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Effects of Climate and Atmospheric Nitrogen Deposition on Early to Mid-Term Stage Litter Decomposition Across Biomes

TaeOh Kwon¹, Hideaki Shibata¹, Sebastian Kepfer-Rojas², Inger K. Schmidt², Klaus S. Larsen², Claus Beier², Björn Berg³, Kris Verheyen⁴, Jean-Francois Lamarque⁵, Frank Hagedorn⁶, Nico Eisenhauer^{7,8}, Ika Djukic^{6*} and TeaComposition Network

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Litter decomposition is a key process for carbon and nutrient cycling in terrestrial ecosystems and is mainly controlled by environmental conditions, substrate quantity and quality as well as microbial community abundance and composition. In particular, the effects of climate and atmospheric nitrogen (N) deposition on litter decomposition and its temporal dynamics are of significant importance, since their effects might change over the course of the decomposition process. Within the TeaComposition initiative, we incubated Green and Rooibos teas at 524 sites across nine biomes. We assessed how macroclimate and atmospheric inorganic N deposition under current and predicted scenarios (RCP 2.6, RCP 8.5) might affect litter mass loss measured after 3 and 12 months. Our study shows that the early to mid-term mass loss at the global scale was affected predominantly by litter quality (explaining 73% and 62% of the total variance after 3 and 12 months, respectively) followed by climate and N deposition. The effects of climate were not litter-specific and became increasingly significant as decomposition progressed, with MAP explaining 2% and MAT 4% of the variation after 12 months of incubation. The effect of N deposition was litter-specific, and significant only for 12-month decomposition of Rooibos tea at the global scale. However, in the temperate biome where atmospheric N deposition rates are relatively high, the 12-month mass loss of Green and Rooibos teas decreased significantly with increasing N deposition, explaining 9.5% and 1.1% of the variance, respectively. The expected changes in macroclimate and N deposition at the global scale by the end of this century are estimated to increase the 12-month mass loss of easily decomposable litter by 1.1–3.5% and of the more stable substrates by 3.8–10.6%, relative to current mass loss.

In contrast, expected changes in atmospheric N deposition will decrease the mid-term mass loss of high-quality litter by 1.4–2.2% and that of low-quality litter by 0.9–1.5% in the temperate biome. Our results suggest that projected increases in N deposition may have the capacity to dampen the climate-driven increases in litter decomposition depending on the biome and decomposition stage of substrate.

Keywords: tea bag, Green tea, Rooibos tea, litter decomposition, carbon turnover, nitrogen deposition, TeaComposition initiative

INTRODUCTION

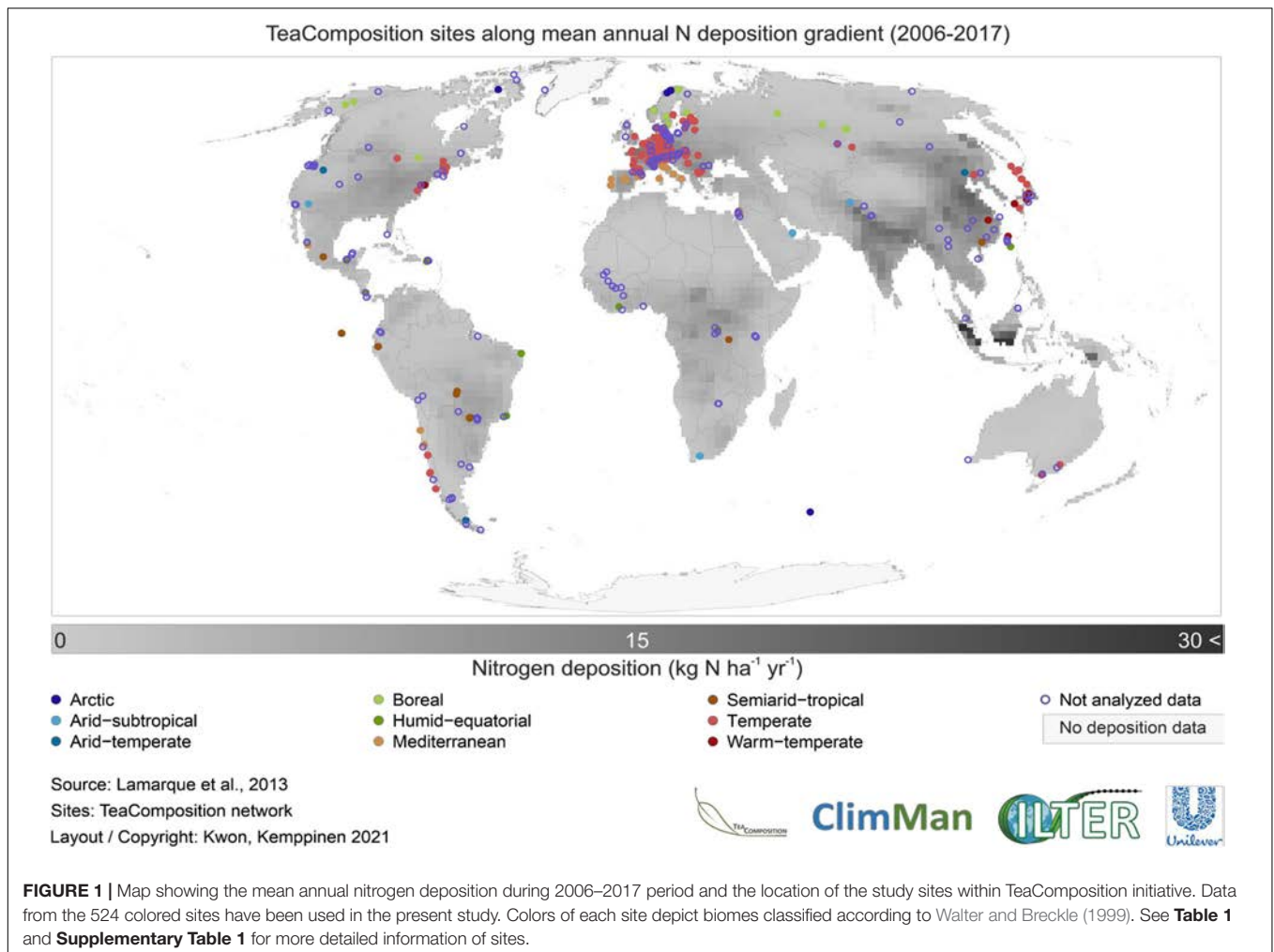
Litter decomposition is a fundamental process in the carbon and nutrient cycling across all ecosystems (Chapin et al., 2011; Berg and McLaugherty, 2020). Decomposition rate is most closely related to litter quality (Cornwell et al., 2008; Djukic et al., 2018; Kotroczó et al., 2020), climate (Davidson and Janssens, 2006; Tóth et al., 2007; See et al., 2019), nutrient availability (Fog, 1988; Luo et al., 2018; Lilleskov et al., 2019; Juhos et al., 2021), and the abundance and diversity of soil organisms (Coûteaux et al., 1995; González and Seastedt, 2001; Pioli et al., 2020). The climate exerts a direct effect on decomposition by stimulation of decomposer activity through the increased temperature and precipitation (Zhang et al., 2008). However, the inhibitory influence of climate might occur when substrate moisture lies below 30% or above 80% and the mean annual temperature below 10°C (Prescott, 2010). The long-term climate conditions shape indirectly the prevailing vegetation and the quality of plant litter, which can have significant impacts on its turnover dynamics. Climate variables can explain up to 68% of the variability in litter decomposition rates on a global scale (Parton et al., 2007); thus changes in environmental conditions may have a significant impact on litter decomposition processes via both direct and indirect pathways. Carbon to nitrogen ratio and lignin content of the initial litter are considered to be good indicators of litter quality as they are related to nutrient availability and chemical properties of the studied substrate. For instance, litter with a high C:N ratio and lignin content decomposes more slowly (Makkonen et al., 2012) than litter with the inverse properties. Yet, the relative importance of diverse drivers may change over the course of the decomposition process. The early stage of litter decomposition (i.e., 0–30% mass loss) where most of the water-soluble compounds are released is especially sensitive to the environmental changes and the decomposition of holocellulose is promoted by higher nitrogen (N) contents in initial litter and soil. In contrast, during the later stage of decomposition (>30% mass loss), N exerts the opposite effect due to the suppressed oxidative enzymatic activities (Berg, 2014; Berg and McLaugherty, 2020). Although the central role of climate and litter quality in controlling litter decomposition rates is widely recognized, results on the effects of increased N input and climate on the decomposition in the field are inconsistent.

Depending on litter quality, responses to atmospheric N deposition may vary from positive for the decomposition of high-quality litter (high N, low C:N ratio) to negative for the decomposition of low-quality litter (high lignin, high C:N ratio; Fog, 1988; Zhou et al., 2017) through affecting the

composition of the decomposer community. Similarly, several studies have shown that in N-poor ecosystems, addition of N is likely to stimulate early-stage litter decomposition (Knorr et al., 2005), whereas in N-sufficient ecosystems inhibitory effects of N deposition have been reported through a reduced oxidative enzymatic activity (Hobbie, 2008; Hagedorn et al., 2012; Norris et al., 2013). A meta-analysis revealed an inhibitory effect of ambient N deposition between 5 and 10 kg N ha⁻¹ year⁻¹ on litter decomposition for a period of 1–72 months (Knorr et al., 2005). Although much is known about the regulatory factors of litter decomposition, the results on the effects of increased N deposition on litter decomposition remain inconsistent (Pei et al., 2020; Hood-Nowotny et al., 2021). Hence, the importance of regulatory factors might be strongly context-dependent and may differ among ecosystems and litter types (Bradford et al., 2016).

Increases of the global mean annual surface temperature (1.0–3.7°C) and mean annual precipitation (28.8–65.0 mm) are projected for the end of this century (IPCC, 2014; Thorpe and Andrews, 2014). The atmospheric total inorganic N deposition rate on land and transitional area is expected to increase by 1.2 kg N ha⁻¹ year⁻¹ (RCP 2.6) to 1.9 kg N ha⁻¹ year⁻¹ (RCP 8.5) by the end of this century (Lamarque et al., 2013). Since N and C cycles are tightly coupled, an increase of N in soil through increased atmospheric N deposition may alter the humification of litter and thus soil C sequestration (Janssens et al., 2010; Prescott, 2010; Berg and McLaugherty, 2020). In addition, not only climate-driven shifts in vegetation composition (Rizzetto et al., 2016; Boutin et al., 2017), but also N driven changes in plant diversity (Bobbink et al., 2010) might not only influence the microclimate but also litter quality, which significantly affects decomposition patterns (Gaudio et al., 2015) and thus might have profound implications for the global C storage and consequently climate change. Therefore, it is crucial to explore potential effects of changes in climate and N deposition on litter decomposition.

To understand the effects of variation in climate, N deposition, and other environmental factors on litter decomposition at the global scale, standardization in experimental materials and methodology is mandatory. The TeaComposition initiative has collected harmonized data on litter mass loss over time using standardized litter (i.e., commercially available tea bags; Djukic et al., 2018). Using this approach, we evaluated the effects of macroclimate and N deposition on the global litter mass loss of fast-decomposing Green tea and slow-decomposing Rooibos tea after 3 and 12 months of *in situ* incubation. For future predictions, two different N deposition and climate scenarios were used. The number and distribution of field



sampling locations often limit our understanding of ecological processes. Therefore, in our analyses we shed more light on the decomposition process in the temperate biome due to the greatest data availability and the largest range of N deposition.

The aims of this study are to determine (1) the relationship between macroclimatic factors, N deposition, and litter quality on mass loss of Green and Rooibos teas across biomes, (2) whether the observed relationships at the global scale hold true for regional scale (i.e., temperate biome where N deposition is highest), and (3) the relationship between predicted changes in macroclimate, N deposition, and first year leaf litter mass loss at global and regional scales. Specifically, we hypothesize (1) that the control of early to mid-stage decomposition will be driven by litter quality > climate > N deposition on the global scale; (2) that the inhibitory effect of N deposition on the progressed stage of decomposition will be more pronounced at the regional scale with higher N deposition rates than at the global scale; (3) that a potential climate change-induced increase of litter decomposition might be mitigated through a potential negative feedback of N deposition on the progressed stage of decomposition.

MATERIALS AND METHODS

Study Sites

We used data gained by the global TeaComposition initiative¹ coming from untreated control plots. Data from 394 sites (5,581 teabags) after 3-month incubation and 423 sites (4,583 teabags) after 12-month incubation are collected across nine biomes (**Figure 1**, **Table 1**, and **Supplementary Table 1**). Each site was assigned to one of nine terrestrial biomes, defined by Walter and Breckle (1999). Sub-sites with different elevations, locations, and vegetation types were considered as separate sites. For 3-month incubation, we used the mean monthly precipitation (MMP), mean monthly air temperature (MMAT), and the mean monthly N deposition (MMN) based on the real incubation period, while for 12-month incubation, mean annual average values of these variables were used. Climate data were extracted from the CHELSA version 1.2 (Climatologies at High resolution for the Earth's Land Surface Areas²; Karger et al., 2017). The atmospheric N deposition at each site was resampled by bilinear

¹<https://www.teacomposition.org/>

²<https://chelsea-climate.org/>

TABLE 1 | Summarized characteristics of the study sites used for the analyses within the TeaComposition initiative.

| Biomes | Ca. 3-month incubation | | | | Ca. 12-month incubation | | | |
|--------------------|--|----------------------------|----------------------------|---------------------------------|---------------------------|----------------------------|----------------------------|---------------------------------|
| | Number ^A of sites (teabags) | Climate (MMP) ^B | Climate (MMT) ^C | N deposition (MMN) ^D | Number of sites (teabags) | Climate (MAP) ^E | Climate (MAT) ^F | N deposition (MAN) ^G |
| Arctic | 3 (124) | 59 (2) ^{bc} | 8 (1) ^c | 0.07 (0.03) ^b | 80 (419) | 487 (6) ^c | −2 (0) ^e | 1.14 (0.04) ^d |
| Boreal | 21 (475) | 63 (3) ^{bc} | 13 (0) ^c | 0.25 (0.03) ^b | 22 (652) | 513 (36) ^c | 1 (1) ^d | 2.84 (0.32) ^{bc} |
| Temperate | 284 (3927) | 80 (2) ^b | 15 (0) ^c | 1.00 (0.02) ^a | 231 (2572) | 862 (21) ^b | 7 (0) ^c | 10.57 (0.31) ^a |
| Warm-temperate | 6 (120) | 182 (41) ^a | 23 (1) ^{ab} | 0.61 (0.09) ^{ab} | 5 (105) | 2451 (361) ^a | 16 (1) ^{ab} | 7.41 (1.31) ^{ab} |
| Arid-temperate | 3 (53) | 32 (14) ^c | 16 (2) ^{bc} | 0.50 (0.38) ^b | 2 (58) | 275 (22) | 9 (2) | 1.81 (0.70) |
| Mediterranean | 40 (428) | 39 (5) ^c | 18 (1) ^b | 0.48 (0.05) ^b | 44 (501) | 755 (51) ^b | 13 (1) ^b | 5.31 (0.53) ^b |
| Arid-subtropical | 9 (141) | 23 (11) ^c | 26 (1) ^a | 0.14 (0.04) ^b | 6 (40) | 340 (98) ^c | 23 (0) ^a | 1.73 (0.78) ^{cd} |
| Humid-equatorial | 14 (104) | 139 (14) ^a | 26 (0) ^a | 0.24 (0.03) ^b | 21 (142) | 1685 (148) ^a | 24 (0) ^a | 2.21 (0.34) ^{cd} |
| Semi-arid-tropical | 14 (209) | 159 (11) ^a | 21 (2) ^{ab} | 0.48 (0.07) ^b | 12 (94) | 1183 (45) ^a | 19 (2) ^a | 4.48 (0.83) ^{bc} |
| Mean | | 89 (11) | 18 (1) | 0.42 (0.08) ^b | | 951 (88) | 12 (1) | 4.17 (0.57) |

Mean (SE) of climates and N deposition at each biome.

Detailed table on the single site characteristics can be found in the **Supplementary Material**.

^ANumber of sites (teabags) is for sites (teabags) used for both the teas, Green tea and Rooibos tea at each incubated period.

^BMMP (mm month^{−1}) = Mean monthly precipitation during real incubation period at each site.

^CMMT (°C) = Mean monthly temperature during real incubation period at each site.

^DMMN (kg N ha^{−1} month^{−1}) = Mean monthly N deposition during real incubation period at each site.

^EMAP (mm year^{−1}) = Mean annual precipitation.

^FMAT (°C) = Mean annual temperature.

^GMAN (kg N ha^{−1} year^{−1}) = Mean annual N deposition. Lowercase letters show the result of multiple comparisons among biomes with Kruskal–Wallis test at the level of $P < 0.05$.

interpolation on a rectilinear 2D grid of Atmospheric Chemistry and Climate Model Intercomparison Project (ACCMIP) dataset with a spatial resolution of 1.9 (latitude) × 2.5 (longitude) degree (Lamarque et al., 2013). The ACCMIP dataset is composed of historical deposition covering the period from 1850 to 2000 and the projected deposition with RCP scenarios until 2100 (Van Vuuren et al., 2011; Lamarque et al., 2013). The data on N depositions are based on the RCP 2.6 scenario from 2007 to 2016 for each site. The mean annual air temperature (MAAT) in our dataset ranges from −2°C to 24°C on the global scale and is 7°C in the temperate biome. The mean annual precipitation (MAP) ranges from 275 mm to 2451 mm at the global scale and is around 862 mm in the temperate biome. The estimated mean annual total inorganic N deposition (MAN) ranges from 1 to 11 kg N ha^{−1} year^{−1} (0.2–22.0 kg N ha^{−1} year^{−1} with a whole range) on the global scale and is around 11 kg N ha^{−1} year^{−1} (0.7–22.0 kg N ha^{−1} year^{−1} with a whole range) in the temperate biome (**Table 1**; site specific data can be found in the **Supplementary Table 1**).

Litter Bag Study

Within the TeaComposition initiative (Djukic et al., 2018), commercially available tea bags of Green tea (C/N ratio of 12.3) and Rooibos tea (C/N ratio of 42.9; Keuskamp et al., 2013) were incubated ($n = 4$ per litter type and sampling period) in the field over a period of 3 and 12 months. The tea was contained in woven nylon bags with 0.25 mm mesh size allowing access only for microorganisms and fine roots. Tea bags were buried in the upper 5 cm of the top-soil in the summer of 2016 in both the northern

and southern hemispheres (i.e., start in summer; June–August in northern hemisphere and December–February in southern hemisphere). After incubation, bags were excavated and carefully cleaned of soil and roots, dried at 70°C for 48 h, and weighed. The remaining mass after the incubation was linearly normalized to 3 and 12 months on dry weight and expressed in percentage (%) of the initial litter weight. When remaining litter was visibly contaminated, remaining mass of litter was estimated by subtracting ash weight (representing mineral portion) obtained after heating the sample in a muffle oven at 500°C for 16 h from remaining mass of visibly contaminated litter.

Data Analyses

Effects of Climate and N Deposition on Mass Loss Between Tea Types and Incubation Time

We linearly normalized all mass loss data to a fixed period because not all tea bags were incubated for exactly 3 (91 ± 8 days; overall mean ± standard deviation; number of sites = 394) and 12 months (369 ± 9 days; number of sites = 423).

To determine the significant differences of the means of mass loss at site level of each tea type across biomes after 3-month and 12-month incubation, the Kruskal–Wallis test was performed. This non-parametric test was used because preliminary analysis indicated at least one of the assumptions of normality and homogeneity of variance was not met. When the result of the Kruskal–Wallis test showed a significant difference across biomes, a non-parametric *post hoc* test was conducted using the “kruskal” function in the package “agricolae” in R Statistical

Software with the Holm-adjusted p -value, set to $p < 0.05$ for statistical significance, for multiplicity correction (Holm, 1979; De Mendiburu, 2017).

To investigate the effects of climatic variables and N deposition on mass loss after 3 and 12 months for both teas or each tea type separately, we applied linear mixed-effects models (Bates et al., 2015) with tea type for both teas, climate, and N deposition as fixed factors and site as random factor. For 3-month incubation, the mean monthly values of climate and N deposition were calculated and used with real incubation period at each site. For 12-month incubation, the mean annual data of climate and N deposition were used. The final model was selected with backward selection by deleting non-significant terms. While determining the final model, we also examined the possibility of multicollinearity between fixed factors using a variance inflation factor (VIF), with an acceptable VIF score < 3 (Kock and Lynn, 2012). The same procedure has been applied separately for data from temperate biome, due to the greatest data availability and the largest range of N deposition at the regional scale.

Projection of Future Litter Decomposition

We used the RCP 2.6 and RCP 8.5 IPCC scenarios to analyze the relationships between the change of mass loss and the change of climate and N deposition by the end of this century (Van Vuuren et al., 2011; Lamarque et al., 2013; IPCC, 2014; **Table 2**). Projected data on MAT and MAP by the end of this century were obtained from IPCC (2014) and the Coupled Model Intercomparison Project 5 (CMIP5; Thorpe and Andrews, 2014), respectively. For the change of atmospheric N deposition, we used the simulated dataset with RCP scenarios from ACCMIP aforementioned, supplied by National Center for Atmospheric Research in United States (Lamarque et al., 2013). According to these simulations, the surface temperature is expected to increase between 1 and 3.7°C between 2081 and 2100 relative to the period of 1986–2005, while precipitation is predicted to increase by 28.8 to 65.0 mm year⁻¹ between 2079 and 2098 in comparison to 1986–2005. In addition, N deposition is expected to increase by 1.2 to 1.9 kg N ha⁻¹ year⁻¹ by 2090–2099 relative to the period of 2000–2009 (**Table 2**). We calculated the percent changes in mass loss of Green and Rooibos teas, relative to mass loss measured after current 1-year decomposition, by the end of the 21st century by using data on predicted changes in MAT, MAP, and MAN as well as the results of linear mixed-effects models between those factors and mass loss of tea types.

Software Used for Data Processing and Statistical Analysis

All the geographical analyses on climate, N deposition data, and site locations were processed using QGIS (Quantum GIS Development Team, 2017, version 2.18.14). All statistical analyses were carried out with R (R Core Team, 2019, version 3.4.4). To quantify the explained percentage of variance by fixed factors in a linear mixed-effects model using the “lmer” function in the “lme4” package in R, we used the “variancePartition” package in R (Hoffman and Schadt, 2016). Overall, model quality was further quantified by calculating marginal R^2 (fixed

TABLE 2 | Change in mean annual temperature (Δ MAT, °C), mean annual precipitation (Δ MAP, mm year⁻¹), and mean annual N deposition (Δ N deposition, kg N ha⁻¹ year⁻¹) by the late 21st century for two RCP scenarios as compared to the period 1986–2005 for Δ MAT and Δ MAP and to the period 2000–2009 for Δ N deposition.

| Scenario | 2081–2100 | 2079–2098 | 2090–2099 |
|----------|-----------------------------|-------------------|-----------------------|
| | Δ MAT (likely range) | Δ MAP (SE) | Δ N deposition |
| RCP 2.6 | 1.0 (0.3–1.7) | 28.8 (2.9) | 1.2 |
| RCP 8.5 | 3.7 (2.6–4.8) | 65.0 (4.4) | 1.9 |

SE means standard error.

effects only) and conditional R^2 (fixed plus random effects) with “r.squaredGLMM” function in the “MuMIn” package in R (Nakagawa and Schielzeth, 2013).

RESULTS

Effect of Climate and N Deposition on Mass Loss Across All Biomes

Across all biomes Green tea lost 2.4 times more mass [$58.9 \pm 6.5\%$, Mean of mass loss \pm Standard error (SE)] than Rooibos tea ($24.3 \pm 2.8\%$) during the 3-month decomposition period and 1.9 times more mass ($66.4 \pm 2.4\%$) than Rooibos tea ($34.9 \pm 3.2\%$) during the 12-month decomposition period (**Figure 2**). The lowest mass loss after 3 and 12 months of incubation for both tea types was observed under the arid-temperate climate, while the highest mass loss was under the warm-temperate and semiarid-tropical biomes (after 3 months of incubation) and warm-temperate and humid-equatorial biomes (after 12 months of incubation; **Figure 2**).

The 3-month mass loss of both tea types correlated positively with precipitation and temperature (**Table 3**). Tea type explained 72.5%, precipitation 1.6%, and temperature 0.2% of the variance of mass loss. When the analysis was run for each tea type separately, precipitation was positively correlated with mass loss for both Green tea (4.2% of variance) and Rooibos tea (9.2% of variance). In addition, temperature was positively correlated with mass loss of Green tea (0.9% of variance) and Rooibos tea (0.6% of variance; **Table 3** and **Figure 3**).

Similarly, the 12-month mass loss of both tea types was also strongly affected by tea type (explaining 61.8% of the variance) but less affected by tea types than 3-month incubation. As well, precipitation (2.3%), temperature (4.4%), and N deposition (0.3% of variance) were positively correlated with mass loss (**Table 3**). For Green tea, precipitation (8.2% of variance) and temperature (11.7% of variance) were in positive relationships with mass loss. And for Rooibos tea, precipitation (5.9% of variance), temperature (14.9% of variance), and N deposition (2.0% of variance) were positively correlated with mass loss.

Decomposition in the Temperate Biome

When only data for the temperate biome were analyzed, 3-month mass loss of both tea types was also positively related

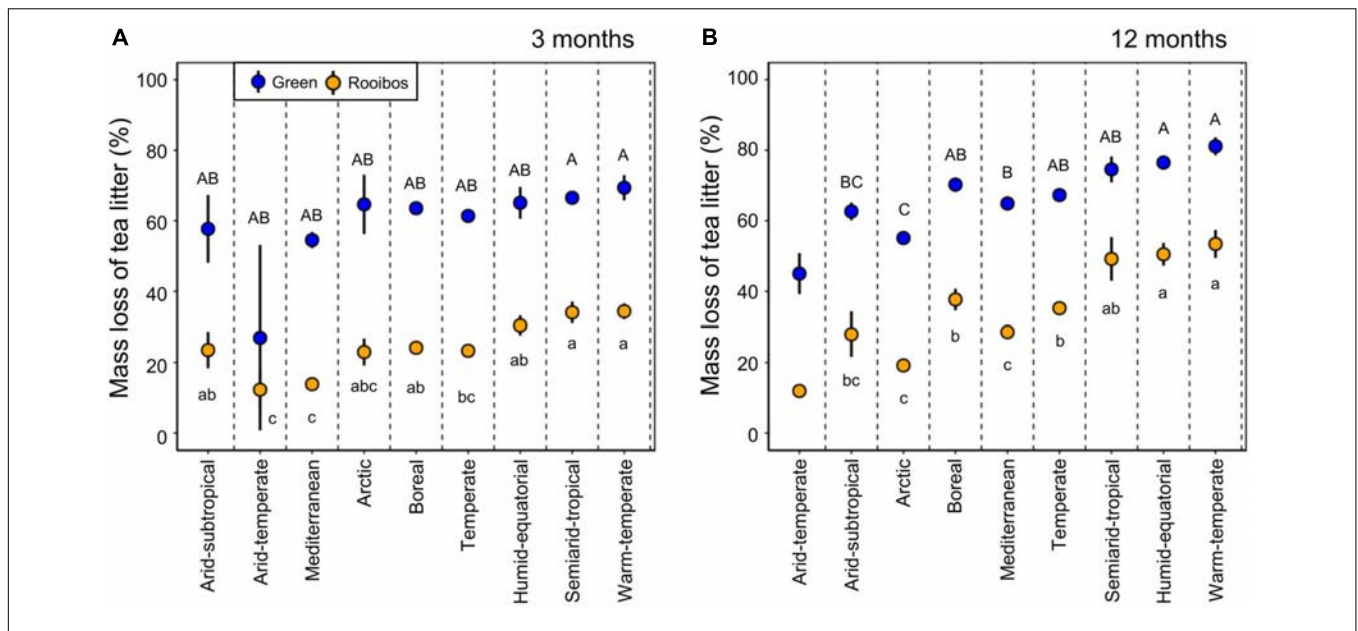


FIGURE 2 | Mass loss of tea litters (%); Green tea (blue) and Rooibos tea (orange) after the field incubation of 3 (A) and 12 months (B) across biomes. Blue and orange circles show the means, and the bars are the standard errors based on the total number of observations. Uppercase and lowercase letters denote significant differences among biomes for Green and Rooibos tea, respectively, based on a Kruskal–Wallis test ($p < 0.05$). The order of biomes follows the order of mean monthly precipitation (mm month^{-1}) for (A) and mean annual precipitation (mm year^{-1}) for (B). In case that the number of sites is <3 sites at each biome, then the data were not included in statistical analysis (i.e., Arid-temperate).

TABLE 3 | The effects of climatic factors and N deposition on the mass loss of Green tea and Rooibos tea after 3 and 12 months of incubation in all biomes.

| Tea type | Fixed effects | 3-month incubation in all biomes | | | | | 12-month incubation in all biomes | | | | |
|----------|---------------|----------------------------------|--------|--------|-----------|-----------|-----------------------------------|--------|--------|-----------|-----------|
| | | Est. (SE) | t | P | Expl. (%) | R2m/R2c | Est. (SE) | t | P | Expl. (%) | R2m/R2c |
| Both | Tea type | 38.69 (0.21) | 186.60 | <0.001 | 72.5 | 0.74/0.89 | 32.65 (0.25) | 129.84 | <0.001 | 61.8 | 0.69/0.84 |
| | Precipitation | 64.33 (9.67) | 6.65 | <0.001 | 1.6 | | 7.33 (1.02) | 7.23 | <0.001 | 2.3 | |
| | Temperature | 0.21 (0.10) | 2.15 | <0.05 | 0.2 | | 0.61 (0.06) | 10.02 | <0.001 | 4.4 | |
| | N deposition | – | – | – | – | – | 0.23 (0.08) | 2.88 | <0.01 | 0.3 | |
| Green | Precipitation | 59.40 (12.60) | 4.72 | <0.001 | 4.2 | 0.05/0.76 | 7.05 (1.08) | 6.50 | <0.001 | 8.2 | 0.20/0.74 |
| | Temperature | 0.29 (0.13) | 2.30 | <0.05 | 0.9 | | 0.51 (0.06) | 7.96 | <0.001 | 11.7 | |
| Rooibos | Precipitation | 70.18 (8.75) | 8.02 | <0.001 | 9.2 | 0.10/0.63 | 7.20 (1.23) | 5.85 | <0.001 | 5.9 | 0.23/0.67 |
| | Temperature | 0.18 (0.09) | 2.08 | <0.05 | 0.6 | | 0.70 (0.07) | 9.28 | <0.001 | 14.9 | |
| | N deposition | – | – | – | – | – | 0.34 (0.10) | 3.57 | <0.001 | 2.0 | |

Mean monthly air temperature ($^{\circ}\text{C}$), precipitation (mm month^{-1}), and N deposition ($\text{kg N ha}^{-1} \text{ month}^{-1}$) were used for the analyses of samples incubated for 3 months, while mean annual air temperature ($^{\circ}\text{C}$), precipitation (mm year^{-1}), and N deposition ($\text{kg N ha}^{-1} \text{ year}^{-1}$) were used for the analyses of samples incubated for 12 months. Est. (SE) = estimates (standard error), Expl. (%) = variance percentage explained by each fixed factor. R2m and R2c are mean marginal R^2 and conditional R^2 , respectively. Only significant fixed effects are shown. For precipitation, models were fitted with precipitation/1000 to avoid too small estimates.

to type of tea (explaining 79.2% of the variance), precipitation (0.4%) and temperature (0.3%), and negatively to N deposition (0.7%) (Table 4). When the analysis was run for each tea type separately, the 3-month mass loss of Green tea was affected by precipitation (2.4%, positively), temperature (3.8%, positively), and N deposition (6.3%, negatively), while the mass loss of Rooibos tea was affected by precipitation (2.1%, positively) and N deposition (1.3%, negatively) without the relationship to temperature.

With the progress of decomposition (12 months), we observed further a positive correlation with tea type (explaining 68.2% of the variance) and temperature (5.0%) as well as a negative correlation with the N deposition (1.7%). However, the precipitation effect was missing (Table 4). When tea types were analyzed separately, also a positive correlation of mass loss with temperature (15.4% for Green tea and 11.0% for Rooibos tea) and a negative correlation between mass loss and N deposition (9.5% for Green tea and 1.1% for Rooibos tea) were recorded.

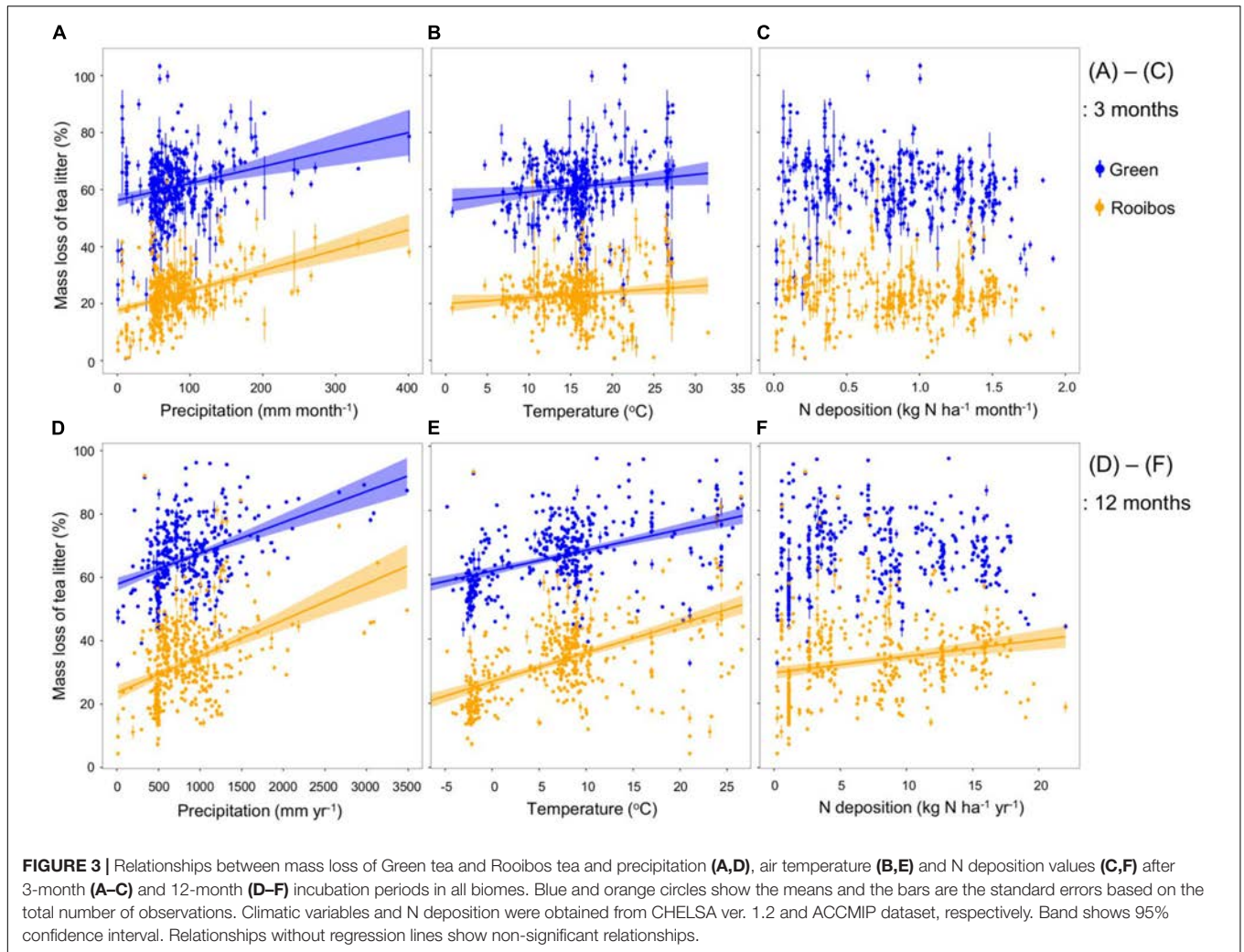
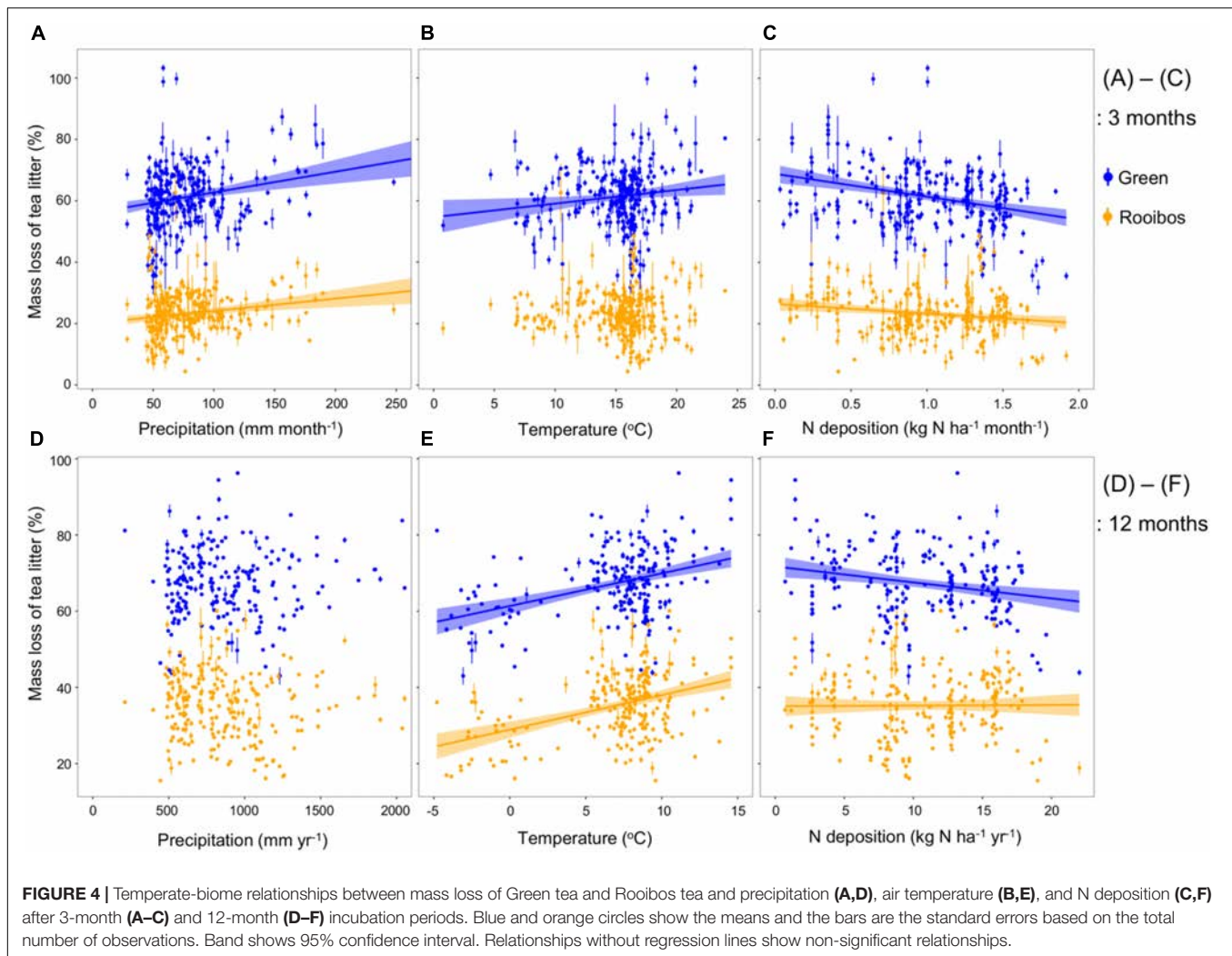


TABLE 4 | The effects of climatic factors and N deposition on the mass loss of Green tea and Rooibos tea after 3 and 12 months of incubation in the temperate biome.

| Tea type | Fixed effects | 3-month incubation in temperate climate | | | | | 12-month incubation in temperate climate | | | | |
|----------|---------------|---|--------|--------|-----------|-----------|--|--------|--------|-----------|-----------|
| | | Est. (SE) | t | P | Expl. (%) | R2m/R2c | Est. (SE) | t | P | Expl. (%) | R2m/R2c |
| Both | Tea type | 38.91 (0.21) | 182.91 | <0.001 | 79.2 | 0.81/0.91 | 33.30 (0.31) | 107.41 | <0.001 | 68.2 | 0.75/0.85 |
| | Precipitation | 42.44 (12.30) | 3.45 | <0.001 | 0.4 | – | – | – | – | – | – |
| | Temperature | 0.37 (0.13) | 2.75 | <0.01 | 0.3 | – | 1.13 (0.12) | 9.19 | <0.001 | 5.0 | – |
| | N deposition | –4.49 (1.11) | –4.06 | <0.001 | 0.7 | – | –0.54 (0.10) | –5.30 | <0.001 | 1.7 | – |
| Green | Precipitation | 50.63 (15.76) | 3.21 | <0.01 | 2.4 | 0.13/0.75 | – | – | – | – | 0.25/0.68 |
| | Temperature | 0.67 (0.17) | 3.92 | <0.001 | 3.8 | – | 1.20 (0.14) | 8.86 | <0.001 | 15.4 | – |
| | N deposition | –6.79 (1.42) | –4.78 | <0.001 | 6.3 | – | –0.77 (0.11) | –6.92 | <0.001 | 9.5 | – |
| Rooibos | Precipitation | 33.12 (12.03) | 2.75 | <0.01 | 2.1 | 0.03/0.61 | – | – | – | – | 0.12/0.49 |
| | Temperature | – | – | – | – | – | 1.02 (0.14) | 7.12 | <0.001 | 11.0 | – |
| | N deposition | –2.16 (1.08) | –2.01 | <0.05 | 1.3 | – | –0.27 (0.12) | –2.32 | <0.05 | 1.1 | – |

Mean monthly air temperature (°C), precipitation (mm month⁻¹), and N deposition (kg N ha⁻¹ month⁻¹) were used for the analyses of samples incubated for 3 months, while mean annual air temperature (°C), precipitation (mm year⁻¹), and N deposition (kg N ha⁻¹ year⁻¹) were used for the analyses of samples incubated for 12 months. Est. (SE) = estimates (standard error), Expl. (%) = variance percentage explained by each fixed factor. R2m and R2c are mean marginal R² and conditional R², respectively. Only significant fixed effects are shown. For precipitation, models were fitted with precipitation/1000 to avoid too small estimates.



No significant effect of precipitation was observed for Green and Rooibos teas (Table 4 and Figure 4).

Effects of Projected Future Climate and N Deposition on Litter Decomposition Across All Biomes

We investigated the effects of future climate scenarios (RCP 2.6 and RCP 8.5; Table 2) on the overall tea mass loss for the 12-month incubation. Across all biomes, we found a 2.2–6.2% increase in predicted mass loss (relative to mass loss in current period) for both types (Table 5). In general, the predicted increase in mass loss appeared to be higher under the RCP 8.5 (3.5–10.6%) than under RCP 2.6 scenario (<3.8%). Positive effects of increased air temperature on mass loss of both litter types were 3.0–4.9 times and 2.0–5.5 times higher than those of the predicted change in precipitation and N deposition, respectively. We noticed a much higher increase in mass loss for the litter material of Rooibos tea (3.8–10.6%) as compared to the more labile litter of Green tea (1.1–3.5%). The effects of air temperature as compared to precipitation seem to be greater on the mass

loss of the more stable material of Rooibos tea (3.3- to 5.7-fold greater) than those of the mass loss of more labile Green tea material (2.7- to 4.0-fold). In addition, mass loss of Rooibos tea increased by the increase of N deposition from 1.2% to 1.9%.

Decomposition in the Temperate Biome

In the temperate biome, models predicted a 0.9–6.2% increase in mass loss (relative to the current conditions) for both types of tea (Table 5). In contrast to the global scale, we noticed only the effect of air temperature change (2.2–8.1%) by RCP 2.6 and RCP 8.5, but not of precipitation, on the overall mass loss of both tea types. Similar to the global scale, the mass loss of the more stable Rooibos tea material showed much higher increase (2.0–9.3%) than that of the more labile Green tea material (0.4–4.4%). Further, the effect of air temperature on mass loss of Green tea (1.8–6.6%) was slightly lower than on Rooibos tea (2.9–10.7%). The predicted change of N deposition in the temperate biome reduced the mass loss of both teas (1.3–2.0%), whereby the mass loss of the Green tea (1.4–2.2%) appeared to be slightly more inhibited than that of Rooibos tea (0.9–1.5%).

TABLE 5 | The percent change of mass loss of Green tea and Rooibos tea by the end of the 21st century relative to the current period, induced by the changes of mean annual temperature (MAT), mean annual precipitation (MAP), and N deposition across all biomes and in the temperate biome after 1 year of decomposition.

| | All biomes | | | Temperate biome | | |
|---------------|------------|-----------|-------------|-----------------|-----------|-------------|
| | Both teas | Green tea | Rooibos tea | Both teas | Green tea | Rooibos tea |
| ΔMAT | 1.2–4.4 | 0.8–2.8 | 2.0–7.4 | 2.2–8.1 | 1.8–6.6 | 2.9–10.7 |
| ΔMAP | 0.4–0.9 | 0.3–0.7 | 0.6–1.3 | – | – | – |
| ΔN deposition | 0.6–0.8 | – | 1.2–1.9 | –1.3––2.0 | –1.4––2.2 | –0.9––1.5 |
| Sum | 2.2–6.2 | 1.1–3.5 | 3.8–10.6 | 0.9–6.2 | 0.4–4.4 | 2.0–9.3 |

DISCUSSION

Climate and N deposition effects on litter decomposition are complex and highly uncertain considering our present knowledge but of significant importance for the global carbon dynamics and assessment of future trajectories. The direct and indirect effects of these environmental changes on litter decomposition are not necessarily consistent between litter quality types (Coûteaux et al., 1995), decomposition stages (Berg, 2014), and environmental conditions (Delgado-Baquerizo et al., 2015; Frøseth and Bleken, 2015). Here we studied the mass loss as the decomposition degree of Green and Rooibos teas across 524 sites with contrasting climate and N deposition conditions. Our results show that litter quality > climate > N deposition are key factors for litter decomposition, with litter quality being most important throughout the observation period, while the effects of climate and N deposition change over decomposition time and space.

Impacts of Climate and N Deposition on Litter Mass Loss

The abiotic and biotic factors regulating decomposition can change over time (Berg and McLaugherty, 2020; Canessa et al., 2021). In our study, litter quality explained a major part of the variance in mass loss both after 3 months (73%) and 12 months (62%) of incubation on the global scale. This is in accordance with several studies showing a positive relationship between litter quality and mass loss or decomposition rate (Zhang et al., 2008; Kang et al., 2009; Djukic et al., 2018; Fanin et al., 2020; Canessa et al., 2021). However, the extent of the effects of climatic variables changed with the stage of decomposition, with precipitation being most important during the 3-month incubation and the air temperature during 12 months of incubation for Green and Rooibos teas. A possible reason for this observation may be due to the fact that initial incubation occurred in the summer months, when precipitation was likely the main limiting factor for the majority of biomes (Prescott, 2010). Moreover, temperature variations during the summer months are smaller compared to the entire year (Karger et al., 2017), and the limiting factor for decomposition during dry seasons is water availability. In addition, during the initial decomposition phase, litter mass loss is dominated by the leaching of soluble compounds (e.g., Hagedorn and Machwitz, 2007; Djukic et al., 2018; Mori et al., 2020; Trevathan-Tackett et al., 2020), which is controlled by precipitation (Ristok et al., 2017). In later stages of decomposition, the microbial degradation of more stable components becomes

increasingly important, which depends on both air temperature and precipitation (e.g., Davidson and Janssens, 2006). Rather optimal ranges between air temperature and precipitation were likely responsible for the high mass loss of both tea types as observed for the warm-temperate, humid-equatorial, and semiarid-tropical climates. In contrast, the extreme ranges of temperature and/or precipitation are likely to explain the low mass loss of both tea types at arid-temperate, arid-subtropical, and arctic climates.

In our study, the effect of N deposition was litter-specific, and only of significant importance for Rooibos tea during the 12-month period at the global scale. Previous studies have shown that N effects on litter decomposition can be positive, negative, or near zero, depending on litter quality, degree of decomposition, as well as N saturation status of the ecosystems (Knorr et al., 2005; Hobbie, 2008; Prescott, 2010; Berg, 2014). The observed positive effect of N deposition on the mass loss of Rooibos tea (~35%) after 12 months, can be related to the stimulated decomposition of the more labile cellulose substrate through the N deposition (Wang et al., 2019; Berg and McLaugherty, 2020) during the early stage of decomposition (0–30% mass loss). In contrast, the progressed decomposition of Green tea (~66% of mass loss) is likely limited by the carbon and nutrient accessibility in the remaining litter, which are essential for the microbial function at the later stage of decomposition (Fanin et al., 2020). In addition, large variability in microclimatic conditions at the global scale as well as very coarse resolution of the available N deposition data (~100 km) is likely masking the effect of N deposition. Hence, it is therefore necessary to consider the variability in the N deposition at the narrower spatial scale for the better understanding of the global decomposition processes.

In the temperate biome, we observed a negative relationship between N deposition and mass loss of both tea types after 3 and 12 months of incubation. Knorr et al. (2005) showed that ecosystems with N deposition rates between 5 and 10 kg N ha⁻¹ year⁻¹ experience an inhibitory effect on litter decomposition. The high N inputs might decrease the demand of decomposers to acquire litter-derived N, when they are supplied with external N. Especially in the progressed decomposition stage, high N inputs may suppress the activity of lignolytic fungi and their oxidative enzymes and consequently suppress decomposition processes (Carreiro et al., 2000; Hobbie, 2008; Hobbie et al., 2012; Berg and McLaugherty, 2020).

Our study underlines the importance of considering the effects of different drivers in time and space for a better

understanding of litter decomposition processes. Especially analyses of litter chemistry, soil properties, soil biodiversity, and their interactive effects (Mori et al., 2021) on decomposition processes are crucial for improved understanding of this fundamental biogeochemical process.

Impacts of Predicted Climate and Atmospheric N Deposition on the Decomposition Process

Our analyses of 1-year mass loss indicate that the expected changes in macroclimate by 2100 at the global scale will increase the mass loss of Green and Rooibos tea. The mass loss of more stable litter seems to be more affected by future warming than that of easily decomposable substrates (Table 5). The intrinsic temperature sensitivity is closely related to the molecular structure of the substrate and increases with its increasing molecular complexity (Davidson and Janssens, 2006), which is also in accordance with our findings across heterogeneous soil environments. However, several other environmental constraints on litter decomposition (such as N deposition) need to be discussed within the context of climate change. Future atmospheric N deposition is expected to have a strong effect on soil biogeochemical processes (Gaudio et al., 2015). In our study, the predicted increase in N deposition by 2100 shows also an enhancing effect on the mass loss of Rooibos tea at the global scale. Moreover, when taking into consideration the combined effects of organic N deposition (~30% of total N deposition globally; Neff et al., 2002; Cornell, 2011) and inorganic N deposition on litter decomposition, the effect of the total N deposition may be higher than our calculated estimates. Thus, the accelerated mineralization of the more stable substrate through the increase in temperature and N deposition might have profound implication for the global C budget. In turn, climate warming as well as higher N deposition might lead to a shift in the structure of plant communities (Cornelissen et al., 2007), changes in microclimate (Wang et al., 2019), increases in plant growth (Prescott, 2005; Bobbink et al., 2010; Bringmark et al., 2011; Fröberg et al., 2011), changes in litter quality [e.g., increase of litter N (Henry et al., 2005)], changes in soil C:N ratio (Mulder et al., 2015), and changes in soil microbial communities (Carreiro et al., 2000; Hobbie et al., 2012; Leff et al., 2015) with a potentially compensating effect of litter C mineralization.

In the temperate biome with higher average annual N deposition compared with other biomes, however, the predicted change in N deposition may lead to a decrease in mass loss of both high- and low-quality litters. Thus, the negative effect of N deposition on litter mass loss might mitigate, but not offset, the climate change-induced increase of litter decomposition at the regional level (cf. Berg, 2014). The effects of increased N deposition were quite small (means 1–2%) relative to the effect of increased temperature (means 2–8%) and probably irrelevant for plant species occurrence (Dirnböck et al., 2017). Moreover, Forstner et al. (2019) concluded that an accumulation of soil organic carbon in the organic layer through N addition in temperate forests might be even more sensitive to the CO₂ release in case of disturbances or changing environmental conditions

due to the lower degree of physicochemical protection of this soil layer.

Hence assessing the effects of co-occurring global change factors on biogeochemical processes at different geographical scales (e.g., Forstner et al., 2019; Rillig et al., 2019; Bowler et al., 2020) are of significant importance for understanding the relationships between C and N dynamics during different stages of litter decomposition.

CONCLUSION

Our results suggest that litter quality and climate were the most significant drivers of early-to-mid-stage litter decomposition. In addition, climate change and the excess of N deposition might accelerate the decomposition of more stable substrate at the global scale. However, at the regional scale future N deposition seems to have the capacity to dampen the predicted climate change effect. Studying the litter decomposition process over different time and spatial scales requires consideration of complex interplay of different parameters. For a better understanding of global and regional litter decomposition dynamics, we need to increase our basic knowledge on litter-ecosystem interactions in particular on the role of litter chemistry, soil properties (Wang et al., 2019), and biodiversity in decomposition process (Crowther et al., 2019). Moreover, pulsed nature of precipitation and temperature events rather than average annual values needs to be taken into the consideration for the certain biomes (Currie et al., 2010). Considering that the driving factors of litter decomposition at the global scale do not necessarily reflect those at the regional or local scale, a more representative site distribution across the globe is needed to address knowledge gaps in the decomposition process in future studies (Virkkala et al., 2019). There is also a need for better N-deposition products at high spatial and temporal resolutions to capture its variability significant for understanding of N-deposition-decomposition relationships.

Our study indicates that global collaborative research with standard protocols such as the TeaComposition initiative is a powerful approach for global synthesis. Through the collaborative efforts, the valuable add-ons to the ongoing TeaComposition work will be included such as analyses of litter chemistry and soil biodiversity (e.g., Soil BON, Guerra et al., 2021) relevant for a comprehensive understanding of litter decomposition under climate change and atmospheric N pollution.

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DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

ID designed and coordinated the study with extensive input from CB. IS, SK-R, and KL accomplished data preparation. TK conducted statistical analyses and wrote the manuscript with contributions from all authors. The TeaComposition team implemented the study, provided site specific and climatic data, and contributed to manuscript editing.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/ffgc.2021.678480/full#supplementary-material>

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