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Drought Effects on Pine Litter Decomposition and Metal Nutrient Release Are Moderated by Mixed Understory Vegetation Litter

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ABSTRACT: Understory vegetation-mediated forest litter decomposition and nutrient release processes are critical for biogeochemical cycles and ecosystem sustainability. Drought-dominated global change significantly affects relevant processes, but its impact on metal element release from mixed litters of overstory trees and understory vegetation remains unclear. Here, we conducted an 18-month *in situ* decomposition experiment in a *Pinus massoniana*–*Camellia oleifera* mixed forest under three precipitation regimes: control (CK), low-intensity reduction (R30), and high-intensity reduction (R60). Both R30 and R60 treatments significantly inhibited *P. massoniana* litter mass loss by 4.85% and 6.22%, respectively. Only R60 treatment significantly reduced the mass loss in *C. oleifera* and mixed litters. The release of K and Mg from *P. massoniana* litter was suppressed by R30 and R60 treatments, and only R60 treatment significantly impeded K and Mg release from the mixed litter. Furthermore, R60 treatment significantly reduced Ca release from *C. oleifera* litter and Mn release from both single-species litters. These results suggest that mixed understory litter may partially alleviate the inhibitory effects of moderate drought on litter decomposition and metal nutrient release. These findings provide new insights for understanding understory vegetation-mediated forest litter decomposition processes under ongoing climate change.

KEYWORDS: Reduced precipitation; litter decomposition; element release; metal nutrient cycling; *Pinus massoniana*; *Camellia oleifera*

1 Introduction

Metal elements are essential nutrients underpinning plant growth [1,2], playing crucial roles in cell wall stabilization, protein synthesis, water relations, and other key physiological processes [3,4]. In forest ecosystems, they are largely recycled through litter decomposition [5]. However, accumulating evidence shows that drought associated with reduced precipitation can substantially alter litter decomposition and the release of major nutrients such as nitrogen (N) and phosphorus (P), with important implications for biogeochemical cycling under global change [3,6,7]. Yet, the response of metal element release to drought may differ fundamentally from that of N and P because metals are governed by distinct controls, including stronger dependence on complexation and chelation and more closed cycling within forest ecosystems [8].

Despite these potentially contrasting mechanisms, the empirical understanding of how drought regulates metal element release from litter is poorly understood. Given the recycling-dominated pathways of metal elements in forest ecosystems, overlooking their responses may introduce substantial uncertainty into predictions of soil nutrient availability and forest productivity under future climate change [9,10]. Therefore, elucidating how reduced precipitation influences metal element release from decomposing litter is critical for advancing mechanistic understanding of forest biogeochemical cycling.

Litter decomposition is governed by the interplay of abiotic and biotic factors, including climate, litter quality, and decomposer communities [6,11–13]. Reduced precipitation can disrupt metal nutrient release through two primary mechanisms: (1) by directly limiting the physical leaching of soluble ions, and (2) by indirectly suppressing biological mineralization through moisture stress on soil microbial and faunal decomposers [8,14]. Therefore, the effect of reduced precipitation on metal nutrient release rates depends on its biogeochemical dynamics. For instance, the release of highly soluble K is predominantly driven by leaching, making it acutely vulnerable to reduced precipitation [15]. In contrast, Ca, which is often structurally bound in cell walls (e.g., as calcium pectate), is released via microbial decomposition, potentially leading to its relative accumulation under reduced precipitation [16,17]. The release of Mg and Mn involves both leaching and biological processes, making their response to reduced precipitation more unpredictable [7,18,19]. Nonetheless, previous studies have shown that the response of litter metal nutrient (e.g., iron and sodium) release to reduced precipitation varies significantly across ecosystems [20,21]. However, the extent to which reduced precipitation affects the release of K, Ca, Mg, and Mn from litter is still unclear.

Understory vegetation biodiversity can significantly enhance ecosystem stability through compensatory effects and niche complementarity [22]. This principle extends to litter decomposition, where mixtures of different species often decompose at non-additive rates, differing from predictions based on single-species litter [13,23,24]. Under drought conditions, mixed overstory trees and understory vegetation litter can mitigate moisture stress through several mechanisms. For instance, litter layers with varied structural traits can improve water retention and create more favorable microhabitats for decomposers [6,25]. Furthermore, the diverse chemical composition in mixtures can provide complementary resources for microbial communities, supporting a more robust and functionally diverse decomposer consortium that is better able to maintain activity during dry periods [13,23]. These mechanisms may differentially influence drought-induced constraints on measurable decomposition and nutrient release processes. Microclimatic buffering may help sustain mass loss and associated soil moisture conditions that regulate the leaching-driven release of soluble elements (e.g., K). However, resource complementarity may support microbial-mediated processes associated with decomposition rates and the release of structurally bound elements (e.g., Ca and Mg), potentially contributing to more stable decomposition and nutrient release patterns [8]. Consequently, a growing body of evidence suggests that mixed-species litter systems exhibit greater resistance to the negative impacts of drought compared to monospecific litter [26,27]. Recent research results have highlighted that mixed overstory trees and understory vegetation litter decomposition is more resistant to the negative effects of reduced precipitation than that of single-species litter [7,22,24]. However, this compelling narrative has been built almost exclusively on evidence of litter mass loss and decomposition rate [7,24]. The extent to which this stabilizing effect observed in mixed forests translates to the release of metal nutrients remains underexplored. Specifically, it remains unclear whether the physical buffering and biological synergies arising from the presence of understory vegetation litter can mitigate the negative impact of drought on the nutrient release (K, Ca, Mg, and Mn) from the decomposed overstory litter within these mixtures.

Pinus massoniana is a cornerstone and widely planted native coniferous species for afforestation in the subtropical regions of southern China [28,29]. However, long-term monocultures often face challenges of soil degradation and nutrient depletion (e.g., K, Mg, and Mn), partly due to the slow decomposition of pine litter [30,31]. Recent studies have found that *Camellia oleifera* often grows in the understory of *P. massoniana* plantations, forming a mixed forest [32]. Although the effects of drought on N and P release from *P. massoniana* litter have been investigated [33,34], the responses of key metal nutrients remain poorly understood. Moreover, previous studies have shown that understory *C. oleifera* mixed with *P. massoniana* can enhance soil nutrient availability and accelerate biogeochemical cycling [35,36]. However, the potential role of *C. oleifera* litter in moderating drought-induced changes in metal nutrient release from litter remains unclear. To address these knowledge gaps, we conducted an 18-month *in situ* decomposition experiment in a *P. massoniana*–*C. oleifera* mixed forest under three precipitation regimes: control (CK), low-intensity reduction (R30), and high-intensity reduction (R60). This study aims to quantify whether and how mixed understory *C. oleifera* litter mitigated drought effects on the decomposition and K, Ca, Mg, and Mn release in *P. massoniana* forests. We also aim to elucidate metal nutrient cycling in managed *P. massoniana* and *C. oleifera* forests to inform silvicultural strategies under climate change. We test the following hypotheses: (1) Reduced precipitation inhibits litter decomposition and decreases the release of K, Ca, Mg, and Mn from litter; (2) Mixed litter mitigates drought-induced constraints on decomposition and nutrient release processes, reflected in higher mass loss and nutrient release rate compared with single pine litter. Our results suggest that promoting multi-storied forest structures and retaining understory litter are effective management strategies for sustaining soil fertility and buffering the negative impacts of drought.

2 Materials and Methods

2.1 Study Site

This experiment is based at the National Long-term Research Base for *Pinus massoniana*, Guiyang City (106°43' E, 26°43' N). The study site is situated at an elevation of approximately 1300 m and features a subtropical plateau climate with an average annual precipitation of about 1200 mm and an average temperature of 13.5°C. The average height of *P. massoniana* is approximately 21 m, the average diameter at breast height (DBH) is 35 cm, the forest canopy density is approximately 0.7, and the forest age is approximately 60 years in the study plots. The dominant understory shrub is *C. oleifera*, with an average height of approximately 2.5 m and a coverage of approximately 50%. The soil is classified as yellow soil, with a pH of 4.5, a soil depth of approximately 1.2 m, a soil moisture content of 25.1%, TP of 0.85 g/kg, TN of 6.8 g/kg, and soil organic carbon (SOC) of 26.14 g/kg.

2.2 Experimental Design

In October 2021, nine 10 m × 10 m plots were established under the studied mixed forest of *P. massoniana* and *C. oleifera*. An 18-month field decomposition experiment was conducted. The control (CK), low-intensity reduced precipitation (R30), and high-intensity reduced precipitation (R60) treatments were randomly deployed to these plots, with three replicates for each treatment (Fig. A1A). In the R30 and R60 plots, transparent PVC drainage troughs covered 30% and 60% of the study area, respectively (Fig. A1B). Collected rainwater was diverted outside the plots through PVC drainage pipes (Fig. A1B,C). The PVC material had a light transmittance of 85.2%. Additionally, PVC plastic boards were buried 60 cm deep in the soil surrounding the plots to prevent runoff and infiltration (Fig. A1C).

At the end of November 2021, freshly fallen leaf litter from *P. massoniana* and *C. oleifera* was collected from the plots, then air-dried and oven-dried at 60°C until a constant weight was reached. The dried leaves

were weighed and packed into litterbags (15 cm × 20 cm with a mesh size of 0.05 mm) in the following combinations: (1) 10 g of *P. massoniana* and 0 g of *C. oleifera*, representing *P. massoniana* single-species leaf litter; (2) 5 g of *P. massoniana* and 5 g of *C. oleifera*, representing the mixed leaf litter; (3) and 0 g of *P. massoniana* and 10 g of *C. oleifera*, representing *C. oleifera* single-species leaf litter. Ten litterbags of each leaf litter type were collected to determine the initial contents of C, N, P, lignin, cellulose, and metal elements (Table 1). Then, the prepared litterbags were distributed on the surface of each study plot in January 2022 (Fig. A1D). At each sampling, soil temperature and moisture were measured within each plot to obtain dynamic data. Significant variations in both parameters were observed under different levels of reduced precipitation, reflecting the dynamic environmental conditions throughout the decomposition period. In addition, soil samples were collected to determine soil pH, SOC, and TN, and precipitation treatments had no significant effects on these variables.

Table 1: Initial properties of different types of litter.

Initial Properties	<i>P. massoniana</i>	<i>C. oleifera</i>	Mixed
C (g/kg)	496.94 ± 8.85a	420.15 ± 8.31c	468.55 ± 4.95b
N (g/kg)	9.47 ± 0.51a	6.47 ± 0.19b	8.45 ± 0.58a
P (g/kg)	1.11 ± 0.02a	0.67 ± 0.02c	0.88 ± 0.19b
Lignin (mg/g)	162.36 ± 0.55a	131.01 ± 4.42c	150.22 ± 3.33b
Cellulose (mg/g)	138.39 ± 2.96a	118.46 ± 8.03b	130.95 ± 5.11ab
K (g/kg)	4.23 ± 0.25a	2.83 ± 0.06c	3.57 ± 0.21b
Ca (g/kg)	6.39 ± 0.70b	8.62 ± 0.47a	7.69 ± 0.71a
Mg (g/kg)	3.25 ± 0.21b	3.98 ± 0.33a	3.62 ± 0.21ab
Mn (g/kg)	0.38 ± 0.05c	1.24 ± 0.10a	0.85 ± 0.04b

Note: Data in the table are mean ± standard deviation; different lowercase letters indicate significant differences among different types of litter ($p < 0.05$).

2.3 Litter Sampling and Analyses

Litter samples were collected every three months since the beginning of the 18-month field decomposition experiment, namely April, July, and October 2022, as well as January, April, and July 2023. During each sampling event, three bags of each type of decomposing litter were randomly selected from each plot and then brought back to the laboratory. The litter samples were cleaned to remove soil, roots, and other impurities, then dried at 60°C until a constant weight was achieved. The drying method was used to determine the dry weight and moisture content of litter and calculate the litter mass loss. The dried samples were then ground through a 1 mm mesh sieve to determine the metal element content using atomic absorption spectroscopy.

2.4 Statistical Analyses

Litter mass loss rate (M) was calculated by Eq. (1) [37]:

$$M(\%) = [1 - (M_t/M_0)] \times 100$$

Metal elements release rate (R) was calculated by the Eq. (2) [37]:

$$R(\%) = [1 - (W_t X_t)/(W_0 X_0)] \times 100$$

where W_t is the dry mass (g) of the litter at period t of decomposition; W_0 is the initial litter dry mass (g); X_t is the concentration of the metal elements of the litter at period t of decomposition (g/kg); and X_0 is the initial concentration of the metal elements of the litter (g/kg).

The Shapiro-Wilk test and Levene's test were first applied to assess the normality of residuals and homogeneity of variance, respectively. Linear mixed-effects models (LMMs) were employed to evaluate the effects of reduced precipitation, litter type, decomposition time, and their interactions on litter mass loss, metal concentrations, and release rates. Within these models, reduced precipitation, litter type, and decomposition time were used as the fixed factors, and plot was included as a random factor. Post-hoc comparisons among treatments were conducted using Bonferroni-adjusted p -values to maintain a family-wise significance level of $\alpha = 0.05$. Additionally, linear regression models were used to determine the relationship between metal release rates and mass loss rates. All statistical analyses were conducted using SPSS version 29.0.

3 Results

3.1 Effect of Reduced Precipitation on Soil Properties

During the 18-month litter decomposition period, reduced precipitation had no significant effect on soil temperature (Fig. 1A), indicating a limited effect on soil thermal conditions. In contrast, soil moisture declined significantly with increasing precipitation reduction intensity and generally followed the pattern CK > R30 > R60 (Fig. 1B), except in March when no significant difference was observed between CK and R30. These findings suggest that reduced precipitation primarily altered soil water availability while exerting minimal influence on soil temperature.

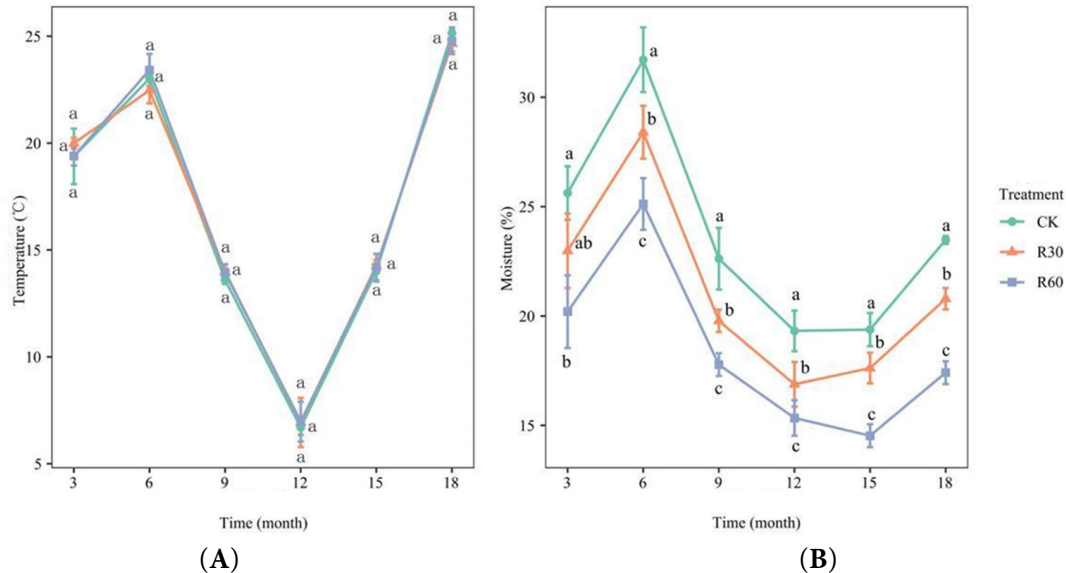


Figure 1: The dynamic changes of soil temperature (A) and moisture (B) under different reduced precipitation. Note: Different lowercase letters indicate significant differences between different rainfall treatments at the same sampling time ($p < 0.05$). Values are the means $\pm$ standard deviations of three replicate plots.

3.2 Effect of Reduced Precipitation on the Rate of Litter Mass Loss

The main effects of reduced precipitation, litter type, decomposition time, and the interaction between reduced precipitation and litter type, as well as the interaction between reduced precipitation and decompo-

sition time, significantly affected the litter mass loss (Table 2; $p < 0.05$). Under the R30 treatment, the mass loss rate of *P. massoniana* litter was significantly lower than that of the CK, whereas the mixed litter did not differ significantly from the CK, indicating that the addition of *C. oleifera* litter may alleviate the inhibitory effects of moderate drought on litter decomposition. However, under the R60 treatment, both *P. massoniana* and mixed litter showed significantly lower mass loss rates than the CK, suggesting that the mitigating effect of litter mixing is insufficient to offset the negative impacts of severe drought stress. After 18 months of litter decomposition, the R30 and R60 treatments significantly decreased the mass loss of *P. massoniana* litter from 6 to 18 months (Fig. 2A; $p < 0.05$), while only the R60 treatment significantly decreased the *C. oleifera* and mixed litter mass loss at the stage (Fig. 2B, C; $p < 0.05$). In addition, the negative effects of reduced precipitation on litter mass loss were increased with the intensity of reduced precipitation (Fig. 2).

Table 2: F and p values for linear mixed-effects model of the effects of reduced precipitation, litter type, and decomposition time on the mass loss of litter.

Source of Variation	F	p
Reduced precipitation (RP)	177.72	<0.01
Litter type (LT)	8.48	<0.05
Decomposition time (DT)	1198.76	<0.01
RP×LT	3.98	<0.05
RP×DT	0.76	0.67
LT×DT	3.13	<0.01
RP×LT×DT	0.35	0.996

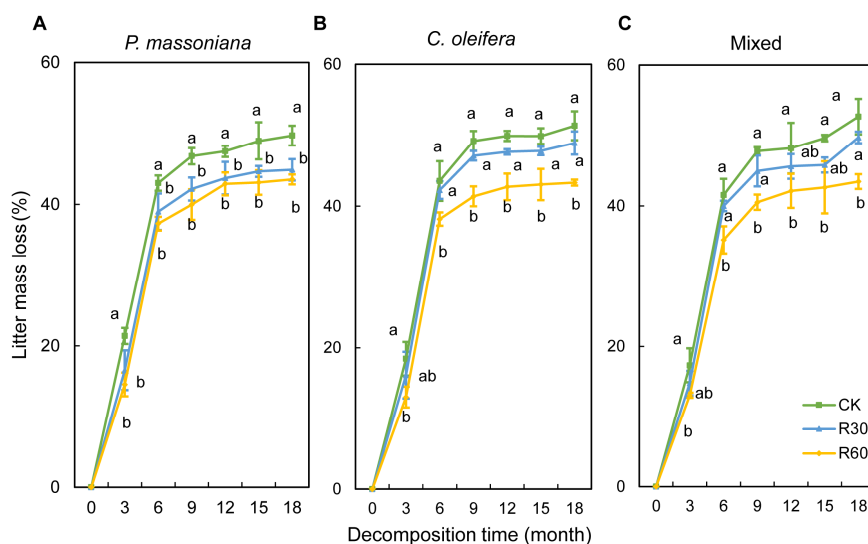


Figure 2: Dynamics of litter mass loss from *P. massoniana* (A), *C. oleifera* (B), and their mixed litter (C) under reduced precipitation. Note: Different lowercase letters indicate significant differences between different rainfall treatments at the same sampling time ($p < 0.05$). Values are the means $\pm$ standard deviations of three replicate plots.

3.3 Effect of Reduced Precipitation on the Release of Metal Elements

The main effects of reduced precipitation, litter type, decomposition time, as well as the interaction between reduced precipitation and litter type, were significant for the content of K and Ca in the litter and the release rates of K, Mg, and Mn (Table 3; $p < 0.05$). After 18 months of litter decomposition, both R30 and R60 treatments increased the K content in *P. massoniana* litter, while only the R60 treatment also

increased K content in mixed litter (Fig. 3A–C; $p < 0.05$). The R30 and R60 treatments reduced the K release rate of *P. massoniana* litter, while only the R60 treatment reduced the K release rate of *C. oleifera* and mixed litter (Fig. 3D–F; $p < 0.05$). Both R30 and R60 treatments increased the Mg content in *P. massoniana* litter (Fig. 4A–C). The R30 and R60 treatments reduced the Mg release rate of *P. massoniana* litter and mixed litter (Fig. 4D–F; $p < 0.05$). Our study revealed that species mixing buffered K and Mg release from *P. massoniana* litter under low-intensity precipitation reduction (R30), but not under high-intensity reduction (R60). In addition, the R60 treatment significantly increased Ca content in *P. massoniana* litter (Fig. 5A–C). The R60 treatment significantly decreased the Ca release rate of *C. oleifera* litter (Fig. 5D–F). The R60 treatment significantly inhibited the Mn release from *P. massoniana* litter; however, no significant effect was observed on Mn release from mixed litter (Fig. 6A–F; $p < 0.05$). These results indicate that the responses of Ca and Mn release to reduced precipitation differed among litter types and elements.

Table 3: *F* and *p* values for linear mixed-effects model of the effects of reduced precipitation, litter type, and decomposition time on the K, Ca, Mg, and Mn release from litter.

Source of Variation		Metal Content		Metal Release Rate	
		<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
K	Reduced precipitation (RP)	522.11	<0.01	590.37	<0.01
	Litter type (LT)	35.44	<0.01	93.87	<0.01
	Decomposition time (DT)	211.67	<0.01	716.91	<0.01
	RP×LT	15.88	<0.01	3.54	0.1
	RP×DT	14.14	<0.01	14.00	<0.01
	LT×DT	5.20	<0.01	5.62	<0.01
	RP×LT×DT	4.00	<0.01	3.16	<0.01
Ca	Reduced precipitation (RP)	89.96	<0.01	6.08	<0.01
	Litter type (LT)	3588.29	<0.01	564.63	<0.05
	Decomposition time (DT)	249.02	<0.01	114.35	<0.01
	RP×LT	6.05	<0.01	3.00	<0.05
	RP×DT	6.64	<0.01	1.21	0.30
	LT×DT	93.17	<0.01	27.68	<0.01
	RP×LT×DT	6.53	<0.01	2.17	<0.01
Mg	Reduced precipitation (RP)	1.37	0.26	131.54	<0.01
	Litter type (LT)	407.53	<0.01	30.55	<0.01
	Decomposition time (DT)	309.82	<0.01	292.56	<0.01
	RP×LT	1.17	0.33	3.06	<0.05
	RP×DT	1.86	0.06	4.69	<0.01
	LT×DT	11.03	<0.01	4.86	<0.01
	RP×LT×DT	2.66	<0.01	6.05	<0.05
Mn	Reduced precipitation (RP)	7.35	<0.01	425.32	<0.01
	Litter type (LT)	3232.09	<0.01	657.27	<0.01
	Decomposition time (DT)	148.40	<0.01	502.01	<0.01
	RP×LT	1.94	0.11	15.21	<0.01
	RP×DT	1.29	0.25	18.29	<0.01
	LT×DT	12.29	<0.01	127.27	<0.01
	RP×LT×DT	3.62	<0.01	27.22	<0.01

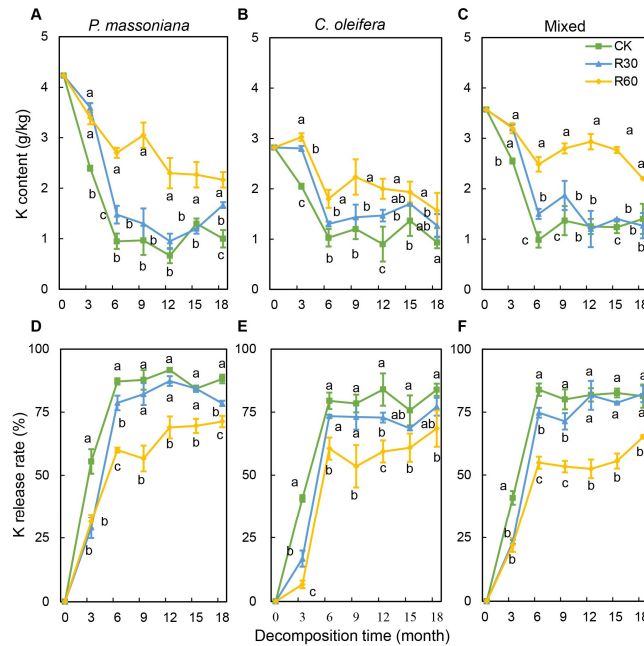


Figure 3: Dynamic changes in K content ((A–C), unit: g/kg) and K release rate ((D–F), unit: %) during 18 months of litter decomposition. Panels A and D represent *P. massoniana* single litter; B and E represent *C. oleifera* single litter; C and F represent mixed litter. Values are means $\pm$ standard deviations of three replicate plots. Note: Different lowercase letters indicate significant differences between different rainfall treatments at the same sampling time ($p < 0.05$).

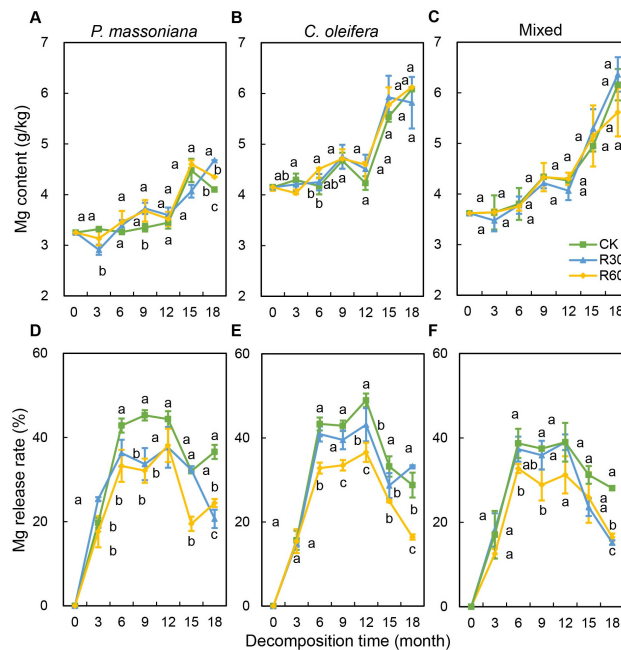


Figure 4: Dynamic changes in Mg content ((A–C), unit: g/kg) and Mg release rate ((D–F), unit: %) during 18 months of litter decomposition. Panels A and D represent *P. massoniana* single litter; B and E represent *C. oleifera* single litter; C and F represent mixed litter. Values are the means $\pm$ standard deviations of three replicate plots. Note: Different lowercase letters indicate significant differences between different rainfall treatments at the same sampling time ($p < 0.05$).

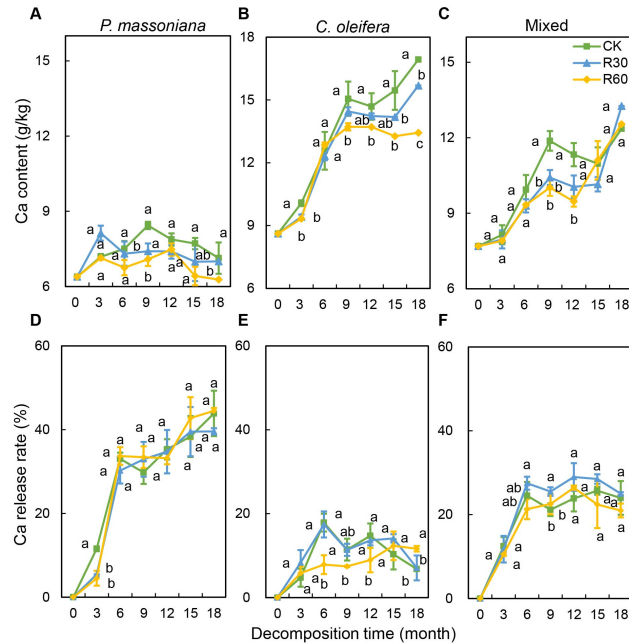


Figure 5: Dynamic changes in Ca content ((A–C), unit: g/kg) and Ca release rate ((D–F), unit: %) during 18 months of litter decomposition. Panels A and D represent *P. massoniana* single litter; B and E represent *C. oleifera* single litter; C and F represent mixed litter. Values are the means $\pm$ standard deviations of three replicate plots. Note: Different lowercase letters indicate significant differences between different rainfall treatments at the same sampling time ($p < 0.05$).

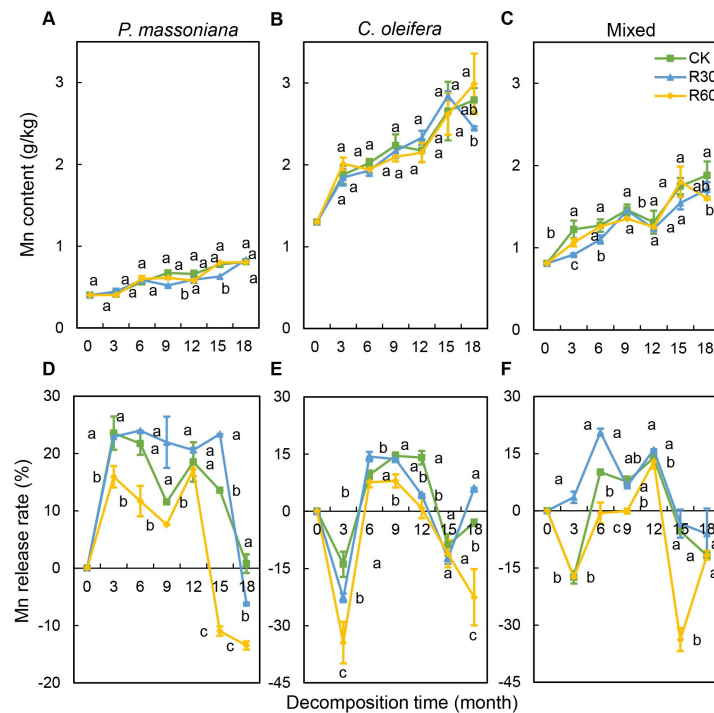


Figure 6: Dynamic changes in Mn content ((A–C), unit: g/kg) and Mn release rate ((D–F), unit: %) during 18 months of litter decomposition. Panels A and D represent *P. massoniana* single litter; B and E represent *C. oleifera* single litter; C and F represent mixed litter. Values are the means $\pm$ standard deviations of three replicate plots. Note: Different lowercase letters indicate significant differences between different rainfall treatments at the same sampling time ($p < 0.05$).

3.4 Relationship between Litter Mass Loss and Metal Nutrient Release

The results showed that there were significantly positive correlations between the rate of K release and the rate of litter mass loss (Fig. 7A; $R^2 = 0.78$; $p < 0.01$), the rate of Ca release and the rate of litter mass loss (Fig. 7B; $R^2 = 0.20$; $p < 0.01$), the rate of Mg release and the rate of litter mass loss (Fig. 7C; $R^2 = 0.36$; $p < 0.01$), and the rate of Mn release and the rate of litter mass loss (Fig. 7D; $R^2 = 0.04$; $p < 0.05$). The litter mass loss rate showed a significant increasing trend with increasing concentrations of K, Ca, Mg, and Mn.

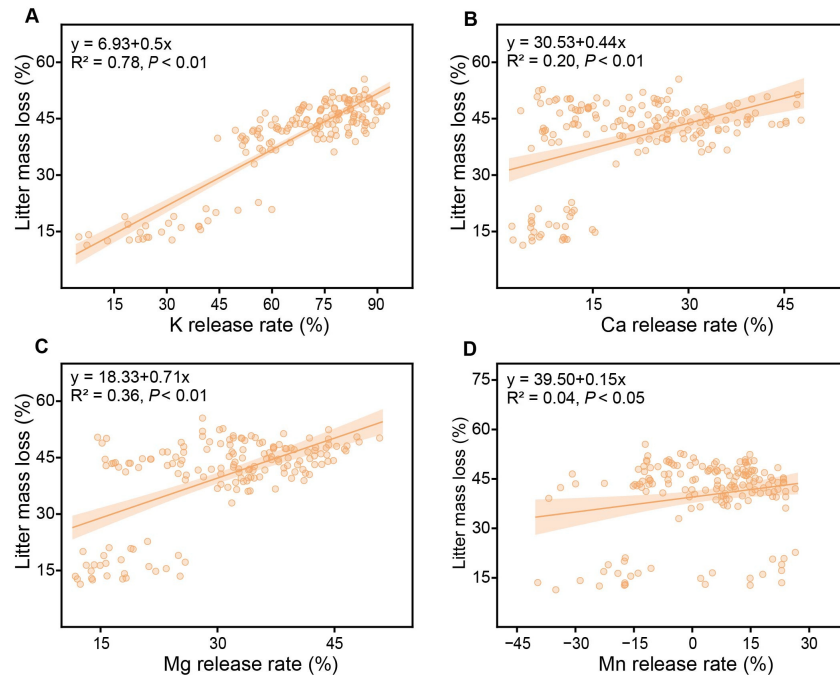


Figure 7: Regression analysis of the mass loss rate of litter and the release rate of K (A), Ca (B), Mg (C), and Mn (D) during decomposition. Data come from six sampling times and three treatments.

4 Discussion

4.1 Effect of Reduced Precipitation on Litter Decomposition

The results showed that the decomposition of *P. massoniana*, *C. oleifera*, and their mixed litter was rapid during the initial nine months, followed by a gradual decline in the decomposition rate thereafter until the 18th month, at the end of the experiment. This pattern is consistent with previous studies reporting rapid initial mass loss followed by a slower decomposition phase [38,39]. A likely explanation is that during the early stages of decomposition, litter mass loss was primarily driven by leaching, leading to faster litter decomposition [6]. In contrast, decomposition during the later stage is constrained by recalcitrant compounds such as lignin and cellulose, resulting in a significantly slower mass loss rate [6,38,40]. *P. massoniana* litter is characterized by relatively high lignin and cellulose contents, whereas *C. oleifera* litter contains a higher proportion of more readily decomposable components. In the mixed litter, the lignin and cellulose contents were intermediate between the two single-species litters, thereby having a relatively lower proportion of recalcitrant substances than that of pine. This compositional difference may help alleviate the constraints imposed by recalcitrant substrates on decomposition processes under drought conditions, which at least partly explain the weaker response of mixed litter to low-intensity precipitation reduction. However, the current findings may not fully represent the later stage of decomposition because

complete decomposition of pine litter often extends beyond 18 months. Therefore, more long-term research is needed for a more comprehensive understanding.

This study showed that the R30 and R60 treatments reduced the mass loss rate of *P. massoniana* litter, while only the R60 treatment significantly decreased mass loss in the mixed litter of *P. massoniana* and *C. oleifera* (Fig. 8). These findings suggest that the mixed litter may mitigate the inhibitory effects of low-intensity reduced precipitation on *P. massoniana* litter decomposition (Fig. 8). In particular, this finding is consistent with the results reported by Zeng et al. [41], who observed that mixed *P. massoniana* and *Cupressus funebris* litter facilitated a faster decomposition process than *P. massoniana* single-species litter. In addition, our study found that the initial N and P concentrations in the mixed litter were intermediate between those of the two single-species litters and were not significantly higher than those of *P. massoniana* litter (Table 1). Moreover, during litter decomposition, precipitation treatments had no significant effects on N and P. This is not entirely consistent with previous studies [42,43], which suggested that mixed litter can promote decomposition rates due to elevated N and P concentrations. Our results suggest that the facilitative effect of mixed litter decomposition may be driven by mechanisms other than nutrient enrichment. Overall, under reduced precipitation conditions, mixing *P. massoniana* litter with *C. oleifera* may regulate the decomposition processes and nutrient cycling.

Furthermore, litter mass loss was significantly positively correlated with the release of K, Ca, Mg, and Mn, highlighting that factors beyond N and P contents, such as K, Ca, Mg, and Mn dynamics, should also be considered when assessing the effects of reduced precipitation on decomposition processes. Although the regression coefficient for Mn was statistically significant ($p < 0.05$), the very low coefficient of determination ($R^2 = 0.04$) indicates limited contribution. The relationship between Mn and litter decomposition rate might be regulated by additional factors. Therefore, we recommend that future studies include additional potential drivers, particularly microbiological indicators and background soil Mn content, to more comprehensively elucidate the underlying mechanisms.

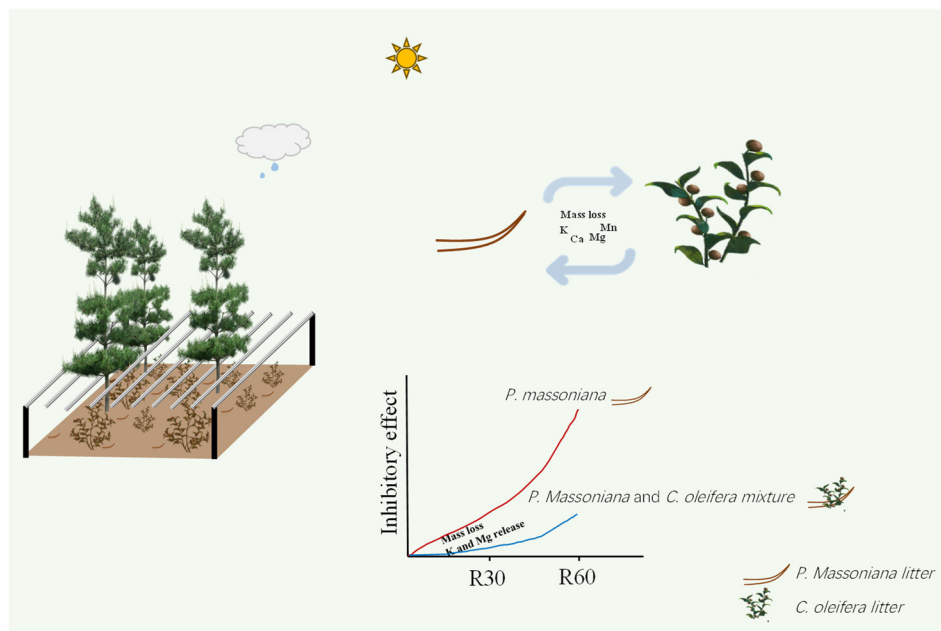


Figure 8: Schematic graph of reduced precipitation effects on *Pinus massoniana* and *Camellia oleifera* litter decomposition. R30 treatment indicates low-intensity reduced precipitation; R60 treatment indicates high-intensity reduced precipitation.

4.2 Effect of Reduced Precipitation on the Release of Metal Elements during Decomposition

After 18 months of decomposition, both the R30 and R60 treatments reduced the K and Mg release rates from the *P. massoniana* single-species litter, while only the R60 treatment significantly reduced the rate of K and Mg release from *C. oleifera* and mixed litter ($p < 0.05$). This result suggests that the mixed litter may mitigate the inhibitory effects of low-intensity reduced precipitation on K and Mg release from *P. massoniana* litter. Furthermore, these results also suggested that the greater the intensity of reduced precipitation, the more pronounced the inhibition of the K and Mg release from litter. Previous studies have reported that increased intensity of reduced precipitation further limits decomposition, potentially exacerbating the suppression of K and Mg release rates [44,45]. This effect can be attributed to the relatively mobile, water-soluble nature of K in litter, as well as the role of rainfall in enhancing soil water flow and moisture [46]. Under higher precipitation regimes, increased leaching and soil wetness promote the loss of exchangeable K and Mg from both soil and decomposing litter, resulting in progressively lower K and Mg concentrations over time [7,44,47], consistent with our findings. Reduced precipitation decreased soil moisture, with the lowest under the R60 treatment (Fig. 1), which may reduce the leaching processes of elements. As K and Mg are primarily released from litter through leaching processes [15,24], reduced leaching likely inhibited their release from litter [47]. However, mixed litters can accelerate litter decomposition (as discussed above), so that only the high-intensity reduced precipitation inhibited K and Mg release from mixed litter in this study. These results suggest that mixing *P. massoniana* with *C. oleifera* can buffer the negative impacts of moderate drought on K and Mg release, highlighting the potential of species mixing to sustain nutrient cycling under climate stress. This suggests that forest management practices (e.g., planting mixed forests) may help support nutrient cycling under reducing precipitation by influencing metal element release from litter.

Our results showed that only the R60 treatment reduced the Ca release rate during the 18-month decomposition period of *C. oleifera* single-species litter. This may be attributed to the stronger water limitation under the R60 treatment, which likely slowed litter decomposition and associated nutrient leaching processes, thereby reducing Ca release [7,48]. However, previous studies have shown that Ca content in decomposing litter may be relatively increased under reduced precipitation due to the tight binding of Ca to pectin in plant tissues [16,17], which was inconsistent with our findings. The inconsistent results may be because the effect of reduced precipitation on the Ca release during litter decomposition depends on vegetation species and initial litter quality [49]. In this study, *C. oleifera* litter has higher initial Ca content; drought (R60) can suppress its release. The stability observed in mixed litter further underscores how species interactions can buffer Ca release under climatic stress. These findings underscore that Ca cycling during litter decomposition can vary substantially among species and ecosystems [50,51]. Future studies should integrate species-specific litter traits to improve predictions of cation release under climate change.

Mn plays a crucial role in the catalytic process of the lignin-degrading enzyme manganese peroxidase (MnP), which is a key enzyme in lignin degradation [23]. Compared to K, Ca, and Mg, Mn exhibited a higher degree of accumulation in this study. This is likely because microorganisms need to absorb more Mn from their environment for the synthesis of MnP [49]. Consequently, Mn displayed an enrichment pattern during the latter nine months of litter decomposition [52,53]. In addition, Mn was shown to play a key role in litter decomposition in temperate forests, primarily by catalyzing the enzymatic breakdown of recalcitrant organic matter [53]. However, its role in litter decomposition may vary across ecosystems, and the response of Mn release to environmental changes remains inconsistent among studies. For example, Singh et al. [8] found no significant relationship between Mn and decomposition rates, suggesting that the role of Mn in decomposition may be complex and not yet fully understood. After 18 months of decomposition, the R60

treatment significantly inhibited Mn release from *P. massoniana* single-species litter. This is consistent with previous studies showing that reduced precipitation inhibits Mn release from litter [7]. However, neither the R30 nor the R60 treatment significantly affected Mn release from mixed litter at the end of the experiment. This indicates that reduced precipitation may not suppress MnP activity during the decomposition of mixed litter [23]. As a result, the effects of reduced precipitation—at least at low intensity—on the decomposition of *P. massoniana* litter and the release of metal elements were not significant when *C. oleifera* litter was present. In addition, the initial Mn concentration in *P. massoniana* litter was lower than that in *C. oleifera* and mixed litter, indicating its inherently limited Mn supply capacity, which may constrain decomposition [54].

4.3 Limitations and Implications

This study highlights the mitigating effects of understory *C. oleifera* on the decomposition of *P. massoniana* litter and the release of metal nutrients under drought conditions. In forest management and ecological practices, understory vegetation should be appropriately retained to enhance the buffering capacity of ecosystems against drought stress, thereby maintaining the stability of litter decomposition processes and nutrient cycling. However, several limitations should be acknowledged. First, the relatively short duration of the experiment limits our understanding of late-stage decomposition processes, particularly for pine litter. Future studies should adopt long-term, multi-site monitoring to better capture decomposition dynamics across different forest types and climatic regions, thereby improving the generality of the findings. Second, the use of fine-mesh litterbags excluded soil meso- and macrofauna, thereby altering natural decomposition pathways. While this design allowed us to investigate microbial- and microfauna-driven processes, it may underestimate the contribution of soil fauna. Future work could incorporate litterbags with different mesh sizes or open-field decomposition experiments to better capture the full decomposer community. Third, this study did not measure microbial community composition, biomass, or extracellular enzyme activities. This limits the mechanistic interpretation of metal nutrient release processes. Future research combining high-throughput sequencing and enzyme assays (e.g., manganese peroxidase, MnP) would help clarify the microbial mechanisms underlying litter decomposition and nutrient cycling. Despite the limitations, our study still demonstrates that understory *C. oleifera* litter can effectively mitigate drought-induced suppression of *P. massoniana* litter decomposition and metal nutrient release, particularly under moderate drought conditions. This highlights the important role of understory vegetation in regulating decomposition processes and nutrient cycling in forest ecosystems under climate change.

5 Conclusion

This study demonstrated that reduced precipitation not only inhibited the decomposition process but also reduced the release of K, Mg, and Mn from *P. massoniana* single-species litter. Moreover, this inhibitory effect intensified with increasing severity of precipitation reduction. However, the presence of understory *C. oleifera* litter alleviated the suppressive effects of low-intensity reduction (R30 treatment) on the decomposition and release of K, Mg, and Mn from *P. massoniana* litter. From a forest management standpoint, our findings provide new implications for *P. massoniana* plantations in response to drought. Reasonably retaining understory *C. oleifera* litter may alleviate moderate drought restrictions on litter decomposition and metal nutrient release. Maintaining mixed understory vegetation has the potential to sustain litter-based nutrient recycling under moderate drought, which is essential for improving soil nutrient sustainability and ecosystem productivity.

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Availability of Data and Materials: The data that support the findings of this study are available from the corresponding author upon reasonable request.

Ethics Approval: Not applicable.

Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

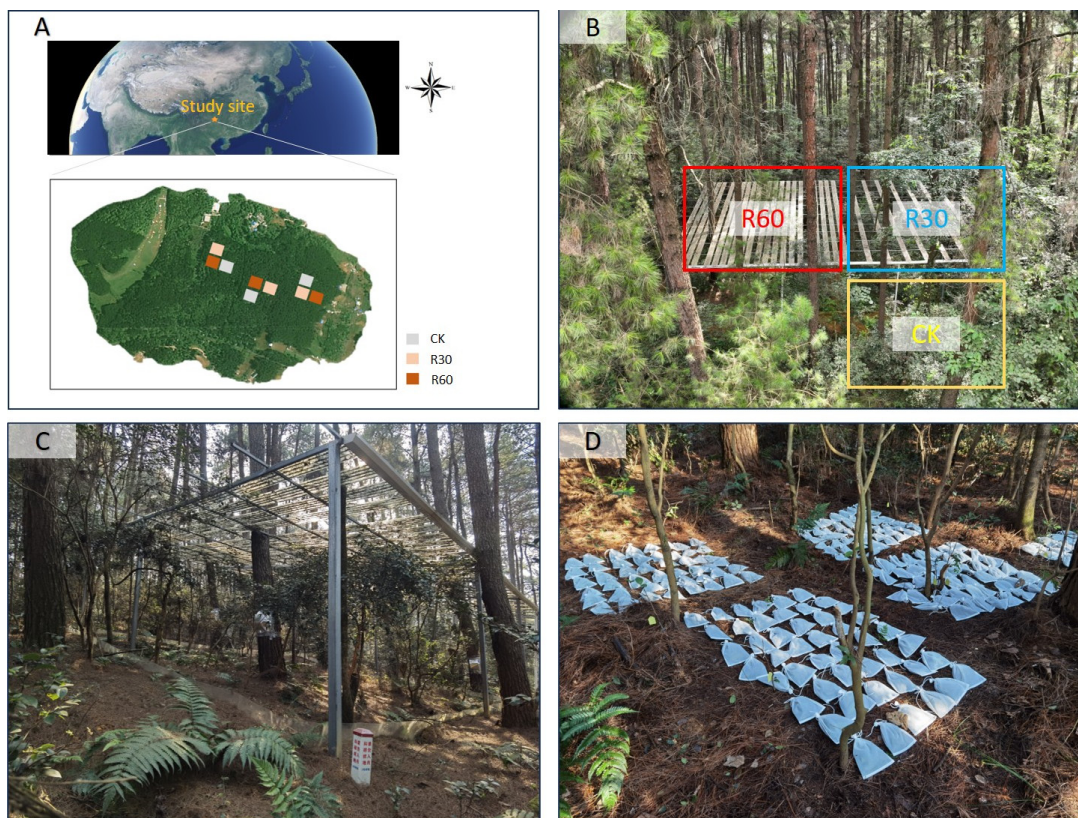


Figure A1: Study area location and experimental design. (A) Location and plot distribution; (B) plots under control (CK), 30% reduction (R30), and 60% reduction (R60) treatments; (C) structure of the precipitation interception system and lateral seepage prevention; (D) litterbag deployment.

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