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Impacts of extreme precipitation events on leaf litter and wood decomposition rates

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Abstract

Global hydrological cycles are shifting due to climate change, and projected increases in the frequency and intensity of extreme precipitation events will likely affect essential ecosystem processes driven by climate, such as forest decomposition. Our objective was to determine the effects of drought and intense rainfall on leaf litter and wood decomposition rates. We used a precipitation manipulation experiment to demonstrate that extreme precipitation projections for the Northeastern United States will significantly impact wood but not leaf litter decomposition and that variations in substrate quality will continue to drive differences in decomposition rates. We found that drought and high rainfall reduced wood decomposition compared to historic rainfall patterns. The median mass remaining of wood stakes after three years within drought, control, and inundation treatments was 84.2%, 57.0%, and 67.5%, respectively. Furthermore, labile litter and wood substrates decomposed more rapidly than recalcitrant substrate types. Thus, our findings suggest a greater sensitivity of wood decomposition to changing precipitation regimes compared to leaf litter. Since wood represents a substantial forest carbon pool, our results underscore the possible significant impacts of projected extreme precipitation scenarios for forest functions, including carbon cycling and sequestration.

KEYWORDS
climate change, deadwood, decomposition, drought, forest carbon cycle, leaf litter, precipitation, woody material

INTRODUCTION

Global hydrological cycles are projected to continue shifting under climate change, including increasing the frequency and intensity of extreme precipitation events, which will likely have consequences for critical ecosystem processes such as decomposition (Guilbert et al., 2015). Indeed, average annual precipitation in the Northeastern United States has increased each decade since the late 1900s (Huang et al., 2021). Furthermore, the region is projected to experience more frequent and intense precipitation events with longer drying periods in between (Allen et al., 2010; Sun et al., 2007). Extreme precipitation events, including severe droughts and intense flooding, have already had numerous economic, social, and ecological consequences within the region and may also impact critical forest processes, including decomposition and forest carbon storage (Alexander et al., 2006). Since northern forests have been a substantial carbon sink over the past several decades, it is essential to understand and anticipate the effects of climate change on forest carbon (C) cycling and sequestration (Goodale et al., 2002; Myneni et al., 2001).

Climate is a key driver of forest decomposition rates (Dai et al., 2021; Dyer et al., 1990). Large-scale syntheses have found a dominant influence of climate on leaf, root, and wood decomposition (Adair et al., 2008; Smith et al., 2011; Zanne et al., 2022). In cases where temperature and oxygen are not limiting, decomposition and respiration rates increase with the moisture content of the decomposing material and the surrounding microenvironment (Aerts, 1997; Boddy, 1983; Cisneros-Dozal et al., 2007; Crockatt & Bebber, 2015; Herrmann & Bauhus, 2013; Lee et al., 2014). For instance, increasing moisture increases respirational C loss in both litter and wood mostly due to the activities of saprophytic fungi that release respirational C (Djukic et al., 2018; Keuskamp et al., 2013). The activities of saprophytic fungi are moisture-limited and include the production of the hydrolytic and oxidative extracellular enzymes that allow for the breakdown of recalcitrant litter and wood components, such as lignin, cellulose, and hemicellulose (A'Bear et al., 2014; Ataka et al., 2014; Herrmann & Bauhus, 2013; Sinsabaugh et al., 2008). Conversely, at extremely high moisture levels, oxygen availability may limit decomposition, while microbial metabolisms can become limited at deficient moisture levels, thereby reducing decomposition rates (Chapin et al., 2012; Panshin & de Zeeuw, 1980; Progar et al., 2000; Stokland et al., 2012).

In addition to climate, substrate quality significantly contributes to variations in forest decomposition rates due to differences in the chemical composition and physical structure of leaf litter and wood (Jomura et al., 2022; Strickland et al., 2009). Litter consists of various forms of organic carbon, including cellulose and hemicellulose, and tends to have relatively high nitrogen (N), making it a labile source of organic material (Cornwell et al., 2008). In contrast, wood has low N concentrations and is rich in lignin, a complex polymer resistant to decomposition (Aber et al., 1990; Kahl et al., 2017; Meentemeyer, 1978). Such variations in the chemical composition of leaves and wood, often described using C:N ratios or lignin content, also contribute to differences in decomposition rates among species and litter types by influencing the composition of decomposer communities inhabiting the substrate (Ge et al., 2013; Liu et al., 2013; Weedon et al., 2009; Yang et al., 2024). Therefore, interactions between climate and substrate quality will have varying impacts on leaf litter and wood decomposition rates (Bradford et al., 2017; Dai et al., 2021).

Given the importance of moisture in affecting leaf litter and wood decomposition rates, ongoing and future shifts in precipitation regimes will play a significant role in forest decomposition (Dyer et al., 1990; Salamanca et al., 2003; Su et al., 2023). For example, Lensing and Wise (2007) found that high-rainfall events accelerated litter decomposition rates by 50%. Direct impacts of rainfall on litter and wood include the leaching of soluble compounds (e.g., phenolics, carbohydrates, and amino acids) during the initial stages of decomposition (Swift et al., 1979). Rainfall indirectly affects litter and wood decomposition by regulating microbial activities that contribute to the degradation of organic material (Bradford et al., 2008). Thus, shifts in extreme precipitation events will impact the rate at which litter and wood decompose in forested ecosystems.

Extreme precipitation events, including intense and heavy rainfall or droughts, may have contrasting effects on the rate at which leaf litter and wood decompose due to altered micro-climatic moisture conditions and the resulting influence on microbial activities; however, these dynamics have been little studied. Our objective for this study was to determine the effects of varying future extreme precipitation scenarios, including drought and extreme rainfall events, on leaf litter and wood decomposition rates using a precipitation manipulation experiment. The questions we sought to answer were (1) how will leaf litter and wood decomposition rates respond to extreme precipitation scenarios and (2) how will extreme precipitation scenarios and substrate quality interact to affect leaf litter and wood decomposition rates? We hypothesized that (1) a heavy and intense precipitation regime would accelerate leaf litter and wood decomposition rates and that this would be particularly true for high-quality, labile substrates due to enhanced leaching of soluble compounds and (2) that extreme drying periods (i.e., drought) would slow leaf litter and wood decomposition rates, regardless of substrate quality.

METHODS

Study site

This study was conducted at the University of Vermont Jericho Research Forest (44.445° N, 73.003° W). The portion of the 192-ha experimental forest used for this work is primarily comprised of naturally regenerated second-growth northern hardwood forests and is dominated by maple (*Acer* spp.), birch (*Betula* spp.), American beech (*Fagus grandifolia*), eastern white pine (*Pinus strobus*), northern red oak (*Quercus rubra*), and eastern hemlock (*Tsuga canadensis*), with minor components of various deciduous and coniferous species. Soils are sandy glaciofluvial deposits. Mean annual temperatures range from −7°C (January) to 21°C (July), and annual precipitation is 107.5 cm (NOAA, 2020). The experiment occurred within three 0.1-ha canopy gaps created during winter 2017–2018 (for more details, see Clark & D'Amato, 2023).

Experimental design

To determine the effects of future extreme precipitation scenarios on leaf litter and wood decomposition, we conducted a precipitation manipulation experiment that was active for two years during the 2018 and 2019 growing seasons (described in detail in Clark & D'Amato, 2023). The experiment included a 27-m^2 precipitation manipulation shelter in the central portion of three recently created 0.1 ha canopy gaps (i.e., three sites). The following precipitation treatments were applied within each shelter to emulate various extreme drought and inundation rainfall scenarios projected for this region:

1. Historic (control): "typical" rainfall, calculated as the median daily volume and frequency of nontrace rainfall (>1-mm total daily rainfall). Values were calculated for each growing season month and derived from historical meteorological records (1917–2017). This treatment represents our experimental control.
2. Drought: "once-in-a-century" (1st percentile) growing season drought, statistically defined using the 95th percentile of consecutive rainless days (<1 mm total daily rainfall) for each growing season month. To control for the amount of water distributed, the total allocated during each irrigation event was also based on the median daily volume, similar to the per-event volume used in the historic treatment.
3. Inundation: characterized as historic rainfall punctuated by periodic, high volume (95th percentile) extreme precipitation. Modeled after historical conditions, this treatment is defined by "typical" daily precipitation volume and frequency (see "Historic treatment"), interspersed by pulsed extreme precipitation events. The frequency and interval for extreme precipitation events were derived from regional projections less than RCP 8.5 (Ning et al., 2015), based on the forecasted number of days with precipitation larger than the 95th percentile of daily precipitation amount (from 1917 to 2017). To control for frequency, the time between irrigation events was statistically determined based on the 95th percentile of consecutive rainless days (<1 mm) per month.

Each experimental precipitation treatment unit was applied beneath each shelter unit ($N = 3$; one replicate per precipitation treatment per shelter/site) (Clark & D'Amato, 2023).

To quantify the effects of extreme precipitation or drought on leaf litter and wood decomposition rates, we deployed tea bags (as described in Keuskamp et al., 2013) and wood stakes beneath each shelter canopy and within each treatment. To study leaf decomposition, we deployed green and rooibos tea in tetrahedron-shaped synthetic tea bags in all treatments. All tea bags were oven-dried at 75°C for 48 h before being weighed and numbered with a unique ID. Within each treatment, 12 bags per tea type were buried pairwise at a depth of 8 cm in June 2018. Tea bags from each treatment were collected, oven-dried, and weighed at five intervals (every 4–5 months) over approximately 24 months (~2 years) to determine mass remaining and decomposition rates over time.

We used commercially available tea bags following the Tea Bag Index method as outlined by Keuskamp et al. (2013) and further refined by Djukic et al. (2018). This approach standardizes decomposition rates across studies by using litter with known chemical compositions and consistent quality parameters, ensuring comparability across environments or treatments. We used green tea, which has a relatively high nitrogen content (C:N ratio = 12.229), and red tea, which has a lower nitrogen content (C:N ratio = 42.870) (Keuskamp et al., 2013). Several studies have observed increased decomposition rates of "native" leaf litter compared with "nonnative" leaf litter in what has been described as the home-field advantage theory; however, the tea bag method has been cited in a large number of global experiments as a proven indicator of how experimental treatments impact leaf litter decomposition (Djukic et al., 2018; Duddigan et al., 2020).

To study wood decomposition, wood stakes were manufactured in size 2.54 × 2.54 × 20 cm from locally harvested, knot- and defect-free sugar maple (*Acer saccharum*) and quaking aspen (*Populus tremuloides*) wood and oven-dried at 75°C for eight days (Fraver et al., 2018). Each stake was weighed and numbered with a unique ID. Within each treatment, eight stakes per species were positioned pairwise (10 cm apart) on the ground surface in June 2018. Six stakes per species per treatment were collected, oven-dried, and weighed at five intervals over three years to determine mass loss over time. During the post-treatment period (year 3), stakes were in the field for one additional year and were exposed to ambient climate conditions. Mean starting mass of wood stakes was 73.01 g. Some samples could not be recovered or processed for various reasons, including missing samples, missing identification tags, or broken, torn, or fragmented samples, resulting in a reduced sample size for some treatments and the third year of the experiment.

Statistical analyses

To assess the rates of tea bag decomposition, we fit the asymptotic decomposition model

$$X = A + (1 - A)e^{-k_a t}, \quad (1)$$

to the proportion of leaf litter mass remaining, where X is the proportion of initial mass remaining at time t, A is the fraction of the initial mass with a decomposition rate of zero, while the remaining fraction $(1 - A)$ decomposes with a rate of k_a (Berg, 2000; Hobbie et al., 2012). While the decomposition rate of A would never actually equal zero, the asymptotic model assumes that this litter fraction decomposes so slowly that its decomposition rate is approximately zero. Thus, A can be considered the fraction of recalcitrant litter that decomposes extremely slowly (Hobbie et al., 2012). The model was fit to each site, tea type, and treatment combination using nonlinear regression and the nls function in the "stats" package in R (R Core Team, 2021).

To determine the effects of extreme precipitation events on leaf litter decomposition rates, we compared decomposition model parameters—the decomposition rate k_a, and the fraction of litter that did not decompose, A—using a mixed model with plot as a random effect and a constant variance function for treatment (lme in the package nlme; Pinheiro & Bates, 2023; R Core Team, 2021). We fit a linear mixed model to measure interactions between treatment and tea type to determine the effects of extreme precipitation events and substrate quality on leaf litter decomposition rates and the fraction of substrate whose decomposition rate was, or approached, zero (k_a, A). Our final models included decomposition model parameters as response variables and interactions between treatment and tea type as predictor variables. In cases with a significant main effect, a post hoc analysis was performed using the Tukey–Kramer method to identify where differences in decomposition model parameters existed among the treatments.

The estimates for wood stake decomposition rates were calculated by dividing the final dry weight of the stakes by the initial weight and multiplying by 100 to determine the percentage of mass remaining over time (note that there were not enough time points to fit Equation 1 to these data). To determine the effects of extreme precipitation events on wood decomposition, we performed a mixed model ANOVA with percent mass remaining as the response variable and treatment, species, and years stakes were in the field as the predictor variables. Our final mixed-effects model included interactions among treatment, species, and the number of years stakes were in the field, with site as a random variable. A constant variance structure was applied to account for heterogeneity in variance across the number of years stakes were in the field. We could not test a three-way interaction between treatment, number of years stakes were in the field, and species of wood stakes due to missing data/samples in the third year. For all models, we also calculated marginal and conditional R^2 values using piecewiseSEM (Lefcheck, 2016). Marginal R^2 describes the proportion of variance explained by fixed factors (e.g., treatment, species). Conditional R^2 describes the proportion of variance explained by fixed and random (e.g., site) factors (Nakagawa & Schielzeth, 2013).

RESULTS

Leaf litter decomposition

The impact of extreme precipitation treatments varied with substrate quality (Table 1). Green tea decomposition rates (k_a) ranged from 0.040 to 0.067, approximately 4 times higher than those of red tea, which ranged from 0.009 to 0.018. Surprisingly, decomposition rates did not vary among treatments (Figure 1a, Table 1). The fraction of substrate that did not decompose (A) after two years in red tea ranged from 0.386 to 0.494 (or 38.6%–49.4% of tea), which was approximately 1.6 times greater (or 57% more) than the fraction that did not decompose (A) after two years in green tea, which ranged from 0.230 to 0.331 (23%–33.1%) (Figure 1b, Table 1). A marginal interaction between treatment and substrate quality was found for the fraction that did not decompose (A), and post hoc analysis revealed that the fraction of substrate that did not decompose (A) for green tea was 22% greater within the drought treatment compared to inundation (Figure 2, Table 1).

Wood decomposition

Treatment effects on the remaining mass of wood stakes depended on the number of years stakes were in the field (Table 1). After the first year (2018), mass

TABLE 1 ANOVA results showing differences in leaf litter and wood decomposition rates.

Response variable and effects	Marginal R^2 (conditional R^2)	numDF	denDF	F	p
Leaf litter k_a	0.938 (0.939)				
Treatment		2	10	2.6	0.12
Substrate quality		1	10	591.6	<0.0001
Treatment:substrate quality		2	10	2.9	0.1
Leaf litter A	0.879 (0.923)				
Treatment		2	10	1.3	0.32
Substrate quality		1	10	370.4	<0.0001
Treatment:substrate quality		2	10	3.5	0.07
Wood mass remaining (%)	0.793 (0.793)				
Treatment		2	57	0.2	0.67
No. years		2	57	6.8	0.002
Species		1	57	30.9	<0.0001
Treatment:species		2	57	2.3	0.108
No. years:species		2	57	11.8	0.0001
Treatment:no. years		4	57	3.3	0.018

Note: Response variable k_a is the decomposition rate of the tea bags while A is the fraction of the initial mass with a decomposition rate of zero or the fraction of litter that did not decompose. Wood mass remaining (in percentage) is an estimate of wood stake decomposition rates.

remaining was 1.4% lower within the inundation treatment than in the control and was not significantly different from the drought treatment. No significant difference was observed after the second year (2019). However, mass remaining after the third year (2020) was 32% lower in the control than the inundation treatment and 53% lower than in the drought treatment (Figure 3a, Table 1). Median mass remaining of wood stakes after three years within the drought, control, and inundation treatments was 84.2%, 57.0%, and 67.5%, respectively. Mass remaining differed significantly between species in the second and third years as aspen stakes decomposed faster than maple stakes (Figure 3b, Table 1). Mean final mass of wood stakes was 69.81 g.

DISCUSSION

Global climate change will substantially impact future forest dynamics by altering regional hydrological cycles. Forest functions, including C cycling and storage, may be disrupted during prolonged droughts or intense precipitation events due to shifts in forest decomposition. We used a precipitation manipulation experiment to demonstrate that future extreme precipitation scenarios will impact wood more than leaf litter decomposition. Overall, we found that drought and extreme precipitation slowed wood decomposition.

Decomposition rates

Our results suggest that the future extreme precipitation scenarios projected to impact Northeastern US forests will have minor impacts on leaf litter decomposition, but that impact may vary with litter quality. We found that, on average, drought tended to increase decomposition rates by 17%, and inundation tended to decrease decomposition rates by 20% for high-quality litter (green tea), but decomposition rates were not significantly different among treatments (Figure 1a). These findings contradict previous studies that found increasing precipitation significantly accelerates leaf litter decomposition, regardless of litter quality, due to greater leaching from high-rainfall events (Lensing & Wise, 2007; Salamanca et al., 2003). Furthermore, drought effects on labile leaf litter substrates (i.e., green tea) also resulted in a larger "slowly decomposing" fraction (Hobbie et al., 2012) than in the inundation treatment, though neither treatment was significantly different than the control (Figure 2). These results are consistent with Berg and Ekbohm (1991), who found nutrient-rich litter exhibited multiple stages of decomposition where the labile fractions of litter decomposed more rapidly during the initial stages (12–18 months) than during the later stages (3–4 years).

In contrast to leaf litter, our results indicate that extreme precipitation scenarios will have a larger and more consistent impact on wood decomposition. Both drought and inundation treatments reduced wood

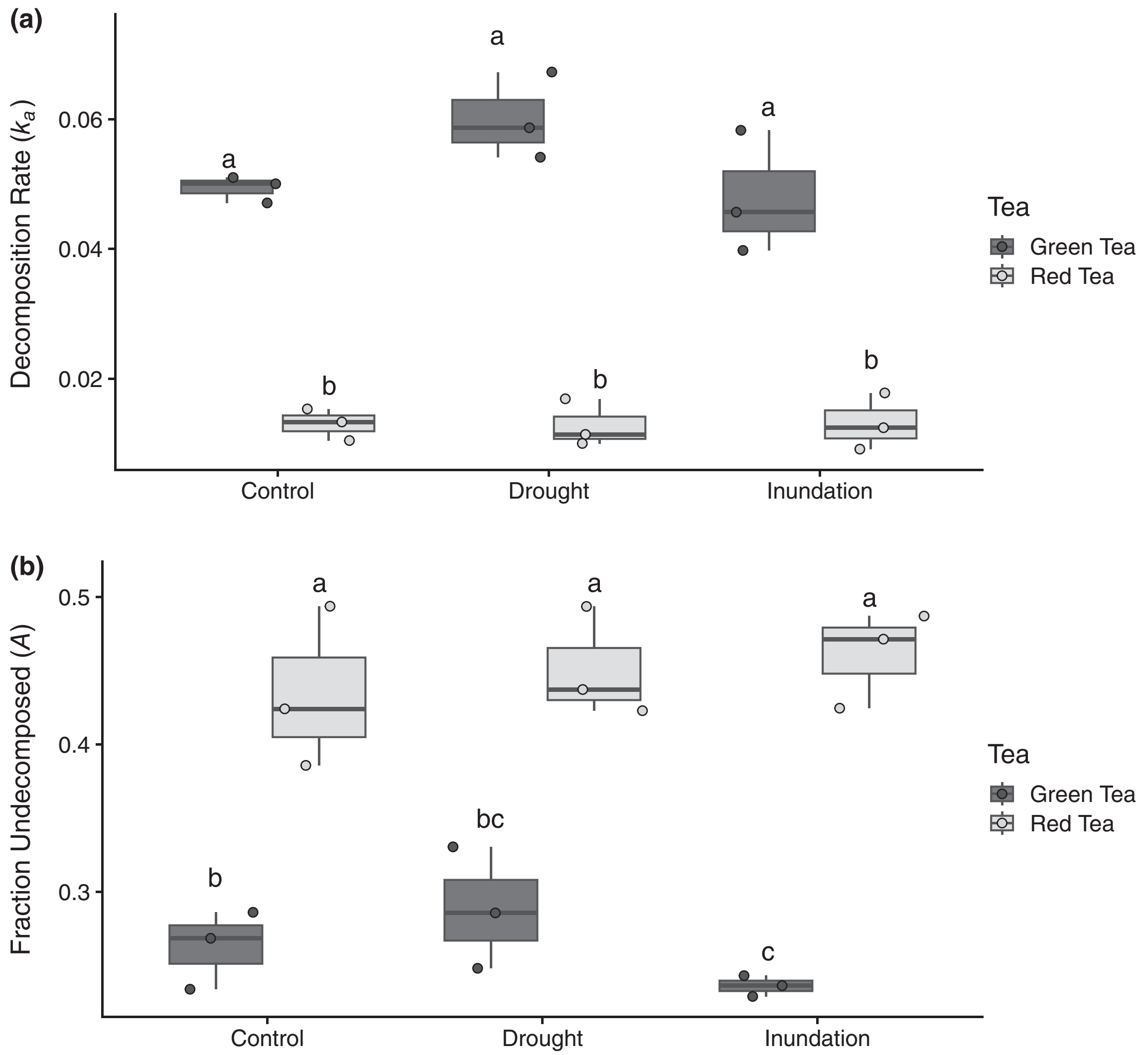

FIGURE 1 Decomposition model parameters obtained from fitting an asymptotic model to show differences between leaf litter substrate types under different future precipitation regimes: (a) k_a and (b) A is the fraction of initial litter that did not decompose (note that $A \times 100\%$ is the percent of litter that did not decompose). Letters ("a," "b," and "c") indicate significant differences within treatments and tea type.

decomposition compared to historical conditions during the experiment (Figure 2a). During the post-treatment period, the stakes experienced ambient conditions. The large observed difference among treatments in the third year may reflect a lag effect from the previous two years of treatment conditions as samples acclimated to ambient conditions in the final treatment year. The overall observed trends in wood decomposition reflect what might be expected under future variations in precipitation extremes in which excessively dry or wet growing seasons are followed by ones reflective of more historic conditions. After three years, wood decomposition was greater under historic than inundation conditions (Figure 3a), where increased rainfall likely disrupted microbial activity by creating anaerobic conditions, whereas moderate, historical precipitation provided consistent moisture conditions that were more suitable for microbial organisms within leaf litter and wood (A'Bear et al., 2014). Decomposition in both substrates relies heavily on microbial activities, particularly those of fungi and bacteria which respond differently to varying moisture levels (Boddy, 1983). While moderate moisture generally supports microbial growth, excessively high moisture conditions may limit oxygen availability and slow decomposition, particularly for fungi which are obligate aerobes (Panshin & de Zeeuw, 1980). Similarly, excessively low moisture conditions may also limit microbial decomposition (Jones et al., 2022; Schlesinger et al., 2016). These moisture-driven dynamics underscore why extreme precipitation events can have variable impacts on decomposition processes.

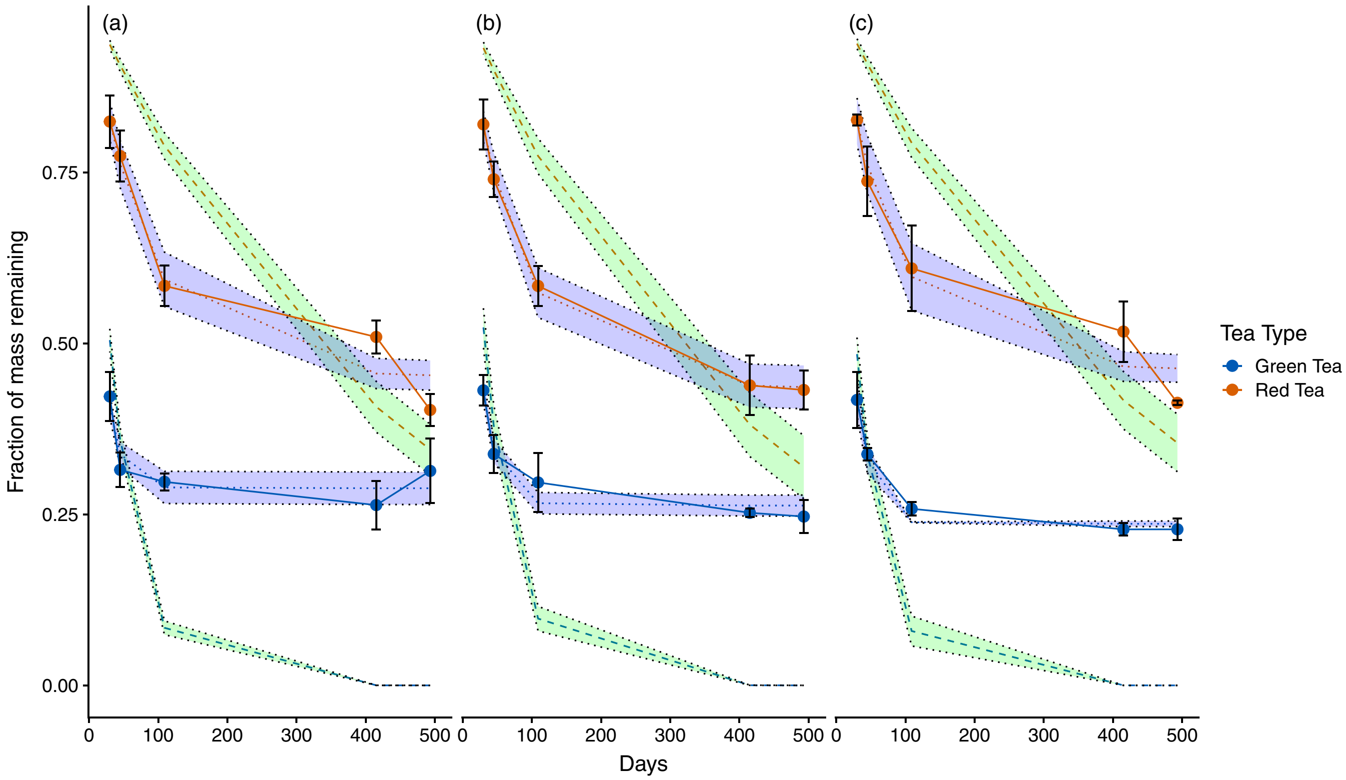

FIGURE 2 Average mass remaining by tea type and treatment with predictions from the single pool and asymptotic models. The dashed line with green shading represents the single pool predictions. The dotted line with blue shading represents the asymptotic predictions. The shaded areas are ±1 SE around predictions. Data error bars are ±1 SE.

Substrate quality

As expected, labile leaf litter substrates decomposed more rapidly than recalcitrant ones (Figure 1a). Climate and substrate quality strongly predict decomposition rates across ecosystems and act synergistically to control decomposition (Adair et al., 2008). At global scales, temperature and moisture are highly related to decomposition rates. Still, within individual ecosystems, the chemical composition of the decomposing substrate becomes a better predictor and is often expressed in terms of lignin content or C and N concentrations or ratios (Aerts, 1997; Gholz et al., 2000). Labile leaf litter substrates tend to have higher N concentrations and lower lignin contents, making them more decomposable (Aber et al., 1990; Meentemeyer, 1978). Therefore, it is not surprising that green tea had greater decomposition rates than red tea.

Similarly, wood decomposition rates differed between sugar maple and aspen stakes, a finding similar to that of Forrester et al. (2023) (Figure 3b). However, this difference was not evident until after the second year of the experiment. After Year 2, aspen stakes decomposed more rapidly than sugar maple stakes, likely due to differences in chemical composition and wood traits. These results agree with the established idea that differences in wood physical, chemical, and structural properties across tree species and their interactions with microbial communities contribute to variations in their general decomposability (Forrester et al., 2023; Weedon et al., 2009). Furthermore, previous studies have observed an initial lag time (~2 years) before decomposition rates increased rapidly for aspen species compared with maple species having longer initial lag times (~6–10 years) (Freschet et al., 2012; Johnson et al., 2014). This lag time is potentially due to the initial phases of decomposition when microbial organisms colonize the substrate and can be impacted by wood physical and structural traits (Harmon et al., 1986; Swift et al., 1979; Yang et al., 2024). Thus, the micro-environment provided by low-density and nutrient-rich wood may be more habitable and accessible for microbial decomposers, specifically fungi, and accelerate the initial stages of wood decomposition (Boddy, 1983; Stokland et al., 2012).

Study limitations

Marginal interactions between treatment and substrate quality were detected for litter decomposition rates, specifically labile litter substrates. The effects of these interactions could become stronger over longer periods,

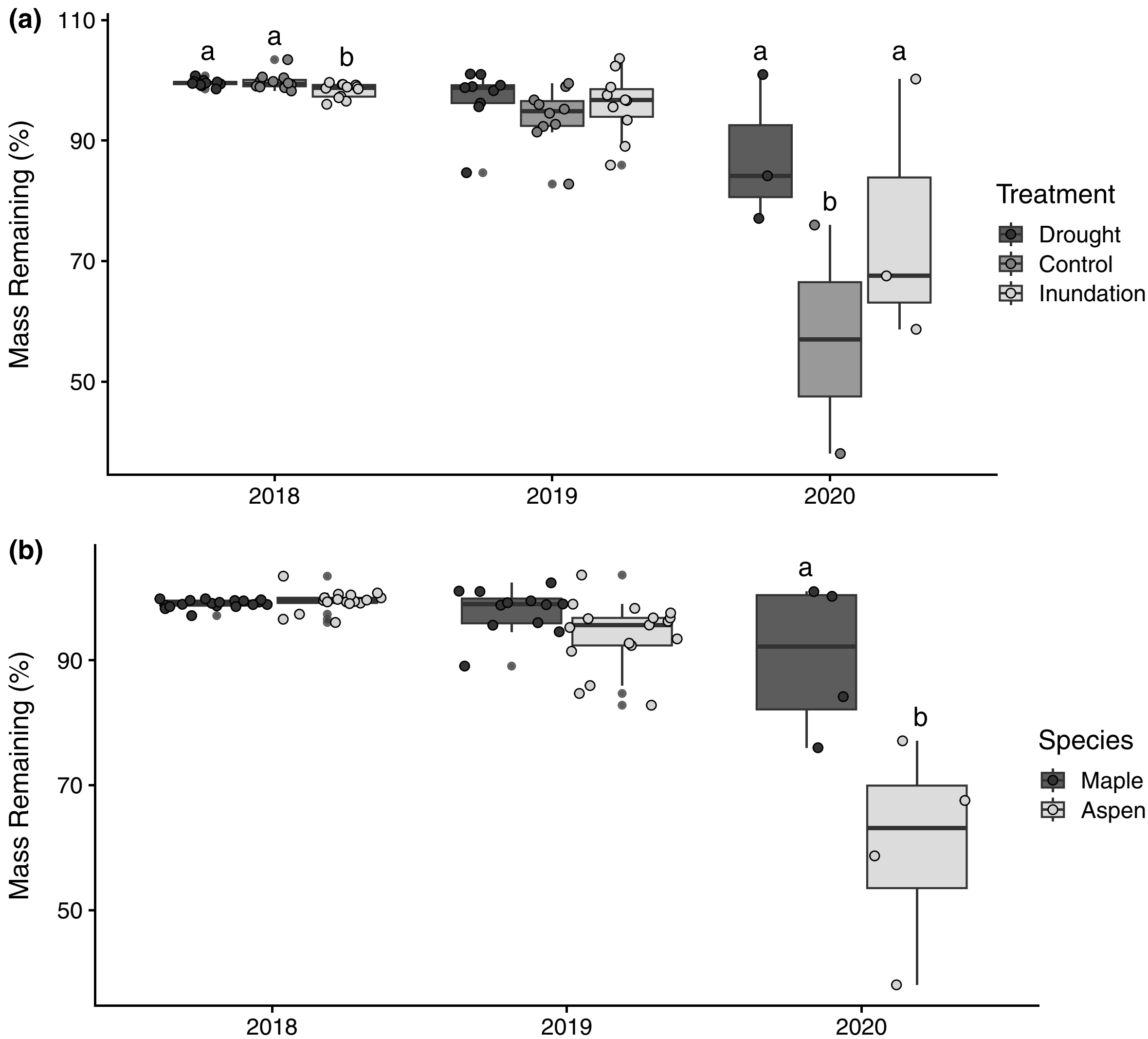

FIGURE 3 Mass remaining (in percentage) of wood stakes over three years (a) by precipitation regime and (b) stake species. The experiment took place over two growing seasons (2018–2019). Stakes were exposed to ambient conditions during the third season (2020). Letters ("a" and "b") indicate significant differences within (but not between) each year.

indicating that variations in extreme precipitation events could have more significant impacts on high-quality litter.

Furthermore, soils on this site are excessively well-drained, potentially resulting in differing decomposition patterns under other soils with greater moisture-holding capacity. For example, drought treatments may respond more similarly to historic treatments, or inundation soils may become saturated under loamy or clay soils. Thus, soil types likely play a large role in determining decomposition patterns.

CONCLUSIONS

Our results provide insight into the ecological impacts of climate change on ecosystem processes that contribute to forest functions, including forest C cycling and sequestration. We found that extreme rainfall and drought had minor impacts on leaf decomposition that varied with litter quality, but that wood decomposition was sensitive to changing precipitation, with drought and inundation treatments slowing wood decomposition. Since wood is a major pool of forest C, these findings have significant implications for forest C storage, suggesting that heavy rainfall and drought may slow wood decomposition and increase forest C storage in wood.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Murray et al., 2024) are available in Figshare at https://doi.org/10.6084/m9.figshare.25105751.v1.

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