

Pulse frequency and soil-litter mixing alter the control of cumulative precipitation over litter decomposition

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Abstract. Macroclimate has traditionally been considered the predominant driver of litter decomposition. However, in drylands, cumulative monthly or annual precipitation typically fails to predict decomposition. In these systems, the windows of opportunity for decomposer activity may rather depend on the precipitation frequency and local factors affecting litter desiccation, such as soil-litter mixing. We used a full-factorial microcosm experiment to disentangle the relative importance of cumulative precipitation, pulse frequency, and soil-litter mixing on litter decomposition. Decomposition, measured as litter carbon loss, saturated with increasing cumulative precipitation when pulses were large and infrequent, suggesting that litter moisture no longer increased and/or microbial activity was no longer limited by water availability above a certain pulse size. More frequent precipitation pulses led to increased decomposition at high levels of cumulative precipitation. Soil-litter mixing consistently increased decomposition, with greatest relative increase (+194%) under the driest conditions. Collectively, our results highlight the need to consider precipitation at finer temporal scale and incorporate soil-litter mixing as key driver of decomposition in drylands.

Key words: arid ecosystem; carbon cycle; Chihuahuan Desert; global change; litter moisture; precipitation regime; water pulses.

INTRODUCTION

Macroclimate has traditionally been considered as the predominant control over decomposition rates (Meentemeyer 1978) and decomposition models based on climate parameters at coarse spatial and temporal scales have generally successfully predicted decomposition in mesic systems. In drylands, however, decomposition models often fail to predict litter decomposition rates (Parton et al. 2007, Adair et al. 2008). Given that drylands cover 45% of the global land area (Pravělie 2016) and play a dominant role on the trend and variability of terrestrial CO₂ uptake (Ahlström et al. 2015), this model-measurement disconnect limits successful prediction of regional-to-global scale biogeochemical cycling. This disconnect led to an important question in dryland ecology: how important is precipitation (PPT) in controlling litter decomposition? Addressing this question, Austin (2011) synthesized data from eight dryland studies and found a striking lack of relationship between cumulative PPT and decomposition rates, leading to the

conclusion that alternative abiotic factors, such as photodegradation, are primary dryland decomposition drivers. Yet, while some individual field studies assessing PPT influence on decomposition also reported no response (Vanderbilt et al. 2008, Gallo et al. 2009), other studies found positive responses (Yahdjian et al. 2006, Brandt et al. 2007), indicating that PPT cannot be dismissed. These contrasting results may be due to the fact that cumulative PPT, typically defined at monthly or annual time scales, fails to reflect the moisture of surface litter and shallow soil and associated decomposer activity. While this disconnect is likely to occur to some extent in all ecosystems, it may be particularly important in drylands due to temperature extremes, localized episodic PPT events, and high spatial heterogeneity of plant cover that causes microclimate variability.

Cumulative PPT may not correlate with decomposition if increasing pulse size does not linearly increase decomposer activity. Indeed, there may be a pulse size threshold above which decomposition rates saturate because litter water-holding capacity and/or decomposer activity are no longer limited by water availability. Such a threshold was documented by Sponseller (2007), who reported that soil microbial respiration saturated at a moderate pulse size. Therefore, when pulse size decreases

but the number of PPT events remain the same, as is typical for rainout shelter studies, there may be no relationship between cumulative PPT and decomposition if the decrease in pulse size does not reduce litter moisture and/or decomposer activity. Instead, compared to cumulative PPT, the frequency of PPT events may play a more important role. Indeed, a 25-mm per month PPT increase in the Chihuahuan Desert increased litter mass loss when added as small weekly pulses, but not when added in larger monthly pulses (Whitford et al. 1986). These more frequent but smaller pulses may have extended the amount of time that litter had sufficient moisture for decomposer activity, while bigger and less frequent pulses may not have increased moisture and decomposer activity. In contrast, Austin et al. (2009) found similar rates of surface litter decomposition in the Patagonian steppe when litter received one 10-mm pulse per week or three 3.3-mm pulses per week. These conflicting results suggest that the effect of PPT frequency depends on the changes in pulse size. The 10-mm addition in Austin et al. (2009) may have been as efficient at triggering decomposer activity as the multiple small, frequent pulses. In contrast, the 25-mm pulse in Whitford et al. (1986) may have exceeded the threshold above which litter moisture and/or decomposer activity saturates, leading this large pulse to be less efficient than the smaller frequent pulses at triggering decomposer activity. Despite these hints that pulse size and frequency may alter cumulative PPT controls on decomposition, the relative importance and interaction remain largely unexplored, limiting our ability to predict the consequences of expected PPT regime changes on decomposition.

A notable characteristic of drylands is the high spatial heterogeneity of plant cover and large areas of bare ground, typically leading to high rates of soil erosion. Soil erosion and subsequent deposition can mix decomposing litter with soil ("soil-litter mixing"), accelerating decomposition (Throop and Archer 2007, Hewins et al. 2013). Soil-litter mixing (SLM) may buffer decomposers from high temperature and desiccation, thereby expanding the windows of opportunity for decomposer activity following PPT events (Barnes et al. 2015). This idea is supported by increased soil-litter mixing effects under oscillating moisture conditions compared to constant moisture conditions in a laboratory study (Lee et al. 2014), but has not been specifically tested so far.

In this study, we aimed to disentangle the relative importance of (1) cumulative PPT, (2) pulse frequency, and (3) SLM on litter microbial decomposition. We hypothesized that (H1) decomposition, measured as litter carbon (C) loss, is positively related to cumulative PPT until a threshold, due to potential saturation of microbial activity and/or litter moisture, (H2) greater pulse frequency enhances decomposition, by potentially extending windows of opportunity for microbial activity, and (H3) soil-litter mixing hastens decomposition, particularly when pulses are small and infrequent, by potentially buffering litter from desiccation. We tested these

hypothesized outcomes by measuring C loss of honey mesquite (*Prosopis glandulosa*) shrub leaf litter in a semi-controlled environment based on Chihuahuan Desert temperature and precipitation conditions. Litter was decomposed in glass jar microcosms, either on the soil surface or mixed with soil. Precipitation pulses were added as factorial combinations of four cumulative PPT levels and four pulse frequencies, simulating a wide range of possible summer monsoon moisture regimes in the Chihuahuan Desert, where there is high variability in cumulative PPT, pulse size, and pulse frequency.

METHODS

We collected soil and litter at the Jornada Basin Long Term Ecological Research site (32°33'31" N, 106°46'29" W; 1188 m a.s.l.) in the northern Chihuahuan Desert, northeast of Las Cruces, New Mexico, USA. This site is characterized by a mean annual PPT of 240 mm (1928–2008), 60% of which occurs as localized monsoonal thunderstorms from July through September (Drewa et al. 2006), and a mean annual temperature of 14.7°C. The site is located on a level upland with coarse-textured, well-drained, sandy loam soils (Typic Paleorthids: pH = 7.3, 0.28 g H₂O g⁻¹ soil water holding capacity, 4.4 mg C g⁻¹ soil, 0.3 mg N g⁻¹ soil). In May 2014, surface soil (top 5 cm) was collected from intercanopy areas, air-dried at 30°C, and passed through a 2 mm sieve. Near-senescent honey mesquite (*Prosopis glandulosa* Torr.) leaf litter was collected in November 2013 (C:N = 15.3, 8.7% ash, 1.56 g H₂O g⁻¹ litter water-holding capacity). This species was selected as it is the dominant shrub and because its litter typically decomposes on or within the soil following leaf drop. Rachises and damaged leaflets were removed. Intact leaflets were air-dried at 30°C and homogenized.

In a full-factorial experiment we manipulated cumulative PPT, pulse frequency, and SLM in 473 mL glass jar microcosms. Cumulative PPT treatments were 30, 60, 90, and 120 mm month⁻¹, spanning a range of possible monthly summer PPT at the site (Drewa et al. 2006). Frequency was manipulated by adding 1/30 of the cumulative PPT every day, 2/30 every 2 d, 3/30 every 3 d, or 4/30 every 4 d (Fig. 1). Precipitation was added as a volume equivalent based on the 30 cm² microcosm surface area. For the SLM treatments, litter was either placed on top of the soil or dispersed throughout the soil such that it was in full contact with soil, replicating common SLM conditions in the Chihuahuan Desert (Hewins and Throop 2016). There were four replicates of each of the 32 treatment combinations ($N = 4$ cumulative PPT levels \times 4 pulse frequencies \times 2 SLM treatments \times 4 replicates per treatment combination = 128 microcosms). Microcosms were filled with 100 g of soil and 2 g of leaf litter. A wet-dry conversion factor for initial litter mass was obtained by weighing initial litter subsamples, drying them at 60°C for 48 h, and reweighing to obtain dry mass. To mimic natural temperature and humidity and

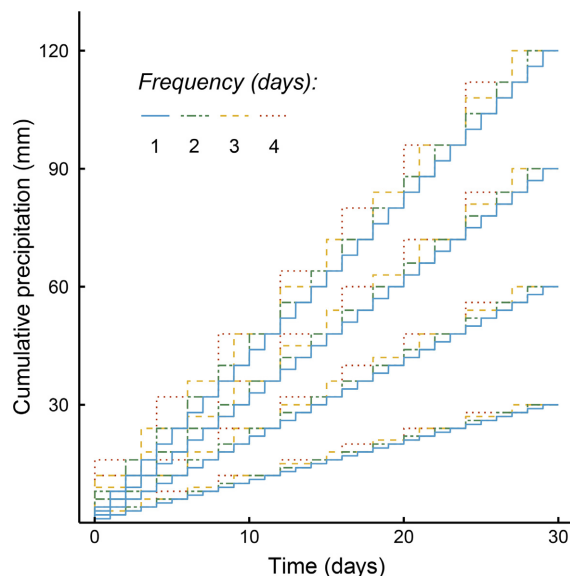


FIG. 1. Simulated precipitation (PPT) patterns throughout the incubation for the different treatments differing in cumulative PPT amounts (30, 60, 90 and 120 mm) and pulse frequency (1/30 of cumulative PPT every day, 2/30 every 2 d, 3/30 every 3 d, or 4/30 every 4 d). [Color figure can be viewed at wileyonlinelibrary.com]

allow soil and litter dry down cycles while still controlling PPT, microcosms were incubated uncovered in a glasshouse ca. 40 km away from the field collection site. Roof and wall vents were open to maintain close-to-ambient humidity conditions. The glasshouse structure and microcosm walls are assumed to have blocked much of the ambient UV. Because the glasshouse temperature could rise significantly above ambient temperature, coolers were turned on when the temperature rose above 35°C. Pulse treatments were applied by carefully adding deionized water with a pipette to the soil/litter surface, ensuring that the water addition did not cause movement. Microcosms were incubated for 30 d, based on prior field and lab studies indicating the potential for substantial mass loss during this time period (Hewins et al. 2013, Lee et al. 2014). Microcosms were dried at 60°C at the end of the incubation. Litter was separated from the soil with a 1 mm sieve, brushed carefully to remove adhering soil, and weighed. Decomposed litter as well as ten samples of undecomposed litter were ground into homogeneous powder using a ball mill (8000D, Spex CertiPrep, Metuchen, NJ, USA). Subsamples (~5 mg) were analyzed for C concentration using an elemental analyzer (ECS 4010, Costech Analytical Technologies, Inc., Valencia, CA, USA). Decomposition was expressed as the percentage of C lost from the litter during the incubation: $\%C \text{ loss} = (M_i \times C_i - M_f \times C_f) / (M_i \times C_i) \times 100$, where M_i and M_f are the initial and final 60°C dry mass, respectively, and C_i and C_f are the initial and final litter C concentration (% of litter dry mass), respectively.

To compare the hypothesized roles of (H1) cumulative PPT and (H2) pulse frequency on C loss, we performed separate two-way ANOVAs on data subsets for surface and soil-mixed litter. In these data subsets, additional one-way ANOVAs were performed for each pulse frequency and PPT level. Tukey HSD post hoc mean comparisons identified among-treatment differences. To test our hypothesis (H3) that SLM hastens decomposition, particularly when pulses are small and infrequent, we quantified the relative SLM effect across PPT treatments as the relative difference in C loss between soil-mixed and surface litter $[(\% \text{ C loss of soil-mixed litter} - \% \text{ C loss of surface litter}) / \% \text{ C loss of surface litter} \times 100]$. We performed a two-way ANOVA to determine how cumulative PPT and pulse frequency affected the relative SLM effects. For all ANOVAs, R^2 values were computed for each term by dividing the sum of squares by the total sum of squares. Carbon loss data were logit-transformed prior to analysis to ensure normal distribution and homoscedasticity of residuals. All statistical analyses were performed using R version 3.3.1 (R Core Team 2016).

RESULTS

Across all PPT treatments, C loss was lower for surface litter (28.4%) than for soil-mixed litter (46.7%) after the 1-month incubation. For surface litter, C loss increased linearly with increasing cumulative PPT for one- and two-day pulse frequencies (Fig. 2a). Patterns were quite different for the three and 4-d pulse frequencies, with C loss saturating at 90 and 60 mm, respectively, such that it did not increase at greater cumulative PPT (Fig. 2a; Table 1). Consequently, for the highest cumulative PPT treatment (120 mm), C loss was slightly higher when pulses were frequent (Fig. 2a, Table 1). Altogether, cumulative PPT was the dominant factor influencing surface litter C loss, explaining 87.2% of variance. In contrast, pulse frequency explained a limited amount of variance (1.5%), while its interaction with cumulative PPT explained 7.1% of variance (Table 2).

Carbon loss in soil-mixed litter was less responsive to cumulative PPT than in surface litter. Carbon loss saturated in response to cumulative PPT for all pulse frequency treatments. This saturation occurred at lower cumulative PPT levels for less frequent pulses (90 mm for 1-d pulse frequency and 60 mm for two- and 3-d pulse frequencies). Carbon loss appeared to saturate at 30 mm cumulative PPT for the 4-d pulse frequency, although there was some fluctuation in C loss with increasing cumulative PPT (Fig. 2b; Table 1). In addition, C loss saturated at lower values for the less frequent pulses. Consequently, C loss was lower for high cumulative PPT with less frequent pulse frequency, ranging from 59.3% C loss for 1-d pulses to 46.9% C loss for 4-d pulses with 120 mm cumulative PPT (Fig. 2b). In contrast, at low cumulative PPT (30 mm), C loss was

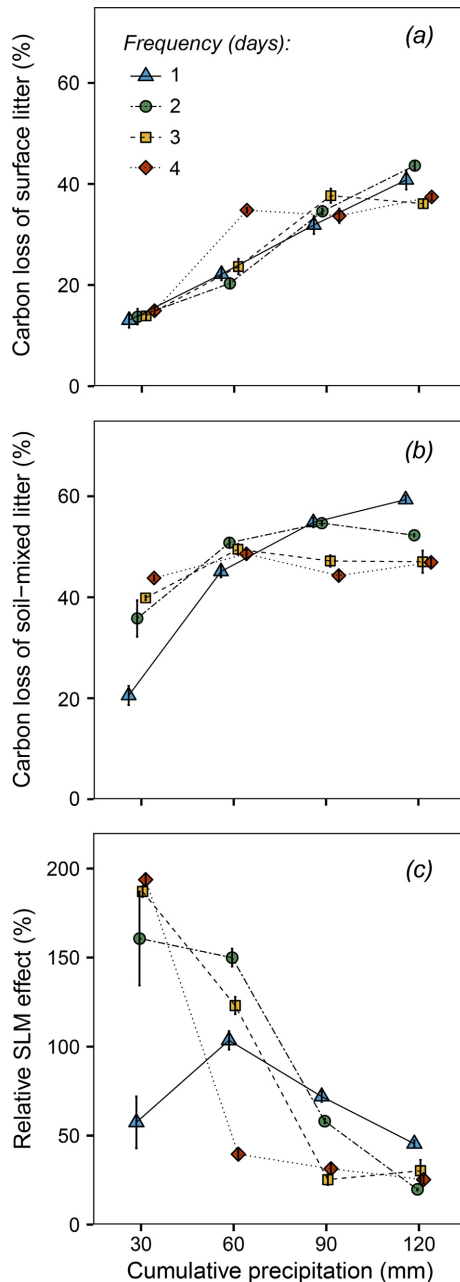


FIG. 2. Percentage of carbon (C) loss in leaf litter decomposing on the soil surface (a) and mixed within soil (b), and (c) relative soil-litter mixing (SLM) effect, i.e. the relative difference in C loss between soil-mixed litter and surface litter (calculated as $[(\% \text{ C loss of soil-mixed litter} - \% \text{ C loss of surface litter}) / \% \text{ C loss of surface litter}] \times 100$), after 30 d of incubation (mean \pm SE, $n = 4$) for different cumulative PPT amounts (30, 60, 90 and 120 mm) added at different pulse frequencies (every 1, 2, 3 and 4 d). Symbols indicate the pulse frequency at which the water was added. X-axis values are jiggered for clarity. Statistical differences among treatment groups are presented in Table 1.

TABLE 1. Statistical significance of differences in litter C loss among (a) cumulative PPT for a given pulse frequency and (b) pulse frequencies for a given cumulative PPT.

	Cumulative PPT (mm)							
	Surface litter				Soil-mixed litter			
Frequency	30	60	90	120	30	60	90	120
(a) Cumulative PPT								
1 d	a	b	c	d	a	b	c	c
2 d	a	b	c	d	a	b	b	b
3 d	a	b	c	c	a	b	b	b
4 d	a	b	b	b	a	b	a	ab
(b) Pulse frequency								
1 d	a	a	a	a	a	a	a	a
2 d	a	a	a	ab	b	b	a	b
3 d	a	a	a	b	b	ab	b	c
4 d	a	b	a	b	b	ab	b	c

Notes: Surface litter and soil-mixed litter are displayed separately. Different letters within (a) a row or (b) a column indicate significant differences in C loss among treatments (Tukey HSD tests). Treatment means and standard error are presented in Fig. 2.

much higher for infrequent pulse treatments, ranging from 43.8% C loss for 4-d pulses to 20.5% C loss for 1-d. Altogether, cumulative PPT was the dominant factor influencing C loss of soil-mixed litter, but cumulative PPT explained a much smaller amount of the variance (49.7%) than for surface litter (87.2%; Table 2). While pulse frequency had a limited effect on C loss (explaining 1.7% of total variance), its interaction with cumulative PPT explained 40.7% of total variance in C loss. This interaction indicates that the effect of pulse frequency on soil-mixed litter decomposition depended on cumulative PPT.

The relative SLM effect, i.e. the relative difference in C loss between soil-mixed and surface litter, was consistently positive but varied among PPT treatments (Fig. 2c). On average, the relative SLM effect decreased with increasing cumulative PPT ($F_{3,47} = 202.7$; $P < 0.001$), from +141% for the 30 mm treatments to +30% for the 120 mm treatments. Cumulative PPT was the dominant factor, explaining 64.4% of variance. In contrast, pulse frequency only had a limited, yet significant effect ($F_{3,47} = 9.2$; $P < 0.001$) explaining 2.9% of variance, but its interaction with cumulative PPT explained 27.7% of variance ($F_{9,47} = 29.1$; $P < 0.001$). In particular, at the lowest cumulative PPT treatments, the relative SLM effect was higher for infrequent than for frequent pulse treatments (+194% and +57%, respectively). With increasing cumulative PPT, the relative SLM effect decreased, particularly with infrequent pulses. At the highest cumulative PPT, differences in relative SLM effect among pulse frequency treatments were small, varying from +20% for 2-d pulses to +45% for 1-d pulses.

TABLE 2. Results of two-way ANOVAS testing the main effects of (i) cumulative precipitation (PPT) and (ii) pulse frequency and their interaction on the percentage of C loss after 30 d of incubation.

Factor	Surface litter (No SLM)				Soil-mixed litter (SLM)			
	df	%SS	F value	P value	df	%SS	F value	P value
Cumulative PPT	3	87.2	317.5	<0.001	3	49.7	98.2	<0.001
Frequency	3	1.5	5.4	<0.01	3	1.7	3.3	<0.05
Cumulative PPT × Frequency	9	7.1	8.7	<0.001	9	40.7	26.8	<0.001
Residuals	46	4.2	-	-	47	7.9	-	-

Notes: Separate ANOVAS were run for surface litter (no SLM, $n = 62$) and soil-mixed litter (SLM, $n = 63$). Variance associated with main effects and their interaction is expressed in percentage sums of squares (%SS).

DISCUSSION

The positive relationship between cumulative PPT and decomposition (defined as litter C loss) for surface litter, explaining 87.2% of the variance, supports the view that the quantity of PPT can be a predominant control of litter decomposition. This result contrasts with previous studies reporting no relationship between cumulative PPT and decomposition (Vanderbilt et al. 2008, Gallo et al. 2009, Austin 2011). However, this relationship was only linear when PPT was added as small and frequent pulses. When added as larger and less frequent pulses, decomposition reached a threshold at intermediate levels of cumulative PPT and did not increase with greater cumulative PPT (Fig. 2a, Table 1). This saturation supports our first hypothesis that decomposition is positively related to cumulative PPT until a threshold, particularly when pulses are infrequent. Similar thresholds were reported for soil microbial respiration (Sponseller 2007), suggesting saturation of soil moisture and/or microbial activity. Regardless of the underlying mechanisms, these saturation thresholds may explain why cumulative PPT typically fails to predict decomposition in drylands. This highlights the need to consider climatic variables at finer temporal scales than the monthly or, more commonly, annual time scales typically used.

In support of our second hypothesis, more frequent pulses enhanced decomposition, particularly at high cumulative PPT. This interaction between pulse frequency and cumulative PPT may explain the conflicting results reported by Whitford et al. (1986) and Austin et al. (2009) who found increased and unchanged decomposition rates when PPT was added as smaller but more frequent pulses, respectively. In fact, in our study the interaction between pulse frequency and cumulative PPT was more important for soil-mixed litter than surface litter, for which it explained 40.7% of decomposition variance. For soil-mixed litter, low decomposition rates at the lowest cumulative PPT for the small and frequent pulse treatments may indicate that smaller pulses did not penetrate the entire litter pool. Consequently, the deeper litter layers may not receive enough moisture to activate microbial activity, as suggested by Jacobson and Jacobson (1998), who found no decomposition of buried cellulose for <9 mm pulses in the Namib Desert. This pattern

of high decomposition for large, infrequent pulses was also reported by Austin et al. (2009) on buried litter. However, in light of our study this pattern might be specific to low levels of cumulative PPT and even reversed at higher levels. This suggests that when pulses are sufficiently large to penetrate the entire litter pool, smaller and more frequent pulses are more efficient at promoting microbial activity than the larger infrequent pulses, as observed in our study. Collectively, our results indicate that smaller and more frequent pulses are more efficient at promoting microbial activity than less frequent and larger pulses, above a certain pulse size threshold. This lower efficiency of larger and less frequent pulses may be due to the saturation of litter water-holding capacity and/or microbial activity. To validate this conjecture, further studies should specifically assess the responses of litter moisture and consequent microbial decomposition to varying pulse sizes and frequencies.

Soil-litter mixing consistently accelerated litter decomposition, consistent with previous studies (Throop and Archer 2007, Hewins et al. 2013, Lee et al. 2014), and particularly, with stronger effects at low cumulative PPT and when pulses were infrequent (Fig. 2c), consistent with our third hypothesis. This observed relationship between SLM and PPT is in line with results from a pan-tropical study where decomposition was enhanced by litter burial at the driest sites and depressed by burial only when MAP was above 3000 mm (Powers et al. 2009). This supports the idea that SLM enhances decomposition by extending periods of moisture availability for microbial activity following rainfall events (Barnes et al. 2015). The strong effect of SLM, increasing decomposition by 20 to 194% depending on the PPT treatments, highlights the need to consider this factor in decomposition studies. Soil infiltration is not unique to drylands and studies in mesic systems also commonly correct for soil contamination. SLM may then enhance decomposition beyond drylands, particularly during dry seasons as suggested by our results.

Collectively, our results indicate that for a given monthly cumulative PPT, a parameter commonly used in biogeochemical models, litter decomposition can vary depending on pulse frequency, and this variability is particularly high when litter is mixed with soil. Although cumulative PPT was still the main driver of C loss in our

study, such results highlight the need to consider PPT characteristics with greater nuance, assessing variables such as PPT pulse size and frequency that may strongly affect the duration that litter is within the moisture range appropriate for decomposer activity. Inclusion of local factors that may alter the effect of moisture pulses on decomposition, such as SLM and factors that affect litter dry down, is also key to refining our understanding of climatic control on litter decomposition and improving predictive capability with modelling. To this end, the effects of pulse size and frequency, SLM, and their interactions should be further tested under field conditions with different litter species and over longer time scales. Additionally, SLM and PPT at small temporal scales may also be relevant in more mesic systems. Indeed, it has been recently pointed out that the regulatory role of climate on decomposition may have been falsely inflated in broad-scale experiments by averaging local-scale variability, thereby undermining the importance of local factors (Bradford et al. 2016). Considering these local factors is essential to move forward on accurately predicting C cycles, particularly in the context of climate change that not only affects cumulative PPT, but also the size and frequency of PPT events.

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