_T$), (f) medium tolerance (red solid line), and (g) low tolerance (black solid line), compared to the $p(s)$ without salinity feedback from Porporato et al., (2004; black thin dashed line), the numerical $p(s)$ with Van’t Hoff approximation (turquoise solid line) and numerical histogram obtained by direct simulation of the corresponding Langvin Equation in (1) (orange bars). Dots represent the mean (red) and the mode (black) of s in the case with and without salinity feedback. Salt tolerance parameters are $\beta = 0.071 \text{ L/g}$ and $C_T = 6.4 \text{ g/L}$ for highly tolerant species, $\beta = 0.084 \text{ L/g}$ and $C_T = 3.84 \text{ g/L}$ for moderately tolerant, and $\beta = 0.12 \text{ L/g}$ and $C_T = 1.92 \text{ g/L}$ for low tolerant (Maas & Hoffman, 1977). Parameters as in (a)–(d) except for initial salt mass, $m = 414 \text{ g}$ (here corresponding to a salt concentration close to C_T for moderately tolerant species).

osmotic effect in the soil (viz., vegetation is not suffering salt stress, and water uptake is unaffected). At the same time, leaching events become rare, and salt concentration C can increase limitless (Figure 2d).

If the Van’t Hoff approximation is introduced, soil moisture dynamics becomes — more realistically — sensitive to the effects of the osmotic potential in the soil. However, the relative soil water content is still overestimated under well-watered conditions, when ET actually approaches ET_{max} and vegetation is not expected to experience salt stress. Additionally, the Van’t Hoff approximation does not account for the species-specific response of vegetation to salt stress, whereas the vegetation-mediated feedback of equation (5) allows to describe the alternation between salt stress and salt-unaffected phases that accompanies the joint evolution of soil moisture and salt-mass dynamics. Here ET is not affected by salinity below the species-specific concentration threshold C_T (i.e., under well-watered conditions or till m values are low). Only when salt concentration C exceeds C_T (mostly during dry outs), transpiration starts to decline till becoming completely impeded at $C = C_{max}$.

3.1. Soil Water Balance of Salt-Affected Soils

Additional insights on the mechanisms regulating the long-term dynamics of soil moisture and salt mass in salt-affected soils can be obtained by studying the steady-state probability density distribution (pdf) of s and m . First, we note that the time scales characterizing salt-mass dynamics are orders of magnitude larger than the ones of the precipitation forcing and wet deposition (Mau et al., 2014; Suweis et al., 2010). As a result, soil moisture typically reaches steady-state conditions within a growing season, while salt-mass balance evolves over much longer time scales (e.g., > decades). This implies that s can reach steady state over a time interval for which the variability of m is expected to be limited, and a *quasi* stationary approximation can be implemented. Namely, the steady-state pdf of the soil moisture, $p(s)$, can be considered dependent on an average or characteristic value of m (at equilibrium). Under this approximation, the master equation associated to the stochastic water balance of equation (1) can be solved analytically at steady state to find the pdf of s conditional to a given level of salinization (m) and prescribed plant salt tolerance $\{C_T, \beta\}$. Following Rodríguez-Iturbe et al. (1999), the general solution for the conditional pdf is given by:

$$p(s|m) = \frac{c}{\rho(s|m)} \exp \left[-\gamma s + \int \frac{du}{\rho(u|m)} \right], \quad (7)$$

which once solved for the water losses in equation (6) gives

$$p(s|m) = \begin{cases} N_T \frac{e^{-\gamma s}}{(s-\theta)} \left(\frac{s-\theta}{s_T-\theta} \right)^{\frac{\lambda}{\eta\chi}} & \theta \leq s \leq s_T \quad (a) \\ N_T \chi \frac{e^{-\gamma s}}{s} \left(\frac{s}{s_T} \right)^{\frac{\lambda}{\eta}} & s_T < s \leq s_1 \quad (b) \end{cases}, \quad (8)$$

where N_T is a normalization constant specific of highly tolerant species. Analogously, for highly sensitive to moderately tolerant species, $p(s|m)$ reduces to equation (8a), with $s_T = s_1$ and salt-sensitive species integration constant N_S . In (8), $p(s|m)$ depends on salt tolerance and level of salinization, m , through the shape factor χ , the minimum relative soil moisture θ , and the salt-stress moisture threshold s_T . Explicit expressions for the normalization constants, together with close forms for the mean and mode of $p(s|m)$ are provided in section S2.

Figures 2e–2g show $p(s|m)$ for *highly tolerant*, *moderately tolerant*, and *highly sensitive* species, respectively, and for prescribed salt mass m , as compared with the direct numerical simulation of the corresponding Langevin equation (orange bars), the analytical $p(s)$ in absence of salinity feedback (black-dashed line; from Porporato et al., 2004), and with the numerically obtained $p(s, C)$ using the Van't Hoff approximation (turquoise solid line).

The lower the salt tolerance, the more the pdf accounting for salinity feedback is shifted toward higher values of s , with higher values of θ and higher probability of reaching the effective field capacity s_1 . This is, again, a consequence of the fact that salt-tolerant plants use soil water more efficiently than the salt-sensitive ones, ultimately hampering leaching events and working toward maintaining higher levels of soil salinization, more favorable to their growth. Note, however, that in this simple modeling framework and under arid climatic conditions, θ could be overestimated since C_{\max} corresponds to the suppression of transpiration but does not account for evaporation. Halophytes are known to show optimal transpiration and growth at intermediate values of salinity and suffer stress for lower (approaching freshwater conditions) and higher salinities (Flowers & Colmer, 2008; Perri et al., 2018). In an ecological perspective, their ability to control soil salinity can be thus seen as a way to compete with less salt-tolerant species (Wendelberger & Richards, 2017).

The comparison of $p(s|m)$ with the numerically obtained marginal pdf, $p(s)$ (Figure S1), indicates that, under well-watered conditions, the conditional pdf represents a good approximation of the actual $p(s)$ (i.e., the right tail of $p(s)$ is well-reproduced), while it can lead to a significant underestimation of C and salinity feedbacks during intense dry outs (i.e., the left tail of $p(s)$ can deviate from the one of $p(s|m)$ for low values of s). This is a consequence of assuming m approximately constant over the typical evolution scales of soil moisture, which also leads to a constant value of the minimum soil moisture θ . However, the impact of such underestimation on the salt-mass balance is limited considering that the soil moisture dynamics drives salt accumulation mainly through leaching events, which take place under well-watered conditions (at s_1), where $p(s|m)$ well approximates $p(s)$.

3.2. Soil Salt-Mass Balance With Linearized Stochastic Leaching Rate

In natural saline soils, salt accumulation takes place over temporal scales typically longer than the ones characterizing soil water dynamics. Consequently, the salt-mass input can be assumed to occur at a constant rate $\Upsilon = \mathcal{M}_d + C_R \lambda \alpha$ (Suweis et al., 2010). At the same time, leaching events remove salt from the root zone through *impulsive* events that can be well approximated by a Poisson process and which occur when relative soil moisture s exceeds the threshold s_1 (Botter et al., 2007). Under this assumption, the salt-mass dynamics in (2) can be written as

$$\frac{dm}{dt} = \Upsilon - \beta_{UP} m - m L'(m), \quad (9)$$

where $L'(m)$ is a marked Poisson noise with leaching frequency $\lambda_L(m)$ and dimensionless exponential mean depth μ (Suweis et al., 2010; Van Den Broeck, 1983). The leaching term in equation (9) represents a multiplicative noise (with jumps) with frequency described by a nonlinear monotonically increasing function of m ; namely, the leaching frequency $\lambda_L(m)$ is state-dependent, accounting for the fact that the higher the soil salinization, the higher the probability of reaching soil saturation.

An approximated solution for $p(m)$ can be found linearizing $\lambda_L(m)$ about a prescribed value of m and interpreting equation (9) in the Stratonovich sense (Stratonovich, 1967; Suweis et al., 2011). The steady-state $p(m)$ can, hence, be obtained in the form (Porporato & D'Odorico, 2004):

$$p(m) = N e^{\frac{\beta m}{\beta_{UP}}} \left(\frac{\beta_{UP} m}{\Upsilon} \right)^{\frac{1}{\mu}} \left(1 - \frac{\beta_{UP} m}{\Upsilon} \right)^{\frac{A}{\beta_{UP}} + \frac{\beta \Upsilon}{\beta_{UP}^2} - 1}, \quad (10)$$

where N is the normalization constant, $A = \lambda_L(m_T) - \beta m_T$, and $B = \lambda'_L(m_T)$. In a similar way, it is also possible to find the approximated pdf of salt mass for $\beta_{UP} = 0$ (i.e., in case of negligible plant salt uptake; see section S3).

However, if λ_L is linearized about a value of m which strongly differs from the mean of the distribution (a priori unknown), the linearization can lead to an underestimation of the leaching frequency and, ultimately, to an overall overestimation of the $p(m)$ right tail. To minimize this effect, we linearize $\lambda_L(m)$ about $m_T = C_T n Z_s s_1$ (representing the salt mass corresponding to the onset of salt stress at $s = s_1$) and then use an iterative procedure in which the mean value of the approximated distribution obtained in the first step is used to set the tangent point of the second iteration. Given the convex shape of $\lambda_L(m)$ (Figure S2), the convergence to the actual mean takes place within few iterations.

Due to their higher capacity to exploit soil water and the consequent lowering of λ_L , highly salt-tolerant species tend to sustain more saline conditions, while salt-sensitive vegetation tends to maintain a lower salinization level (Figure S3). At the same time, halophytes are able to uptake and accumulate salt (salt accumulators), and they can contribute to reduce the stored salt mass over a wide range of climatic conditions, imposing an upper limit to the mass accumulation in the soil (see Figure S3c; Mau et al., 2014). Besides phytoremediation applications, however, salt accumulation in plant tissues can often lead to a lowering of crop quality (Grattan & Grieve, 1998).

3.3. Effects of Climate Forcing and Plant Salt Tolerance on Soil Salt Concentration

The coupled dynamics of soil water content and salt mass determine the time evolution of the salt concentration C in the soil. Despite the substantial separation of scales of the two dynamics, however, soil moisture and salt mass cannot be treated as independent stochastic variables, and at steady-state $p(C)$ cannot be obtained as a simple ratio distribution of m and s . Nonetheless, it is interesting to investigate how the long-term trajectories of C change with the level of salt tolerance and climatic forcing through the numerical simulation of the coupled balance in equations (1) and (2). The level of salt tolerance poses a physical limit $C_{\max} = \frac{\Upsilon}{\beta} = \frac{m}{n Z_s \theta}$ to salt concentration C in the soil. Lower is tolerance, lower is C_{\max} , indicating that through their resilience to salt, tolerant species may be able to compete with glycophytes. Once transpiration is suppressed, evaporation becomes the dominant process, although during dry outs, salt crust formation can have a major role in lowering evaporation (Nachshon et al., 2018). However, whether C_{\max} may represent an underestimation of maximum salinity, it still provides an important indication of how salt tolerance can exert an active forcing on salinization dynamics.

Figure 3 shows typical C temporal evolution patterns and long-term pdfs for semiarid (Figures 3a and 3c) and arid (Figures 3b and 3d) conditions and for different levels of tolerance. In both arid and semiarid climate simulations, the frequency of rainfall occurrence is kept low ($\lambda = 0.1/\text{day}$) to maximize the capacity of rain events to wash away salts. This assumption is consistent with the predominantly convective nature of dryland

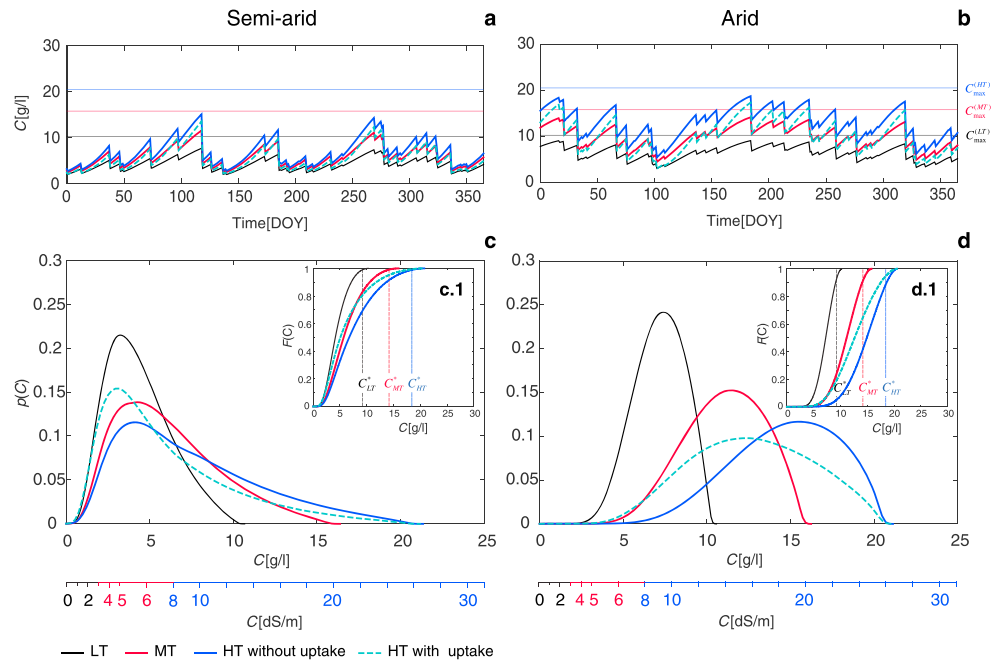


Figure 3. (a and b) Simulations from the simplified physical model with salinity feedback on ET , highlighting the dynamics of salt concentration for LT, MT, and HT species (color coding as in Figures 1–3), under semi-arid (a; $\lambda = 0.1/\text{day}$, $\alpha = 12.3$ mm, annual average precipitation $\langle R \rangle = 450$ mm) and arid (b; $\lambda = 0.1/\text{day}$, $\alpha = 8.22$ mm, annual average precipitation $\langle R \rangle = 300$ mm) conditions. Remaining parameters as in Figure 2. The same rainfall forcing is used across the different salt-tolerance levels. (c and d) Probability density function of salt concentration $p(C)$ obtained from the simplified physical model for the same three levels of salt tolerance in (a) and (b) under semi-arid (c) and arid (d) climatic conditions. The insets in (c) and (d) show the corresponding cumulative density functions $F(C)$. Dashed lines highlight the critical threshold C^* corresponding to the 90% of C_{\max} for different salt-tolerance levels. Colors in (c) and (d) secondary x axes correspond to the here adopted C_T range for sensitive (black), moderately tolerant (red), and highly tolerant (blue) species in deciSiemens per meter. LT = low tolerant; MT = moderately tolerant; HT = highly tolerant.

precipitation, characterized by extremely sporadic, short-duration, and intense events (Kumar et al., 2015; Warner, 2004).

Under semi-arid conditions ($\langle R \rangle = 450$ mm), elevated levels of vegetation salt tolerance result in higher salt concentrations (Figure 3a), and the mode of $p(C)$ is shifted toward higher C values (Figure 3c). However, the probability of exceeding a critical salinity threshold, here defined as $C^* = 0.9 C_{\max}$, remains extremely low (Figure 3, inset c.1), and the $p(C)$ s are positively skewed, with modes mostly below the species-specific stress thresholds C_T . This points out how both glycophytes and halophytes tend to maintain salinization close to their characteristic stress-threshold C_T . Furthermore, fat tails emerge in the case of moderately tolerant, highly tolerant, and salt accumulating species. If, in contrast, species-specific controls are neglected, concentration can grow limitless (in absence of salinity feedback) or reach extremely low values when salinity effects are included also under well-watered conditions (Van't Hoff approximation; Figure S4). It is also interesting to note that under semi-arid conditions, salt accumulators are highly efficient in uptaking salt from the soil, showing the lowest mode of the entire ensemble.

As aridity increases ($\langle R \rangle \approx 300$ mm), concentration trajectories approach the corresponding C_{\max} moving toward a more stable point for the system. The $p(C)$ s become negatively skewed with their mode located at high values of C , and the efficiency of salt accumulators decreases—further pointing out that the new equilibrium of the system is stable and salinization mostly irreversible at this stage. Here scarce precipitation and low soil water content further enhance the $ET - C$ feedback. Also, high-tolerant plants appear to be more likely to reach their C^* threshold compared with medium- and low-tolerant species (Figure 3, inset d.1; low-tolerant species are shown here for reference, since plant mortality starts to have a major impact on sensitive species at these levels of salt stress). In contrast, as precipitation input increases (e.g., in warm Mediterranean climates), the impact of the vegetation-salinity feedback becomes less important, leaching events become more frequent, and salt does not accumulate in the soil (Figure S4). The transition between a semi-arid and an arid

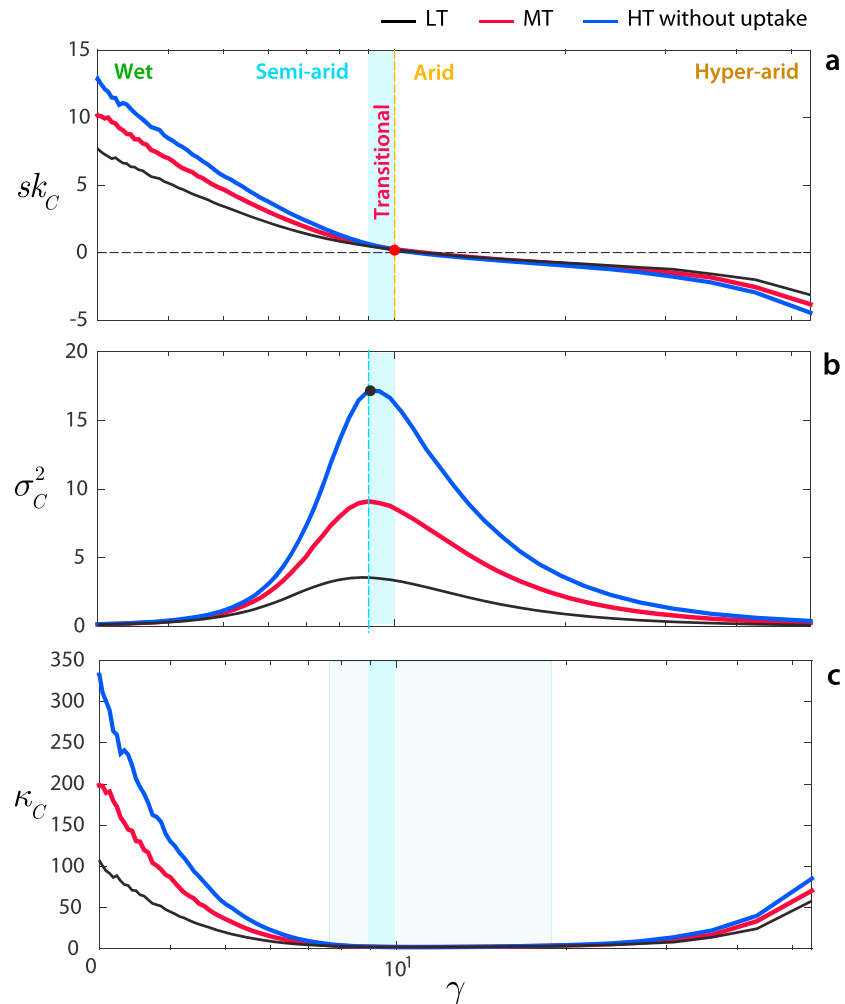


Figure 4. Salt concentration statistics in the transition between semi-arid and arid regimes: (a) skewness, sk_C , (b) variance, σ_C^2 , and (c) kurtosis, κ_C , of the salt concentration C as a function of the dimensionless parameter γ for three degrees of salt tolerance (color code as Figures 1–3). The soil water holding capacity ($nZ_s s_1$) is maintained constant among the different simulations, and the variability in γ is obtained by changing the average precipitation input. LT = low tolerant; MT = moderately tolerant; HT = highly tolerant.

regime is highlighted in Figures 4a–4c, where the skewness, sk_C , the variance, σ_C , and the kurtosis, κ_C , of the salt concentration, C , are represented as a function of hydrological forcing (γ) and plant salt-tolerance level. As the average annual rainfall input decreases, the variance of C increases up to a maximum at $\gamma \cong 9$ (approximately equivalent to a $\langle R \rangle \simeq 450$ mm, representing semi-arid conditions) and just before the transition between positive (mode located at low salt concentrations) and negative (mode shifted toward higher C) values of sk_C . The variance in soil salt concentrations in proximity of the transition point is maximum for highly tolerant species, pointing out the larger uncertainties on the long-term soil water balance and salinization trends associated with the use of halophytes in transitional climates (Figures 4a and 4b). At the same time, highly tolerant species allow for maintaining the highest concentration mode over a wide range of climates, together with the fattest tails of the distribution (Figure 4c). Taken all together, these findings seem to indicate that salt tolerance, together with climate forcing, could have a major role in determining future salinization trends.

4. Conclusions

We presented here a minimalist model of coupled soil water and salt-mass dynamics, accounting for the feedback between salinity and evapotranspiration as mediated by vegetation salt tolerance. Through this simple modeling scheme, we showed that in dryland natural ecosystems and rain-fed agrosystems, salt tolerance can

be considered at the same time a major driver and limiting factor of soil salinization. Elevated salt tolerance corresponds to a higher water use efficiency, lower values of the effective wilting point θ , and higher potential to hamper leaching events and enhance salt accumulation.

Plant salt tolerance also determines the maximum concentration of salt (C_{\max}) that can be reached in the soil, independently from climatic forcing and initial salinization conditions. Salt-resilient plants display elevated C_{\max} and, in an ecological perspective, modify the environment to maintain the most favorable conditions for their survival. Salt-tolerance controls are expected to be especially intense in presence of obligate halophytes, whose transpiration and growth are known to be even favored by salinity (see Perri et al., 2018, and references therein) and in ecologically “unstable” semiarid regions. Here drastic salinization shifts could trigger the transition to more stable permanent-degradation states (D’Odorico et al., 2013) or determine the ecological success of halophytes when competing with glycophytes (Wendelberger & Richards, 2017). At the same time, in nonsaline conditions, glycophytes are significantly more productive than halophytes (Munns & Tester, 2008; Tester & Romola, 2003), which gives them an evolutionary advantage on salt-tolerant species under wet conditions.

The use of highly tolerant species for biomass production, phytoremediation, or as an alternative to traditional crops in salt-affected soils should be therefore carefully evaluated based on long-term effects of salinity on plant-water relations. Halophytes, for instance, could contribute to increase salt accumulation in slightly saline arid and semiarid areas (as a consequence of reduced leaching frequency). However, they will still concur to reduce soil degradation due to erosion and loss of nutrients. More effective would be the use of accumulator-secretor plants (i.e., $\beta_{UP} > 0$) in highly saline/sodic soils that may lead to a reduction of salinization under semiarid conditions. In general, the use of moderately tolerant or highly tolerant plants in salt-affected areas should be planned (i.e., which species to grow) based on both initial salinization conditions and expected climatic forcing.

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