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Consequences of drought tolerance traits for microbial decomposition in the DEMENT model

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ABSTRACT

The frequency and intensity of drought are expected to increase in the future, yet the consequences for soil microbial communities and functioning remain unclear. Processes such as decomposition could be maintained if microbial communities become more drought tolerant. However, increased drought tolerance might involve physiological costs with uncertain consequences for ecosystem processes. Here we used the trait-based model DEMENT to quantify the sensitivity of microbial traits, community dynamics, and litter decomposition to variation in drought tolerance costs. These costs were imposed as a physiological tradeoff between drought tolerance and carbon use efficiency. We ran simulations across a range of drought tolerance costs and with climate forcing from ambient and drought treatments in a Southern California grassland that experiences seasonal summer drought. As expected, zero or low costs of tolerance allowed drought-tolerant taxa to increase in abundance under ambient simulation conditions. More drought tolerant communities had greater microbial biomass but lower extracellular enzyme investment due to biological feedbacks involving enzyme production. These two responses counteracted one another, leaving decomposition unchanged relative to virtual microbial communities with no drought tolerance. Simulated decomposition rates were one-third lower under drought treatment, but there were no differences in microbial drought tolerance compared to simulations forced with ambient climate. This model result suggests that seasonal drought is a more important environmental filter than reduced precipitation during the wet season in our Mediterranean climate system. Overall, our simulations indicate that microbial community responses to drought are not likely to increase decomposition rates, even if CUE costs are low. Using the simulation approach described here, the DEMENT model could be modified to incorporate additional mechanisms of microbial drought tolerance and their associated physiological costs as new empirical data become available.

1. Introduction

Microbes regulate multiple aspects of ecosystem response to environmental variation, including climate change (Allison and Martiny, 2008; Bardgett et al., 2008). In many areas of the globe, especially southwestern North America, drought frequency and intensity are increasing (Cayan et al., 2010; Cook et al., 2015; Seager et al., 2007). These climatic changes could alter microbial communities (Cregger et al., 2012; Sheik et al., 2011) and inhibit microbial processes such as decomposition and respiration that determine carbon fluxes in surface soils (Allison et al., 2013; Evans and Burke, 2013; Manzoni et al., 2012a; Zeglin et al., 2013).

On the other hand, microbes have evolved mechanisms to survive and metabolize at low water potential (Potts, 1994). Such mechanisms could enable microbial communities to sustain biogeochemical fluxes in the face of drought. For example, microbes can accumulate osmolytes (Harris, 1981; Schimel et al., 2007; Warren, 2014), produce exopolysaccharides (EPS) (Roberson and Firestone, 1992), form thick cell walls, or enter a dormant state (Jones and Lennon, 2010; Potts, 1994). At the same time, desiccation tolerance mechanisms could trade off against other aspects of physiology (Raven, 1985; Schimel et al., 2007). For example, microbial taxa that survive better under drought might have lower growth efficiency due to increased metabolic costs (Killham and Firestone, 1984a) or fewer resources to invest in enzymatic

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machinery (Sardans and Peñuelas, 2010).

Predicting biogeochemical responses to drought requires a framework for linking microbial physiology with community and ecosystem processes (Schimel et al., 2007). Desiccation tolerance and associated physiological tradeoffs should affect microbial competitive ability and community interactions (Lennon et al., 2012). Changes in the microbial community should in turn influence ecosystem processes such as decomposition under drought (Bouskill et al., 2016). The goal of this paper is to develop a theoretical basis for predicting how microbial physiological responses might structure communities and their associated decomposition rates under drought. To accomplish this goal, we incorporate drought tolerance mechanisms and tradeoffs into a trait-based model of microbial community dynamics. We aim to generate model predictions that can be compared with molecular-based surveys of microbial drought tolerance strategies (Evans and Wallenstein, 2014; Placella et al., 2012) and field data on decomposition rates under drought conditions (Allison et al., 2013).

Trait-based models are relevant for this aim because they can account for tradeoffs among environmental tolerance and other physiological traits that affect biogeochemical cycling (Bouskill et al., 2012; Follows et al., 2007). Building on prior models of drying and rewetting responses with simplified soil microbial communities (Evans et al., 2016; Zhang et al., 2014), here we update the DEMENT model (Allison, 2014, 2012) to represent drought tolerance traits and tradeoffs in diverse microbial communities with explicit spatial structure. To mimic real communities, DEMENT represents feedbacks and interactions with enzymatic traits involved in decomposition of organic compounds found in litter and soil. Here we focus on predicting decomposition rates in surface leaf litter in Southern California because microbial decomposers in this environment likely experience very low water potentials for much of the year (Dirks et al., 2010; Newell et al., 1991).

Using DEMENT as a conceptual tool, we tested four hypotheses related to microbial drought tolerance and litter decomposition (Fig. 1). Because greater ability to tolerate desiccation should reduce microbial mortality under drought, we hypothesized that 1) introducing trait variation for drought tolerance into the model community should increase litter decomposition rates. However, if there are physiological costs associated with drought tolerance (i.e. a trait tradeoff), the positive effects on decomposition might diminish. Therefore we hypothesized that 2) community drought tolerance, microbial biomass, and litter decomposition should decline with increasing tradeoff costs in terms of carbon use efficiency (CUE). We framed the tradeoff this way because CUE may decline with increasing osmolyte production (Killham and Firestone, 1984a), but we recognize that different costs may apply to other drought tolerance mechanisms (such as dormancy). Because lower moisture levels should select for microbial taxa with greater drought tolerance, we additionally hypothesized that 3) drought treatment (a ~50% reduction in precipitation) would increase the average level of drought tolerance in the microbial community. Following the same rationale, we hypothesized that 4) increasing the sensitivity of microbial death rate to desiccation would increase average drought tolerance.

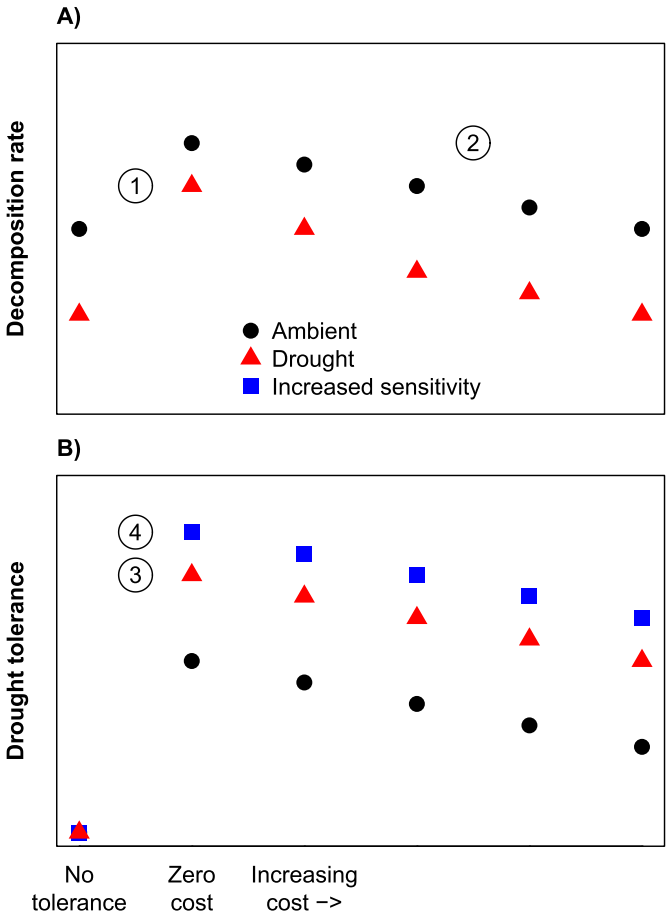

Fig. 1. Conceptual illustration of expected patterns in A) litter decomposition rate and B) community drought tolerance as a function of differing model assumptions. "No tolerance" assumes that there are no drought tolerance traits in the community: mortality rate increases similarly with drought stress across all microbial taxa. "Zero cost" assumes that members of the microbial community possess varying levels of a drought tolerance trait that reduces mortality under dry conditions, but there are no physiological costs. "Increasing cost" assumes that greater drought tolerance correlates with greater physiological cost, and the magnitude of cost increases from left to right. Circled numbers correspond to hypotheses proposed in the main text.

2. Material and methods

2.1. Modeling drought responses

In the DEMENT model, a large number of bacterial and fungal taxa (combined $n = 100$) compete on a spatial grid representing the surface of a decomposing leaf. Microbial growth in DEMENT is a function of multiple factors, including substrate type and stoichiometry, enzyme production rates, uptake investment, and temperature. Cells divide when they reach a threshold biomass and disperse to adjacent grid points. Enzymes produced by the microbial taxa interact locally with substrates to generate monomers for uptake. Simulated extracellular enzymes have a range of kinetic properties, substrate specificities, and constitutive versus uptake-driven mechanisms. Model parameters are described in Table 1, and model code is available on GitHub (https://github.com/stevenallison/DEMENT).

The updated version of DEMENT used here introduces moisture sensitivity of microbial mortality, enzyme kinetics, uptake, and abiotic pathways of monomer loss (leaching, gaseous emissions, physical movement, etc.). Microbial death rates (τ) are assumed to increase as water potential (Ψ, in MPa) declines:

$$\tau = \tau_B(1 - \beta \cdot \Psi(1 - \alpha)) \quad (1)$$

where τ_B is the bacterial death rate at $\Psi = 0$ (τ_F is the analogous rate for fungi), β is a scalar that represents death rate sensitivity to water potential, and α is a drought tolerance parameter that can vary between zero and 1. Increasing values of β imply that death rates increase more sharply as water potential declines. As α approaches

Table 1
Values and units for model parameters.

Variable	Value	Units	Interpretation (with reference if available)
t	365	day	number of iterations
N_E	50		number of enzymes in community
N_S	12		number of substrates
N_U	14		number of uptake transporters
N_B	100		number of taxa
E_a	35	kJ mol^{-1}	activation energy for uptake
E_{aK}	20	kJ mol^{-1}	activation energy for K_m (German et al., 2012)
$K_{mESlope}$	1	mg enzyme day cm^{-3}	slope for $K_m - V_{maxE}$ relationship
K_{mEInt}	0	mg cm^{-3}	intercept for enzyme $K_m - V_{maxE}$ relationship
$K_{mUSlope}$	0.2	mg biomass day cm^{-3}	slope for $K_m - V_{maxU}$ relationship
K_{mUInt}	0	mg cm^{-3}	intercept for uptake $K_m - V_{maxU}$ relationship
V_{maxE}	5–50	mg substrate mg^{-1} enzyme day^{-1}	V_{max} for enzymes
V_{maxU}	1–10	mg substrate mg^{-1} biomass day^{-1}	V_{max} for uptake
λ_{Slope}	−0.8		fractional change in cellulose decay per unit lignocellulose index
E_S	1		minimum number of enzymes capable of degrading each substrate
U_M	1		minimum number of uptake transporters capable of taking up each monomer
E_{max}	40		maximum number of enzymes a taxon may produce
S_E	1		coefficient determining strength of specificity-efficiency tradeoff
α	0–1		drought tolerance level
ε_0	0.5	mg mg^{-1}	intercept for C use efficiency function (Thiet et al., 2006)
m_T	−0.016	mg mg^{-1} °C^{-1}	C use efficiency temperature sensitivity (Allison et al., 2010)
m_E	0	mg mg^{-1}	C use efficiency change with enzyme investment
m_U	0	mg mg^{-1}	C use efficiency change with uptake investment
m_D	−0.35 - 0	mg mg^{-1}	C use efficiency change with drought tolerance
Z_{EC}	1×10^{-6} - 1×10^{-5}	mg C mg^{-1}	per enzyme production cost as a fraction of C uptake rate (inducible)
B_{EC}	1×10^{-6} - 1×10^{-5}	mg C mg^{-1} day^{-1}	per enzyme production cost as a fraction of biomass C (constitutive)
R_{EC}	5	mg C mg^{-1} enzyme C	respiration cost of enzyme production
B_{UC}	0.01–0.1	transporter mg^{-1} biomass C	allocation to each uptake transporter as a fraction of biomass
R_{UC}	0.01	mg C transporter^{-1} day^{-1}	respiration cost of uptake transporters
Z_{EN}	0.3	mg mg^{-1}	per enzyme N cost as a fraction of C cost (Sterner and Elser, 2002)
L_0	0.1	day^{-1}	abiotic monomer loss rate
τ_E	0.04	day^{-1}	enzyme turnover rate (Allison, 2006)
τ_B	0.001, 0.005	day^{-1}	bacterial death rate
τ_F	0.2•τ_B	day^{-1}	fungal death rate
F_{MS}	0	mg mg^{-1}	initial monomer present as a fraction of initial substrate
D_B	0.01		initial bacterial cell density per lattice point
D_F	0.0004		initial fungal cell density per lattice point
C_B	0.825	mg mg^{-1}	bacterial C fraction (Sterner and Elser, 2002)
N_B	0.160	mg mg^{-1}	bacterial N fraction (Sterner and Elser, 2002)
P_B	0.015	mg mg^{-1}	bacterial P fraction (Sterner and Elser, 2002)
C_F	0.900	mg mg^{-1}	fungal C fraction (Sterner and Elser, 2002)
N_F	0.090	mg mg^{-1}	fungal N fraction (Sterner and Elser, 2002)
P_F	0.010	mg mg^{-1}	fungal P fraction (Sterner and Elser, 2002)
C_l	0.090	mg mg^{-1}	tolerance on C fraction
N_l	0.040	mg mg^{-1}	tolerance on N fraction
P_l	0.005	mg mg^{-1}	tolerance on P fraction
C_{min}	0.086	mg cm^{-3}	threshold C concentration for cell death
N_{min}	0.012	mg cm^{-3}	threshold N concentration for cell death
P_{min}	0.002	mg cm^{-3}	threshold P concentration for cell death
C_{Bmax}	2	mg cm^{-3}	C concentration threshold for bacterial reproduction
C_{Fmax}	50	mg cm^{-3}	C concentration threshold for fungal reproduction
β	0.2, 2	MPa^{-1}	desiccation sensitivity of death rate
k_{VE}	0.1	MPa^{-1}	moisture sensitivity of enzyme V_{max}
k_{VU}	0.05	MPa^{-1}	moisture sensitivity of uptake V_{max}
k_L	0.1	MPa^{-1}	moisture sensitivity of abiotic monomer loss rate
F_B	0.5		initial biomass fraction of fungi
ρ_y	0.05		probability of fungi dispersing in y direction
δ	1	lattice point	maximum dispersal distance
x	100		lattice length
y	100		lattice width

1, sensitivity to water potential approaches zero, and τ converges on τ_B. The parameter α is intended to represent drought tolerance, whereby values approaching 1 represent increasing investment in drought tolerance mechanisms. The exact mechanism (osmolytes, EPS, cell walls, etc.) is not specified, so the current representation of drought tolerance is intended to be generic.

Moisture sensitivity of enzyme and uptake kinetics is represented through modification of the per-enzyme reaction velocity V:

$$V = \frac{V_{max}[S]f(T)e^{k_V\Psi}}{K_m + [S]} \quad (2)$$

where V_{max} is the maximum reaction velocity per enzyme mass, $f(T)$ is an Arrhenius function of temperature T, K_m is the half-saturation constant, [S] is substrate concentration, and k_V is a scalar on the water potential. For instance, a value of 0.05 for k_V would result in a

92% decline in V at $\Psi = -50$ MPa (very dry) compared to $\Psi = 0$ MPa (very wet). Zero values for k_V result in no moisture sensitivity of V. Abiotic monomer loss rates L are parameterized with a similar moisture sensitivity function:

$$L = L_0 e^{k_L \Psi} \quad (3)$$

where k_L is a scalar on the water potential that results in $L = L_0$ when set to zero. The one-parameter moisture sensitivity functions for V and L are highly simplified and only intended to represent a general reduction in process rates as water potential declines. We do not attempt to parse out changes in diffusion rates, tortuosity, and effective substrate concentrations. Although relevant, these mechanisms would require a substantial increase in model complexity to parameterize. However, we do assume that moisture constraints are more severe for uptake and abiotic monomer loss than for extracellular enzymes that may still interact with substrates in thin water films (Zhang et al., 2014). Therefore k_V for uptake and k_L were set to 0.10 as opposed to 0.05 for k_V of extracellular enzymes (Table 1), meaning that a 92% decline in uptake or abiotic monomer loss occurs at −25 MPa.

Costs for drought tolerance were implemented through a tradeoff with carbon use efficiency (CUE). CUE is defined here as 1− the fraction of carbon uptake that is associated with growth respiration (Allison, 2014); it does not account for other processes such as cellular maintenance or enzyme production that also generate respiration (Manzoni et al., 2012b). CUE (ε) is assumed to decline with increasing drought tolerance (α) according to:

$$\varepsilon = \varepsilon_0 - m_D \alpha \quad (4)$$

where ε_0 is the reference CUE and m_D is the parameter that controls the cost of drought tolerance.

2.2. Model forcing

Simulations were forced with temperature, moisture, and litter chemistry data from a grassland ecosystem at Loma Ridge, CA, USA (Allison et al., 2013; Parolari et al., 2015). A drought manipulation at this site achieves a 40–50% reduction in precipitation by excluding selected storm events during the winter rainy season (Fig. S1, Parolari et al., 2015). DEMENT requires daily temperature and water potential data for the litter layer (Fig. S1). Water potentials were estimated with fuel moisture sensors that detect the water content of a standardized 1 cm diameter wooden dowel (Campbell Scientific, CS506-L). In each of the ambient and drought treatments, water contents (θ) were averaged from two sensors with continuous records from 14 December 2010 to 13 December 2013, aggregated to daily averages, and converted to water potential values (MPa) based on birch wood relationships described in Dix (1985):

$$\Psi = -10^{0.118 - 0.114 \log_{10}\theta} \quad (5)$$

Water contents generally ranged from 0.05 to 0.70 g water g^{-1} wood. The fuel moisture sensors are subject to instrument drift that could bias the calculated water potentials across the treatments. To correct for this potential bias, we scaled the datasets such that ambient and drought treatments reached equivalent minimum water potentials during the driest summer (2013). Litter chemistry data were taken from ambient conditions in a previous study (Allison et al., 2013) and are also given in Table S1.

2.3. Model simulations

Simulated microbial communities were initiated with 50% bacteria and 50% fungi (by biomass) and total biomass densities of ~1 mg cm^{-3}. Although bacteria dominate leaf litter in our system (Alster et al., 2013), simulations were initiated with 50% fungal biomass because fungi in the model are more vulnerable to extinction due to their larger cell sizes and correspondingly smaller population sizes. Note that DEMENT simulates saprotrophic fungi, as mycorrhizal fungi are rare in grassland leaf litter (Matulich et al., 2015).

Trait values for each taxon were assigned at random from uniform distributions as in Allison (2012, 2014). The limits of the distributions were based on literature values where available, and some traits were assigned based on correlations with other traits. A negative relationship is assumed between enzyme specificity and enzyme efficiency, and a positive relationship is assumed between V_{max} and K_m as in Allison (2012). In contrast to the original model, we do not assume a positive relationship between CUE and enzyme production; there is no direct effect of enzyme traits on CUE. However, the metabolic costs of enzyme production tend to reduce growth efficiency and likely trade off indirectly with drought tolerance. Initial trait values are fixed for each taxon, but community-average trait values change throughout simulations as taxa with different trait values shift in abundance.

For each field treatment, ambient and drought, we conducted 9 simulation scenarios with 13 replicates each (Table 2). The “base” scenario assigned a drought tolerance of zero to all taxa. For the remaining 8 scenarios, drought tolerance was assigned to taxa based on a uniform distribution between zero and 1. Each of the 8 scenarios corresponds to a different magnitude of drought tolerance cost ranging from zero ($m_D = 0$) to high cost ($m_D = 0.35$). We chose this range because the true costs are poorly known but probably cannot represent more than 35% of the substrate uptake rate without severely constraining growth. We also tested the consequences of an increase in drought sensitivity of mortality by conducting additional simulations (10× Beta) under ambient forcing in which β was increased from 0.2 to 2.0, and τ_B (and τ_F) were decreased by a factor of 5.

All simulations were initiated on 14 December 2010 and run on a daily timestep. A new cohort of litter was input to the model every 365 days. There is no dispersal of new taxa into the simulations; however, cell locations are randomized at the start of each year, and taxa that go extinct (reach zero biomass) during a given year may in some cases be reintroduced at the start of the next year. Reintroduction can occur because taxa are assigned to the model grid at the start of each year based on their average frequencies (not their final frequencies) from the prior year. Simulations were run for 3 years (through 13 December 2013) except for the simulations under ambient conditions which were extended to 12 years and forced with the ambient climate record recycled 4 times. The extended simulations were run to test whether communities and average trait values would continue to change after 3 years.

Table 2
DEMENT model simulation set-up and forcing.

Simulation type	Parameters	Forcing	Replicates	Scenarios
Ambient	Ambient	Ambient	13	9[a]
Drought	Ambient	Drought	13	9
10× Beta	$\beta = 2$, $\tau_B = 0.001$	Ambient	13	9
12-year extended[b]	Ambient	Ambient	13	9

[a] Includes base and $m_D = 0.00, 0.05, 0.10, 0.15, 0.20, 0.25, 0.30, 0.35$.
[b] Continuation of the ambient simulations.

2.4. Model output analyses

Output variables for analysis included drought tolerance, CUE, microbial biomass, enzyme investment, and litter mass loss. All analyses were conducted on the third year of the simulation. For drought tolerance, CUE, and enzyme investment, we calculated average values for the initial community as well as community averages weighted by taxon biomass integrated across the third litter cohort. Our metric of enzyme investment was calculated as the sum of constitutive and inducible enzyme production rates across all enzymes, weighted by each enzyme's V_{max}. Microbial biomass is reported as a total carbon concentration (mg cm^{-3}) averaged across the third simulation year. Litter mass loss is the percentage of initial litter mass lost by the end of the simulation (for the third litter cohort); microbial by-products were not counted as mass lost. We also analyzed shifts in microbial trait values with seasonal changes in moisture by plotting biomass-weighted drought tolerance versus enzyme investment for taxa from all 13 ambient replicates at the end of the wet versus dry seasons.

Across all scenarios and treatments, replicate number was treated as a random factor, such that all simulations with the same replicate number started with the same random number seed and thus the same initial conditions (taxon traits, cell positions, etc.). Paired *t*-tests were therefore used to compare means among scenarios and treatments. To account for multiple comparisons, we used 0.05/n as the threshold for statistical significance where n = the number of comparisons (Bonferroni correction).

3. Results

3.1. Model dynamics

Microbial activity in DEMENT was greatest late in the wet season (Fig. 2). Turnover of litter chemical substrates and formation of microbial byproducts was greatest between March and June (Fig. 2C). Likewise, microbial biomass (Fig. 2B) and respiration (Fig. 2D) were elevated during this time period as substrate was converted into microbial biomass and CO_2. In most simulations, there was a pulse of respiration in October corresponding to the first rain event of the wet season that mobilized monomers accumulated during the preceding dry season.

3.2. Drought tolerance

Relative to the base scenario with no drought tolerance, the inclusion of drought tolerance traits in the microbial community had consequences for DEMENT predictions of microbial functioning. After three simulation years, drought tolerance increased in the ambient community only if there was no tradeoff with CUE (i.e. drought tolerance cost = zero, Fig. 3). With weak tradeoffs (low cost scenarios, m_D = 0.05–0.15), drought tolerance did not differ significantly from the initial community average. Stronger tradeoffs (costs of 0.20 or greater) resulted in significant selection against drought tolerance.

3.3. Carbon use efficiency

Average CUE of the initial community reflects the tradeoff with drought tolerance imposed in the model (Fig. 4). With zero tradeoff, there was no effect of including drought tolerance on CUE. As the CUE cost of drought tolerance approached 0.15 in the ambient simulations, biomass-weighted CUE declined to 0.437 ± 0.005 (mean ± SEM), which was not significantly different from the initial community value. As tradeoff costs increased beyond 0.15, biomass-weighted CUE stabilized around 0.434, meaning that taxa with high drought tolerance and therefore low CUE were increasingly selected against.

3.4. Microbial biomass, enzyme investment, and litter mass loss

Relative to the base scenario with no drought tolerance, including zero-cost tolerance in the ambient simulations resulted in greater microbial biomass, although the difference was only marginally significant (P = 0.00625) after Bonferroni correction (Fig. 5A). With further cost increases, microbial biomass declined. In contrast to microbial biomass, enzyme investment declined under low-cost scenarios but then rebounded as costs increased further (Fig. 5B). Trends in litter mass loss reflected offsetting changes in microbial biomass and enzyme investment. Despite higher biomass, there was no significant effect of zero- or low-cost drought tolerance on mass loss (Fig. 5C). Higher costs of drought tolerance reduced mass loss relative to the base scenario, consistent with reduced microbial biomass.

3.5. Drought responses

Simulated drought had almost no effect on biomass-weighted physiological traits yet had strong negative effects on microbial biomass and litter mass loss. Relative to ambient conditions, drought treatment elicited no significant differences in drought tolerance, CUE, or enzyme investment under any of the model scenarios (Figs. 3, 4 and 5B). In contrast, drought treatment significantly reduced microbial biomass by 24–34% (Fig. 5A) and significantly reduced mass loss by 28–37% (Fig. 5C) across the model scenarios.

3.6. Increased moisture sensitivity of mortality

Increasing the sensitivity of microbial death rate to desiccation resulted in significantly greater selection for drought tolerance (Fig. 3) but had no significant effect on litter mass loss (Table S2). Biomass-weighted drought tolerance was significantly greater than the initial community average under zero- and low-cost scenarios (Fig. 3). Under the non-zero cost scenarios, increased sensitivity of death rate to desiccation resulted in lower CUE relative to the ambient and drought simulations with less sensitive death rates (Fig. 4). Although variation in enzyme investment across the cost scenarios was more pronounced, there were no major effects of increased sensitivity to desiccation on trends in enzyme investment, microbial biomass, or decomposition (Table S2).

3.7. Seasonal changes in traits

Biomass-weighted trait values shifted across wet versus dry seasons (Fig. 6). Although a tradeoff between drought tolerance and CUE is imposed in the model, a tradeoff also emerges between drought tolerance and enzyme investment due to the metabolic costs of enzyme production. After the wet season, communities were dominated by taxa with low drought tolerance and high values for CUE and enzyme investment (Fig. 6A). After the dry season, communities shifted to have higher drought tolerance but lower values of enzyme investment and CUE (Fig. 6B). This seasonal shift was observed consistently across the extended simulations, and there was no evidence for a continued directional change in trait values after 3 years. After only 1 year, drought tolerance and enzyme investment traits continued to converge on similar wet and dry season values year after year (Fig. 6C).

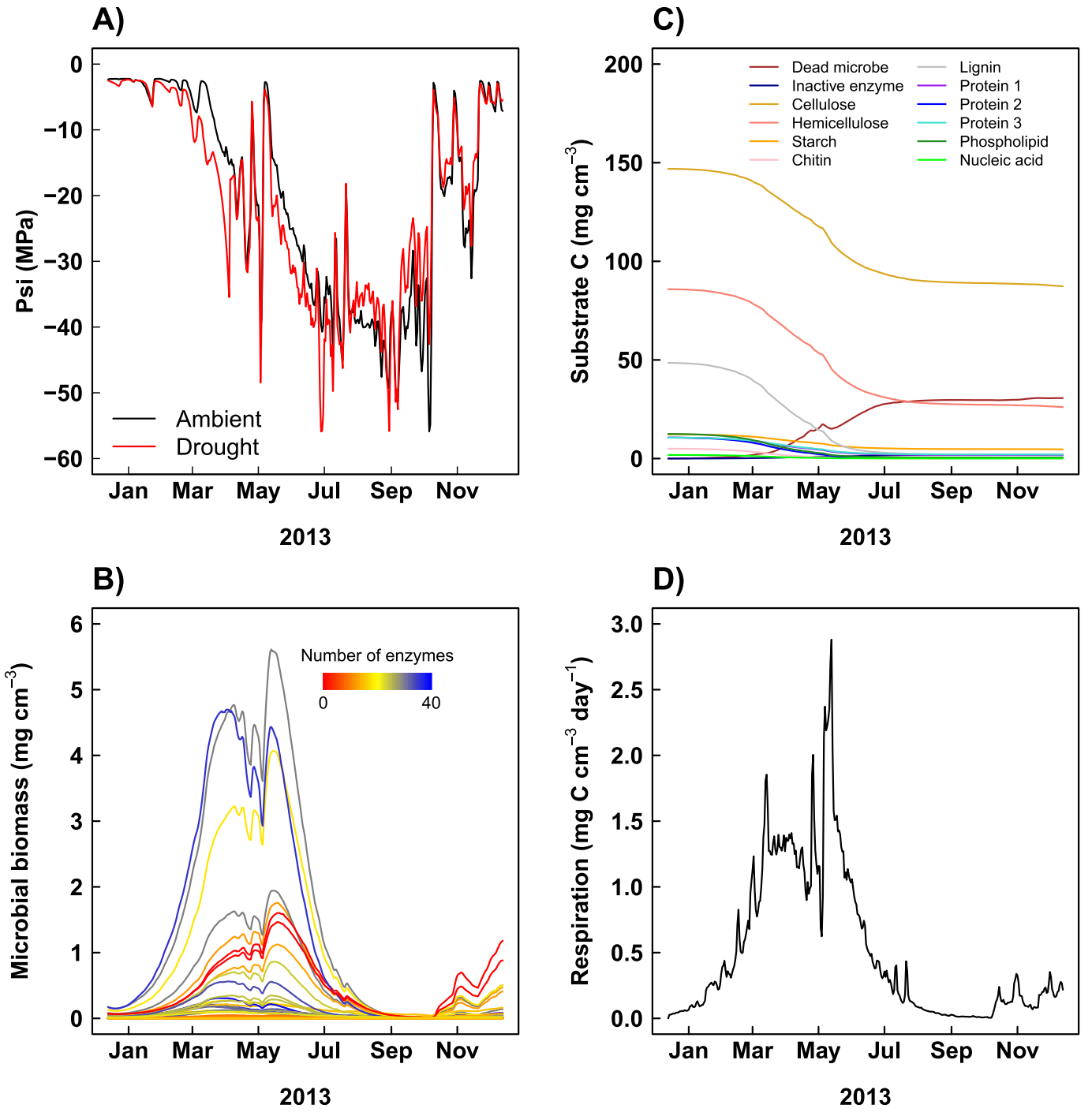

Fig. 2. DEMENT model forcing and outputs from the third year of simulated litter decomposition. Time course of A) litter water potential, B) live microbial biomass, C) substrate pools, and D) respiration. Outputs are from a selected ambient simulation of the base scenario with no drought tolerance. For microbial biomass, lines correspond to individual taxa, and colors correspond to the number of enzymes possessed by each taxon. Total initial biomass density was set to 1 mg cm^{-3}, and initial taxon frequencies were set to the averages across the prior year.

4. Discussion

The physical effects of seasonal and experimental drought were well-represented in DEMENT. Consistent with empirical data from Loma Ridge, CA (Allison et al., 2013; Alster et al., 2013), live microbial biomass declined sharply and there was almost no microbially-driven litter decomposition during the dry season (Fig. 2B and C). However, the decline in microbial biomass may be unique to litter because microbial biomass measured by chloroform fumigation does not decline during the dry season in California grassland soils (Boot et al., 2013). Following the first rains, DEMENT predicted a pulse of respiration due to metabolism of labile organic carbon accumulated throughout the dry season, consistent with observations and models of ongoing enzymatic activity during drought periods in semi-arid soils (Zhang et al., 2014). In the drought treatment, which is only imposed during the wet season, empirical data from Loma Ridge show that litter decomposition rates decline by ~25%, which is consistent with the magnitude of

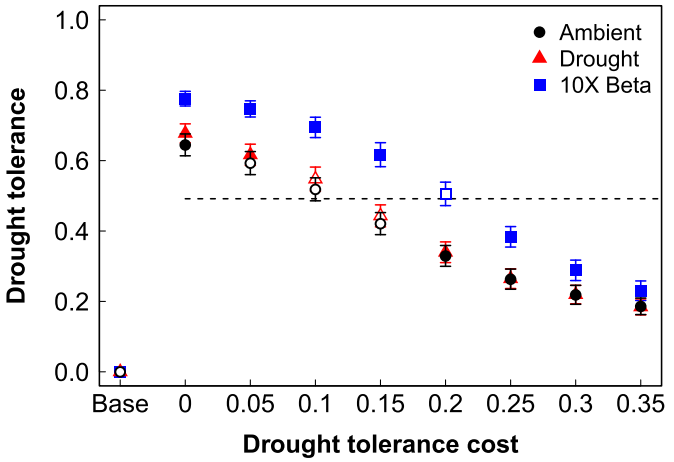

Fig. 3. Biomass-weighted drought tolerance (mean ± SEM) as a function of tolerance cost (Base indicates no drought tolerance in the simulation). Drought simulations were forced with fuel moisture data from a field experiment. 10× Beta corresponds to simulations with $\tau_B = 0.001$ and $\beta = 2$. Open symbols indicate no significant difference ($P > 0.005$, paired t-test) from the initial community average (dashed line).

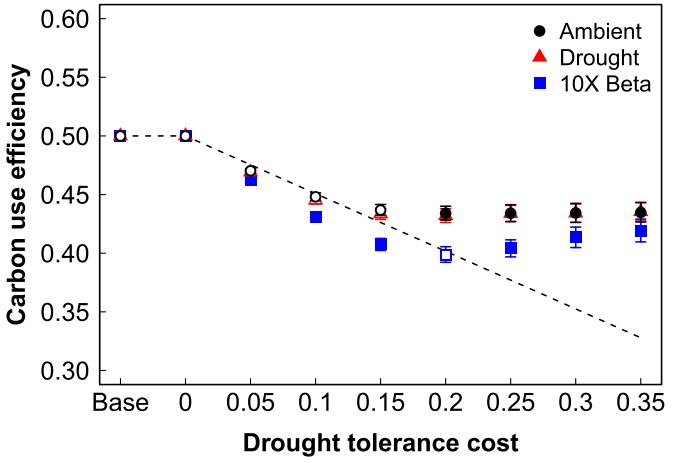

Fig. 4. Biomass-weighted carbon use efficiency (mean ± SEM) as a function of drought tolerance cost (Base indicates no drought tolerance in the simulation). 10× Beta corresponds to simulations with $\tau_B = 0.001$ and $\beta = 2$. Open symbols indicate no significant difference ($P > 0.005$, paired t-test) from the initial community average (dashed line).

decline predicted by DEMENT (Fig. 5C). Thus even small reductions in moisture availability during the wet season have a large impact on decomposition because microbial activity is relatively high.

Surprisingly, model outputs did not support the hypothesis that introducing drought tolerance would increase litter decomposition rates, even when there was no cost for tolerance. Instead our results suggest that biological feedbacks may constrain the effects of drought adaptation on decomposition, consistent with previous studies in which antagonistic microbial interactions limit functioning (Allison, 2005; Gore et al., 2009). Although microbial biomass increased somewhat in communities with drought tolerance traits, biological feedbacks led to an offsetting reduction in enzyme investment (Fig. 5). The feedback involves a shift toward "cheater" strategies in the microbial community, whereby taxa with lower enzyme production (and lower associated costs) increase in abundance. Cheating is favored because higher biomass densities increase access to the enzymatic products of neighboring cells (Allison, 2012). Reductions in enzyme activity have also been

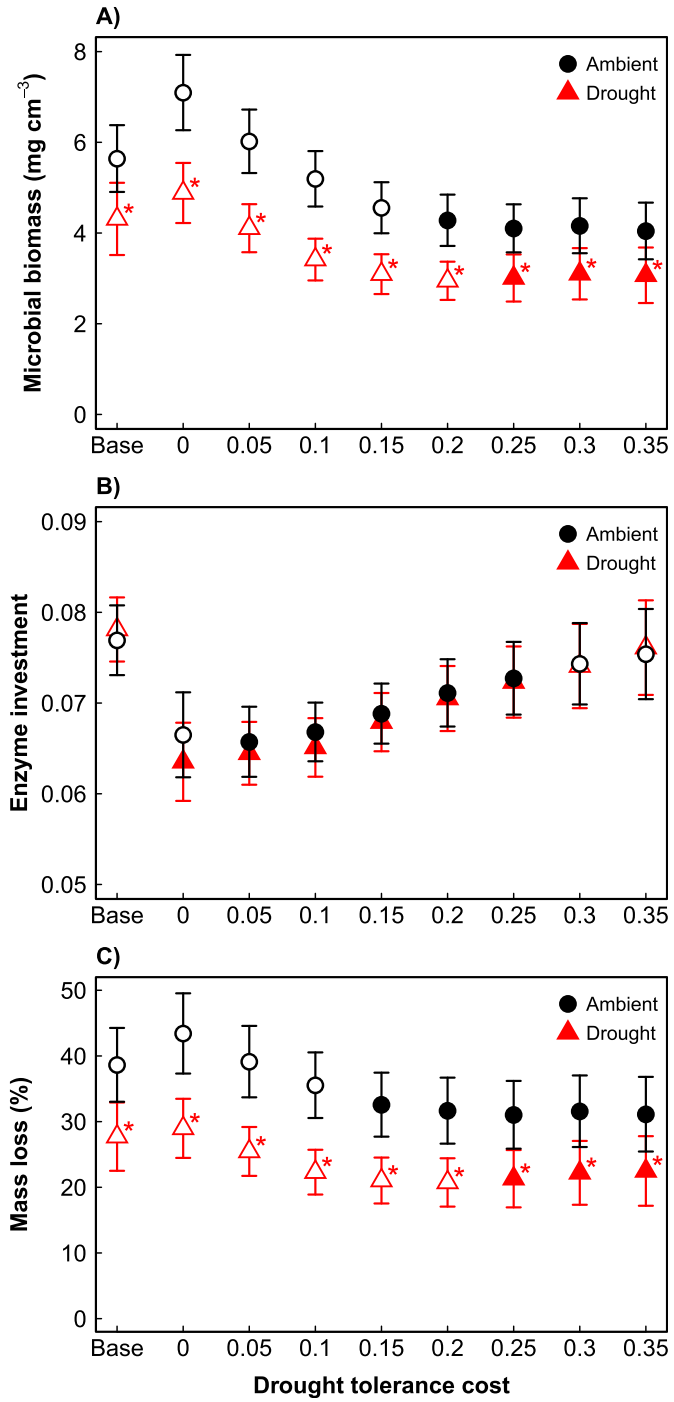

Fig. 5. Mean (±SEM) microbial biomass (A), biomass-weighted enzyme investment (B), and litter mass loss (C) as a function of drought tolerance cost (Base indicates no drought tolerance in the simulation). Drought simulations were forced with fuel moisture data from a field experiment. Open symbols indicate no significant difference ($P > 0.005$, paired t-test) from the base scenario. Asterisks indicate significant differences between ambient and drought simulations.

observed empirically in response to drought (Sardans and Peñuelas, 2010, 2005).

Consistent with hypothesis 2, our results indicate that drought tolerance traits and decomposition rates decline with increasing tradeoff costs in terms of CUE. CUE is an important determinant of growth rate and therefore competitive ability in real microbial populations and the DEMENT model (Allison, 2014; Sinsabaugh

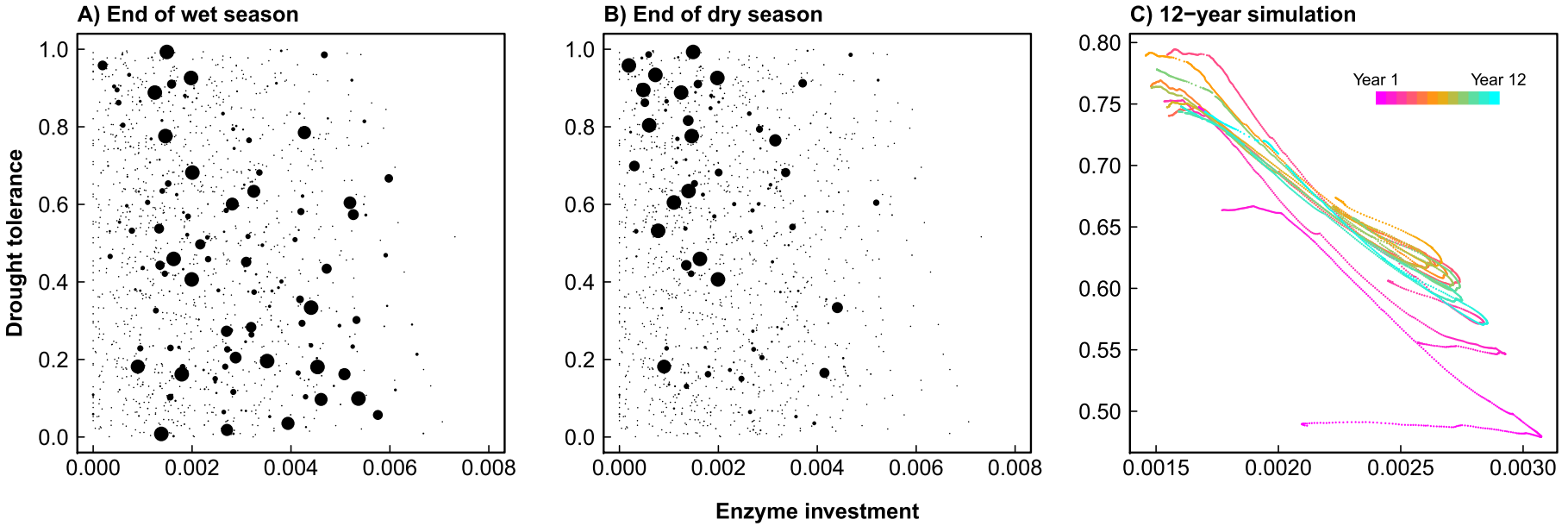

Fig. 6. Community-level tradeoffs among drought tolerance and enzyme investment for microbial taxa at (A) the end of the wet season (13 March 2013) versus (B) the end of the dry season (16 September 2013) in 13 replicate ambient simulations (drought tolerance cost = 0.10). Each point corresponds to an individual taxon, and point sizes are proportional to taxon biomass normalized to the most abundant taxon within each simulation at each time point. (C) The biomass-weighted average drought tolerance and enzyme investment for the same simulations run for 12 years. Points represent daily averages across the 13 simulations. Discontinuities occur between years because each year was re-initiated with taxon frequencies averaged across the prior year. Note difference in x- and y-axis scales.

et al., 2013). Our model formulation reflects evidence that strategies such as osmolyte and EPS production require additional metabolic machinery whose maintenance reduces growth efficiency (Killham and Firestone, 1984a, 1984b; Schimel et al., 2007). Still we recognize that our version of the drought tolerance-CUE tradeoff is a simplification of many physiological mechanisms potentially involved in drought tolerance (Manzoni et al., 2014).

Nonetheless, any drought tolerance strategy is likely to involve physiological costs. Under desiccating conditions, microbial respiration declines (Manzoni et al., 2012a) and cells must maintain protein conformation, membrane integrity, and other vital functions to avoid death. In a classic review, Potts (1994) described the physiological challenges of desiccation and emphasized osmolyte and EPS production as strategies to stabilize proteins and membranes through water replacement. More recently, osmolyte production has been observed in drying soils, but with increased costs in terms of carbon demand (Bouskill et al., 2016; Warren, 2016, 2014). Biofilm production also promotes drought tolerance but reduces microbial growth potential under culture conditions (Lennon et al., 2012). Alternative strategies such as dormancy may entail unique physiological costs, such as synthesis and maintenance of spore structures (Lennon and Jones, 2011).

Aside from drought tolerance costs, other factors also influenced the average level of drought tolerance observed in our model simulations. Even with cost-free tolerance and high sensitivity to desiccation, not all taxa remaining in the community were completely drought tolerant after 3 years. The maximum biomass-weighted average drought tolerance achieved by a single community was 0.927, and the average maximum across communities was 0.776, not 1.0 (Fig. 3). Our extended simulations suggest that these values do not increase further over time (Fig. 6C), meaning that the simulated communities will never become completely drought tolerant. The reason is probably that in DEMENT and in real communities, multiple traits determine taxon performance (Martiny et al., 2015). Due to stochastic trait assignment in DEMENT and evolutionary history in real microbes, taxa with optimal drought tolerance traits (i.e. $\alpha = 1.0$) need not have optimal values for other traits, such as resource acquisition potential.

In contrast to our third hypothesis, simulated drought treatment had essentially no effect on drought tolerance traits, although there were clear negative effects of drought on microbial biomass and decomposition rate. This result can potentially be explained by strong seasonal variation in moisture availability. Microbial taxa in DEMENT, and in the field, experience intense drought every summer season. Seasonality explains the majority of variation in microbial community composition at Loma Ridge (Matulich et al., 2015), and seasonal shifts in drought tolerance and enzyme investment are evident in DEMENT. Together these patterns suggest that drought treatment (40–50% reduction in annual precipitation) is a much weaker selective force on microbial communities than seasonal drought (Matulich et al., 2015). Microbial taxa that can survive the seasonal drought are probably pre-adapted to survive experimental drought, especially given the high degree of inter-annual precipitation variation in this system (Parolari et al., 2015).

Consistent with hypothesis 4, increasing the sensitivity of microbial death rate to desiccation resulted in stronger selection for drought tolerance across cost scenarios. This result provides insight into the level of CUE cost that microbes might tolerate under different conditions. Reducing the baseline death rate while increasing the desiccation sensitivity of mortality effectively increased the survival benefit of the drought tolerance trait by a factor of two. This benefit can be expressed as the change in death rate for an increment in drought tolerance, or the derivative of Eq. (1) with respect to α, which equals $\tau_B \beta \Psi$. This value is two-fold greater under the high-sensitivity scenario, explaining why more sensitive communities tolerated nearly two-fold greater costs for the same level of drought tolerance (Fig. 3).

4.1. Conclusions

This modeling exercise shows how tradeoffs in microbial traits might affect ecosystem processes such as respiration and litter decomposition. Although the true costs of drought tolerance are uncertain, the DEMENT model predicts that moderate to high CUE costs severely constrain drought tolerance within the microbial community. Surprisingly, at low—even zero—costs, increasing drought tolerance may not help maintain decomposition rates under dry conditions. Although DEMENT predicts increased survival and greater biomass in microbial communities with traits conferring drought tolerance, microbial interactions in the model reduce enzyme investment, effectively canceling out any biomass-driven impacts on decomposition. These feedbacks suggest a potential mechanism for sustaining carbon storage in surface litter under drought. Future empirical studies of drought tolerance mechanisms, physiological tradeoffs, and community consequences would be useful for validating and generalizing DEMENT model predictions.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2017.01.001.

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