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Climate control of litter decomposition and nutrient release in tropical and sub-tropical forest biomes of Northeast India

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ABSTRACT

Litter decomposition is fundamental to nutrient cycling in forest ecosystems across the globe and is affected by abiotic and biotic factors. Thus, patterns of litter decomposition and nutrient release vary among different terrestrial ecosystems depending on climatic conditions. We followed the decomposition of litter from four species as well as a mixed litter in contrasting sub-tropical (STF) and tropical (TF) forests of North-east India to assess the factors influencing decomposition between them. Mass loss and concentrations of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), manganese (Mn) and sulfur (S), as well as acid-unhydrolyzable residue (AUR) ('lignin') were followed over a one-year period. We found clearly different decomposition patterns in the two forest types. In the TF, decomposition followed the single exponential function indicating a complete disappearance of litter material within a year. In contrast, in the STF, the mass loss pattern followed an asymptotic function with a limit value indicating a stable fraction. The AUR decomposition rate was about twice as fast in the TF as compared to the STF. Litter decomposition and nutrient release were faster in the TF compared to the STF, and hence carbon and nutrients were accrued in the soil organic matter in the latter but not in the former due to contrasting environmental conditions. It is concluded that the mechanism for complete decomposition in TF as compared to STF is strongly influenced by the climate rather than any intrinsic factors.

1. Introduction

Globally, tropical forest biomes harbor over half of the world's species, cycle key nutrients, exchange large quantities of carbon (C) and water with the atmosphere, and thus play a critical role in global biogeochemical cycling (Slik et al., 2013; Lewis et al., 2015). These forests are being degraded due to expanding human populations and increasing demand for agricultural land (Lewis et al., 2015). Tropical moist deciduous forests and sub-tropical broad-leaved forests account for about 30 % of the total forested area globally (Pan et al., 2013). These two forest types show distinct differences in climate and tree species composition; therefore the production of litter, its decomposition and nutrient dynamics are likely to differ between them, affecting their ecological functioning.

In forests, litterfall is a major source of organic matter and nutrients to the soil, and in tropical forests, foliar litter accounts for about two-thirds of the aboveground litter production (Krishna and Mohan, 2017), with non-foliar litterfall composed of small branches, twigs, and reproductive structures (Proctor et al., 1983; Lalnunzira and Tripathi, 2018). The soil fertility of a site determines how much litterfall falls there, while other factors like soil moisture content and air temperature can also affect how much litter is produced in the forest (Pitman, 2013).

In both tropical and sub-tropical forests, the variation in temperature and soil moisture influence the rate of litter decomposition and mineralization of nutrients in the soil (Tripathi and Singh, 1992a,1992b; Paudel et al., 2015) by regulating the activity of decomposer microbes (De Marco et al., 2018) and larger organisms such as macro- and mesofauna (Powers et al., 2009). Nutrients contained in the litter are released during the process of decomposition, becoming available to plants (Aponte et al., 2012; Ge et al., 2017; Sun et al., 2019), but different nutrients may be released from leaf litter at differing rates depending upon their relative limitations to the decomposition process, with nutrients that limit the decomposition process being accumulated and/or immobilized, whereas those that are in excess of the requirements of the decomposers will be released more rapidly from the litter (Tripathi and Singh, 1992b; Aponte et al., 2012). Litter decomposition is also influenced by different abiotic factors that vary with the ecosystem (Sellan et al., 2020; Singh and Tripathi, 2020; Singh et al.,

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2022) and the quality of the litter (Berg and McClaugherty, 2008; Powers et al., 2009).

In tropical forests, litter decomposition rates are fast, and consequently, there is rapid nutrient release with high mass loss due to the dominance of white-rot fungi (Yamada et al., 2005). Furthermore, in tropical rain forests, litter decomposition and nutrient release rates increase with increasing precipitation (Liu et al., 2022). In contrast, in sub-tropical forests, the lower soil temperature results in slower litter decomposition (Liu et al., 2005).

In addition to abiotic factors, the high variation in the initial chemistry (substrate quality) affects decomposition rates and nutrient release patterns. Substrate quality, *viz.*, concentrations of e.g. lignin and nutrients, is widely reported to strongly influence litter decomposition (Yamada et al., 2005; Pandey et al., 2007; Lalnunzira and Tripathi, 2018; Sun et al., 2018; Bohara et al., 2019). Further influential factors are polyphenol concentrations, the lignin-to-nitrogen (N) ratio, C:N ratio (Pérez-Harguindeguy et al., 2000; Krishna and Mohan, 2017; Qu et al., 2019) and the litter's concentration of manganese (Mn) (Hatakka 2001; Berg and McClaugherty, 2008). Among these factors, concentrations of N and lignin have been suggested as the most important factors to regulate decomposition (Gartner and Cardon, 2004). While N concentrations may promote the process of litter decomposition in the initial stages, it also retards the process of litter decomposition in the later stages, i.e., the stage in which decomposition is dominated by lignin (Berg and McClaugherty, 2008). In addition, the leaf litter of evergreen species usually decomposes more slowly than that of deciduous species (de Paz et al., 2017) due to a lower specific leaf area and tougher leaves (Cornelissen et al., 1999; Rahman and Tsukamoto, 2013).

The present study was designed to assess litter production and decomposition in a moist tropical deciduous forest and a semi-evergreen sub-tropical forest that have clear differences in climate as well as in species composition, thus resulting in litter with different properties. We focus on two litter species from each forest type and a mixed, standardized litter. This study hypothesizes that the litter production, decomposition rates, and nutrient release patterns would vary between the two forest types having different climates and biota.

2. Materials and methods

2.1. Study sites

Study sites were selected based on Champion and Seth's (1968) Indian forest classification type. They were both found in Mizoram, a state in Northeast India, and both were forests over 80 years old. The first site was a sub-tropical forest (STF) at Hmuifang Forest Reserve, located at 23°27′ N; 92°45′ E and an elevation of 1455 m a.m.s.l. The second site was selected in the tropical forest (TF) area at Sairang Forest, located at 23°49′ N; 92°39′ E and an elevation of 100 m above mean sea level (Singh et al., 2021). The sites differed in vegetation and climate; at the STF site, the climate was cool, with daily temperatures ranging from 20 to 30°C in summer and 4 to 21°C in winter, with a mean annual precipitation of 2960 mm, whereas at the TF site, the climate was humid, with temperatures ranging from 25 to 34°C in summer and 9 to 26°C in winter with a mean annual precipitation of 3080 mm (Fig S1). At the STF site, the dominant plant species were *Quercus floribunda* (Fagaceae) and *Drypetes indica* (Putranjivaceae). At the TF site, *Melocanna baccifera* (Poaceae) and *Tectona grandis* (Lamiaceae) were dominant. At each site, a plot with a size of 1 ha was selected for measurements of litterfall and litter decomposition.

2.2. Climate data and soil sampling

Data on air temperature and precipitation were collected from the nearest weather stations, namely at the Agriculture Department in the village of Sialsuk for the STF and at the town of Lengpui for the TF. Both climate stations are located approximately 10 km from each site and at the same altitude (Fig. S1). Data on soil temperature and soil moisture was collected during monthly field visits.

At each site, soil samples (0 to 15 cm depth) were collected from three random locations using a soil corer of 4.2 cm diameter. Bulk density (BD; g cm^{-3}) was calculated using soil cores of known volume (4.2 cm diameter and 10 cm depth) and expressed as dry soil weight (Brady, 1984). Soil texture was determined using the hydrometer method (Gee and Bauder, 1986). Soil pH was determined in 1:2.5 soil/distilled water suspension using a Mettler-Toledo pH meter. Soil microbial biomass carbon (MBC) was determined by the chloroform fumigation extraction method (Brookes et al., 1985). Within a few days of collection, soil samples were divided into two 25 g subsamples. One subsample was transferred to a 50 ml beaker and fumigated with chloroform for 24 h in a desiccator, whereas the other subsample remained unfumigated. Soils were extracted with 100 ml 0.5 M K_2SO_4 on an orbital shaker for 30 min at 200 rpm. The extracts were filtered using Whatman No 42 filter paper and 10 ml of supernatant was used for the determination of C using the wet oxidation method (Walkley and Black, 1947). The difference in C content between fumigated and non-fumigated extracts was multiplied by the constant $k_{EC} = 0.38$ (Vance et al., 1987; Wu et al., 1990; Dilly and Munch, 1998) (Table S1). Soils were air-dried, ground, sieved through a 1-mm mesh, and oven-dried at 40°C for 48 hrs. Carbon and N concentrations were determined using a Euro Vector Euro EA3000 CHNS/O elemental analyzer. Available phosphorus (P) was determined by the method of Bray and Kurtz (1945), using a spectrophotometer at 660 nm.

2.3. Litterfall

Litter input at each forest site was determined using 10 randomly placed nylon net litter traps, located within the 1-ha permanent plots, at 15 to 25 m distance from one another. Each trap measured 50 cm × 50 cm, was 15 cm deep, with a 1.5-mm mesh net, and was installed 50 cm above the ground. Litter traps were emptied at monthly intervals from June 2015 through May 2016. Collected litter was sorted into foliar and non-foliar fractions, oven-dried at 60 °C for 72 hrs and weighed.

2.4. Collection of litter and preparation of litter bags

Litter intended for the decomposition study was taken from the two dominant species at each site, namely *Q. floribunda* (QF) and *D. indica* (DI) from the STF, and *T. grandis* (TG) and *M. baccifera* (MB) from the TF. Freshly senesced leaves were collected from 15 to 20 different trees per species at each site by shaking the branches/culms. In addition, we prepared a mixed litter, by combining equal proportions of litter from *M. baccifera, T. grandis, Q. floribunda, D. indica* and a *Castanopsis* species (Fagaceae) which was a common species at both sites. This mixed litter, identical for both sites, was denominated M1 for the STF and M2 for the TF site.

Air-dried leaf litter (10 ± 0.01 g) was enclosed in nylon litter bags (15 × 15 cm with 1-mm mesh). The exact moisture content (c. 5-7 %) in the initial air-dried litter samples was determined by placing them ($n = 10$) in an oven at 60 °C for 72 hrs and the litter mass of the samples was expressed on an oven-dry mass basis. A total of 432 bags (216 at each site) were placed randomly on the soil surface among six locations with 15 to 25 m distance between them. Monthly, 18 litter bags (6 bags from each litter type) were retrieved from each site, cleaned by removing adhering soil particles and dried at 60 °C for 72 hrs. Dried litter samples were ground and sieved through a 1-mm mesh for further analysis.

2.5. Chemical analysis of leaf litter samples

Ash content of litter samples was determined as loss-on-ignition at 500 °C for 4 hrs. Carbon and N content were analyzed using a Euro Vector EuroEA3000 CHNS/O elemental analyzer. For the analysis of phosphorus (P), potassium (K), magnesium (Mg), calcium (Ca),

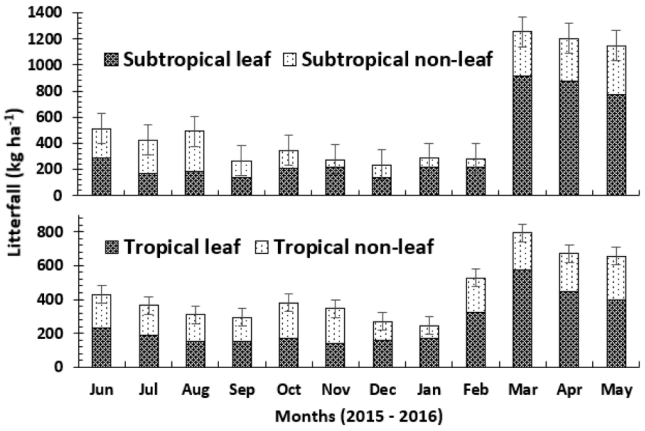

Fig. 1. Monthly litterfall of leaf and non-leaf litter fractions at a sub-tropical and tropical forest site in Mizoram, North-east India, over the period from June 2015 to May 2016. Vertical lines above all bars represent ± 1 SE.

manganese (Mn) and sulfur (S), samples (0.1 g) were digested in 10 ml of 'reverse' aqua-regia (HNO_3 + HCl, 3:1 ratio) using a Mars Xpress 5 (CEM Corporation) microwave oven. The samples were diluted 1:10 in deionized water and then analyzed using a Thermo Scientific iCAP 6300 inductively coupled plasma optical emission spectrophotometer. For quality control, a certified reference material (Strawberry Leaves, LGC 7162) was analysed alongside the samples.

2.5.1. Gravimetric lignin/acid-unhydrolysable residue (AUR)

Gravimetric lignin was analyzed using a Fibrotron Automatic Fibre Analysis (Model: FRB 6; Tulin Equipments, Chennai, India). Lignin was determined by Acid Detergent Solution (ADS) hydrolysis, using 1 N H_2SO_4 plus 2 % Cetyl Trimethyl Ammonium Bromide (CTAB). Samples (0.5 g) were weighed and placed in oven-dried glass crucibles that were boiled for 10 min at 350 °C with 100 ml ADS, followed by 30 min at a lower temperature of 250 °C. The remaining mass was determined after drying at 60 °C for 48 hrs until constant weight. Lignin content was calculated as a percentage of the original sample mass. We adopted the term acid-unhydrolyzable residue (AUR) as, to some extent, gravimetric lignin includes cutins and tannins (Preston et al., 2009).

2.5.2. Decomposition patterns and rate constants

We used two equations to estimate rate constants and decomposition patterns. The annual decay constant (k_S) was calculated using the negative exponential model of Olson (1963):

$$W_t/W_o = \exp^{(-kt)} \quad (1)$$

where W_t = weight remaining after time t, and W_o = initial weight. As suggested by Olson (1963), the time required for 50 % and 95 % weight loss was calculated as $t_{50} = 0.693/k$ and $t_{95} = 3/k$. We also used the asymptotic function (Wider and Lang, 1982), which is applied for accumulated mass loss:

$$L_t = m\left(1 - e^{-k_A t/m}\right) \quad (2)$$

where L_t is the accumulated mass loss (in percent), t is time in days and k_A is the decomposition rate. m represents the asymptotic level or limit values that the accumulated mass loss will finally reach before decomposition declines markedly or even stops; this value is often considerably less than 100 % (Berg, 2014). The k_A of this function is variable.

2.6. Statistical analyses

One-way ANOVAs were performed to compare mean values of C and nutrient concentrations in initial leaf litter among the litter types. Least Significant Differences (LSD) were employed for various soil physico-chemical properties to test the significant differences between soils at the two sites. Further, LSD tests were performed to assess significant differences in rates and limit values for the different litter types. Linear regressions were made between litter variables, i.e. N, P, lignin and accumulated litter mass loss followed by multiple comparisons (post-hoc tests) to test significant differences among the slopes of the linear relationships obtained. All the above analyses were conducted using MS Excel and IBM SPSS v. 18.0 software Pearson's correlations were performed to identify the significant relationship between climatic factors and the patterns of decomposition of various litter types using OriginPro v. 22.

3. Results

3.1. Annual litter production

Total annual litter production was 6720 and 5290 kg ha^{-1} yr^{-1} in the STF and TF sites, respectively (Fig. 1). Litterfall was highly seasonal with the main fall occurring during the dry period of the year (March to May), and a lower fall more evenly distributed during the period from June to February (Fig. 1). Foliar litter production accounted for 64 % of the total litterfall at the STF site and 59 % at the TF site.

3.2. Chemical composition of the initial litter

The initial concentrations of the important elements (e.g. C, N, P, S, K, Mg, Ca and Mn) and AUR varied among the four species (Table 1). There was no general difference between the litters from the two sites, but rather a variation among species. The litter of *M. baccifera* was

Table 1
Mean (±1 standard error) concentrations of the main nutrients, C, AUR/lignin as well as ash in the newly shed leaf litters and in mixed leaf litter in a tropical and a sub-tropical forest in Mizoram, North-east India.

Litter type	C	N	P	S	K	Mg	Ca	Mn	AUR/lignin	Ash content
Drypetes indica	434 ± 0.1^{c}	10.1 ± 0.06^{d}	0.06 ± 0.01^{d}	0.17 ± 0.02^{c}	0.24 ± 0.02^{d}	0.16 ± 0.01^{d}	2.77 ± 0.14^{b}	0.07 ± 0.01^{bc}	148 ± 0.61^{a}	51 ± 0.5^{b}
Quercus floribunda	479 ± 1.5^{b}	11.9 ± 0.14^{c}	0.07 ± 0.02^{cd}	0.17 ± 0.02^{c}	0.38 ± 0.01^{c}	0.28 ± 0.01^{c}	1.49 ± 0.01^{d}	0.16 ± 0.02^{a}	147 ± 1.0^{a}	44 ± 1.1^{bc}
Melocanna baccifera	370 ± 0.7^{d}	22.1 ± 0.09^{a}	0. 29 ± 0.01^{a}	0.51 ± 0.01^{a}	0.99 ± 0.05^{b}	0.52 ± 0.01^{a}	2.07 ± 0.04^{c}	0.11 ± 0.01^{ab}	125 ± 0.82^{b}	32 ± 0.8^{c}
Tectona grandis	487 ± 1.2^{a}	10.2 ± 0.07^{d}	0.14 ± 0.01^{b}	0. 19 ± 0.02^{bc}	1.15 ± 0.01^{a}	0.34 ± 0.02^{c}	1.51 ± 0.06^{d}	0.02 ± 0.02^{c}	154 ± 1.1^{a}	73 ± 0.5^{b}
Mixed litter*	480 ± 1.1^{b}	15.1 ± 0.11^{b}	0.11 ± 0.01^{bc}	0.25 ± 0.01^{b}	0.30 ± 0.01^{cd}	0.42 ± 0.01^{b}	3.58 ± 0.03^{a}	0.13 ± 0.01^{a}	148 ± 1.7^{a}	72 ± 4.1^{b}

*Mixed leaf litter contained five species in equal proportions, namely of all four local litter types plus a *Castanopsis* species. Significance was determined as per multiple comparison (post hoc) tests by performing LSD (Least Significant Different). All values are mg g^{-1}; $n = 3$ except for the mixed leaf litter ($n = 6$). Different letters in superscript indicate significant differences at $p < 0.05$ within each column.

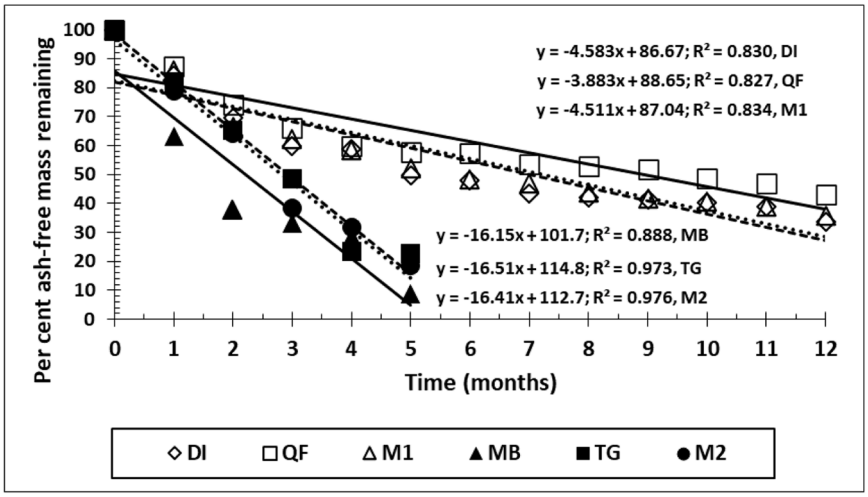

Fig. 2. Linear relationships between remaining ash-free litter mass and time for two local leaf litter types in a tropical forest (TG = *T. grandis*, MB = *M. baccifera*) and a sub-tropical forest (QF = *Q. floribunda*, DI = *D. indica*) as well as two mixed leaf litter preparations incubated in the two forest sites in Mizoram, North-east India. All linear relationships were significant, for the tropical forest at least at $p < 0.05$ and for the sub-tropical forest at least at $p < 0.001$. See also slopes in Table 2.

Table 2
Decay constant (k_S, yr^{-1}), limit values, initial asymptotic rates (k_A), and slopes for remaining mass versus time, as well as measured remaining ash-free leaf litter mass at the end of the study, viz. at 365 days in a subtropical forest and at 153 days in a tropical forest in Mizoram, North-east India.

Site	Litter type	Remaining litter mass (ash free) (%)	Decay constant (k_S) (yr^{-1})	R^2	Limit value (%)	k_A	Slope remaining mass (% m^{-1})	Slope remaining AUR mass (% m^{-1})
Subtropical local	*Drypetes indica*	33.8^a	1.34^a	0.88	64.6^a	225^a	-4.55^a	-4.34^a
	Quercus floribunda	43.3^b	1.01^b	0.85	55.8^b	178^b	-3.88^b	-3.81^b
Tropical local	*Melocanna baccifera*	8.7^a	4.87^a	0.97	93.6^a	240^a	-16.2^a	-18.9^a
	Tectona grandis	22.7^b	3.23^a	0.96	263^b	537^b	-16.5^b	-17.2^b
Mixed litter	M1	35.7^c	1.33^a	0.86	63.7^a	220^a	-4.51^a	-6.26^a
	M2	18.6^c	3.41^a	0.98	153^b	272^b	-16.4^b	-11.1^b
Mean ± 1SE	All subtropical	37.6 ± 1.0	0.87 ± 0.02		60.7 ± 1.4	208 ± 5.3	−4.30 ± 0.1	−4.83 ± 0.7
	All tropical	16.6 ± 1.4	4.30 ± 0.12		170 ± 17.2	349 ± 32.3	−16.3 ± 0.1	−15.7 ± 2.3

Note: One way ANOVA was used to calculate the least significant difference (LSD). The values for k_s and k_A in the tropical forests as well as slope for remaining mass were significantly ($p < 0.05$) greater than the sub-tropical forest. Limit values in the two forests were significantly different at $p < 0.01$. Significant differences ($p < 0.05$) across the leaf litter types in the forests are shown by different superscript letters within each group (viz. subtropical, tropical and mixed litter).

richest in N (22.1 mg g^{-1}) and S (0.51 mg g^{-1}) and this species, along with *T. grandis*, was richer in P than the two STF species. There was no significant difference between sites in litter Ca, but *M. baccifera* and *D. indica* had greater concentrations than *T. grandis* and *Q. floribunda*. The two litters from the TF had significantly greater K and Mg concentrations than the two STF litters. The greatest Mn concentration was observed in *Q. floribunda* litter and the lowest in that of *T. grandis,* whereas the litter of the other two species had intermediate concentrations. Carbon concentrations were greatest in the *T. grandis* litter and least in that of *M. baccifera*, which was similar to the differences in AUR concentrations.

The initial chemical concentrations in the mixed litter at both sites were within the ranges of the local litters, with one exception: Ca (3.58 mg g^{-1}), which was significantly greater in the mixed litter than the local litters (Table 1).

3.3. Litter mass loss patterns

The litters at the TF site clearly decomposed faster than that of STF site (Fig. 2; Table 2). After the first three months, there was already a difference in mass loss between the litter types and sites. After one year, the litter of *D. indica* and *Q. floribunda* had lost 64.5 % and 55.8 % of their mass, respectively; in contrast, the litter of *T. grandis* had lost 77.3 % of its mass and that of *M. baccifera* lost 91.3 % in less than half that time. There were significantly greater values for both the single exponential rate constant (k_S) and the initial asymptotic function (k_A) for the two TF litters compared to the STF litters (Table 2). The STF litters followed the asymptotic function well and gave limit values for *D. indica* (64.6 %) and *Q. floribunda* (55.8 %). At the TF site, *M. baccifera* litter decomposed more completely and gave a limit value of 93.6 %, which was not significantly different from 100 %. The *T. grandis* litter did not give any limit value as the calculated asymptote was well above 100 %. For the TF site, the single exponential function fitted better than the asymptotic function (Table 2). Comparing the slopes for remaining mass versus time showed negative linear relationships at both sites (Fig. 2). In the STF, the slopes of these relationships were significantly less steep ($p < 0.001$) than those in the TF (Table 2).

At the STF site, the mixed litter (M1) decomposed at about the same rate as the local litter (Table 2) with the slope for the remaining mass versus time being 4.5 % mo^{-1}; this slope was not significantly different from that of the *D. indica* litter. For the TF site, the mixed litter (M2) slope had a value of −16.4 % mo^{-1}, which was not different from that of the two local litters. Furthermore, similar to the two local litters, the mixed litter at the TF site gave a limit value that indicated complete decomposition, namely well above 100 % (Table 2). In contrast, at the STF site, the mixed litter gave a limit value of 63.7 %.

Table 3
Relationships between concentrations of elements and AUR versus accumulated mass loss in the decomposing leaf litters of four species in a tropical and a sub-tropical forest in Mizoram, North-east India.

Element/Species	Regression	R^2	*P*-value
AUR			
D. indica	$y = 0.0019x + 0.138$	0.924	<0.0001
Q. floribunda	$y = 0.0023x + 0.175$	0.878	0.003
Mixed litter M1	$y = 1.5705x + 165.9$	0.860	0.003
T. grandis	$y = -0.00005x^2 + 0.0046x + 0.163$	0.936	0.003
M. baccifera	$y = -0.0004x + 0.126$	0.816	0.022
Mixed litter M2	$y = 1.8267x + 149.3$	0.950	0.0004
Nitrogen			
D. indica	$y = 0.0009x^2$ - 0.0126x + 10.51	0.827	0.013
Q. floribunda	$y = 0.1462x + 12.17$	0.985	<0.0001
Mixed litter M1	$y = 0.017x + 0.195$	0.826	0.002
T. grandis	$y = 0.0708x + 11.86$	0.713	0.072
M. baccifera	$y = -0.0047x + 0.5104$	0.953	0.001
Mixed litter M2	$y = 0.004x + 14.75$	0.043	0.74
Phosphorus			
D. indica	$y = 0.0004x + 0.0641$	0.501	0.15
Q. floribunda	$y = 0.0003x + 0.0749$	0.300	0.34
Mixed litter M1	$y = 0.0007x + 0.0963$	0.751	0.016
T. grandis	$y = -0.000003x^2 + 0.0021x + 0.1414$	0.828	0.35
M. baccifera	$y = -0.0025x + 0.2702$	0.921	0.001
Mixed litter M2	$y = -0.015x + 0.1200$	0.989	<0.0001
Sulfur			
D. indica	$y = 0.004x + 0.1829$	0.060	0.82
Q. floribunda	$y = 0.0012x + 0.1726$	0.233	0.050
Mixed litter M1	$y = 0.0019x + 0.2072$	0.601	0.12
T. grandis	$y = 0.001x + 0.1985$	0.870	0.021
M. baccifera	$y = -0.0047x + 0.5104$	0.873	0.017
Mixed litter M2	$y = -0.026x + 0.2810$	0.977	0.0014
Potassium			
D. indica	$y = -0.0018x + 0.2438$	0.755	0.0023
Q. floribunda	$y = 0.0001x^2$ - 0.0099x + 0.3798	0.994	0.0001
Mixed litter M1	$y = -0.0015x + 0.2548$	0.526	0.027
T. grandis	$y = -0.0145x + 1.226$	0.792	0.010
M. baccifera	$y = -0.0111x + 0.8369$	0.976	0.0001
Mixed litter M2	$y = -0.066x + 0.3560$	0.973	0.0005
Calcium			
D. indica	$y = 0.0083x + 3.000$	0.178	0.26
Q. floribunda	$y = -0.001x^2$ +0.0765x +1.583	0.935	0.029
Mixed litter M1	$y = 0.008x + 2.981$	0.004	0.85
T. grandis	$y = 0.0003x^2 - 0.0009x + 1.517$	0.934	0.007
M. baccifera	$y = -0.0003x^2$ +0.0142x +2.046	0.681	0.13
Mixed litter M2	$y = -0.0426x + 3.505$	0.987	0.0001
Magnesium			
D. indica	$y = 0.001x + 0.2008$	0.193	0.39
Q. floribunda	$y = -0.002x + 0.3071$	0.679	0.030
Mixed litter M1	$y = -0.003x + 0.4420$	0.102	0.53
T. grandis	$y = 0.0021x + 0.3511$	0.405	0.39
M. baccifera	$y = -0.0027x + 0.4856$	0.997	<0.0001
Mixed litter M2	$y = -0.029x + 0.4390$	0.985	0.0008
Manganese			
D. indica	$y = 0.003x + 0.0810$	0.240	0.098
Q. floribunda	$y = 0.001x + 0.1640$	0.000	0.62
Mixed litter M1	$y = -0.0001x + 0.1150$	0.013	0.51
T. grandis	$y = 0.001x + 0.0010$	0.893	0.015
M. baccifera	$y = -0.0003x + 0.1161$	0.997	<0.0001
Mixed litter M2	$y = -0.002x + 0.1446$	0.965	0.003

Note: *Drypetes indica, Quercus floribunda* and mixed leaf litter (M1) were found in the sub-tropical site and with $n = 9$ whereas *Tectona grandis, Melocana baccifera* and mixed leaf litter (M2) were found in the tropical sitewith $n = 5$. See also Figures 3 and 5.

3.4. Changes in acid-unhydrolysable residue (AUR or lignin) during decomposition

At the STF site, *D. indica* and *Q. floribunda* showed AUR loss rate slopes of 4.34 and 3.81 % mo^{-1}, which were significantly different. The AUR loss rates at the TF site were significantly faster with rates of 18.9 and 17.2 % mo^{-1} for *M. baccifera* and *T. grandis,* respectively. Concentrations of AUR gave different relationships among species when related to accumulated mass loss (Table 3; Fig. 3). Both the local litters at the STF site had positive linear relationships versus accumulated mass loss (Fig. 3). At the TF site, *T. grandis* litter had a negative quadratic relationship, whilst *M. baccifera* litter had a weak negative linear relationship.

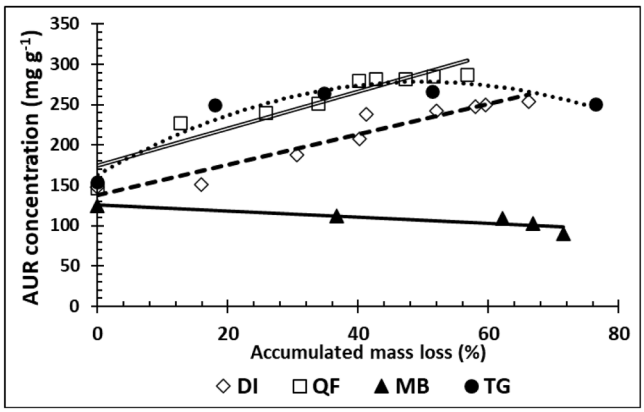

Fig. 3. Relationships between AUR concentration in decomposing local leaf litter and accumulated mass loss in a tropical and a sub-tropical forest of Mizoram, North-east India. DI indicates *D. indica*, QF indicates *Q. floribunda* (sub-tropical site), MB indicates *M. baccifera*, and TG indicates *T. grandis* (tropical site).

The mixed litter showed similar patterns for AUR changes during decomposition in both the STF and TF sites with positive linear relationships versus accumulated mass loss (Table 3; Fig. 5). When related remaining AUR mass to time, we found significant linear relationships at both sites with a slope of −6.26 % mo^{-1} in the STF and −11.1 % mo^{-1}, almost twice as fast, in the TF (Table 2).

3.5. Changes in litter nutrient concentrations during decomposition

Nitrogen concentrations increased in the *T. grandis, D. indica* (positive quadratic relationships) and *Q. floribunda* (positive linear relationship) litter (Fig. 4a; Table 3). The relationships for P were similar but not significant (Fig. 4b; Table 3). Sulfur concentrations also increased linearly for *Q. floribunda* and *T. grandis*, whereas those for *D. indica* were not significant (Fig. 4c; Table 3). In marked contrast to the three litter types noted above, the N, P and S concentrations in the *M. baccifera* litter decreased linearly with accumulated mass loss (Fig. 4; Table 3). Potassium concentrations decreased linearly for three of the litters as decomposition proceeded, whereas a quadratic relationship was found for *Q. floribunda* (Fig. 4d; Table 3). For Ca, quadratic relationships were only significant for *Q. floribunda* and *T. grandis* (Fig. 4e; Table 3). In contrast, Mg concentrations linearly decreased in *Q. floribunda* and *M. baccifera* (Fig. 4f; Table 3). For Mn, only the *M. baccifera* litter showed a significant decrease during decomposition (Fig. 4g; Table 3).

Nutrient concentration patterns in the mixed litter were different between sites and among nutrients (Fig. 5; Table 3). Thus, decrease in concentrations was significant for P, S, K, Ca and Mg at the TF site, whereas the litter at the STF site had significant increases in N, P and S but decreases in K, Ca and Mg. For Mn there was a negative relationship in the TF, whereas there was no relationship with accumulated mass loss in the STF (Fig. 5; Table 3).

3.6. Net nutrient dynamics in the decomposing litters over time

At the STF site, the litter of *Q. floribunda* showed an initial immobilization of N, P, Ca, Mn and S followed by a gradual release. Similar patterns were observed for P, Mg and Mn in *D. indica*. All other nutrients decreased consistently, notably K, in both litters (Fig. 6). At the TF site, remaining nutrient mass was measured at 120 days: *M. baccifera* litter showed a rapid release of all nutrients. This was in contrast to the litter

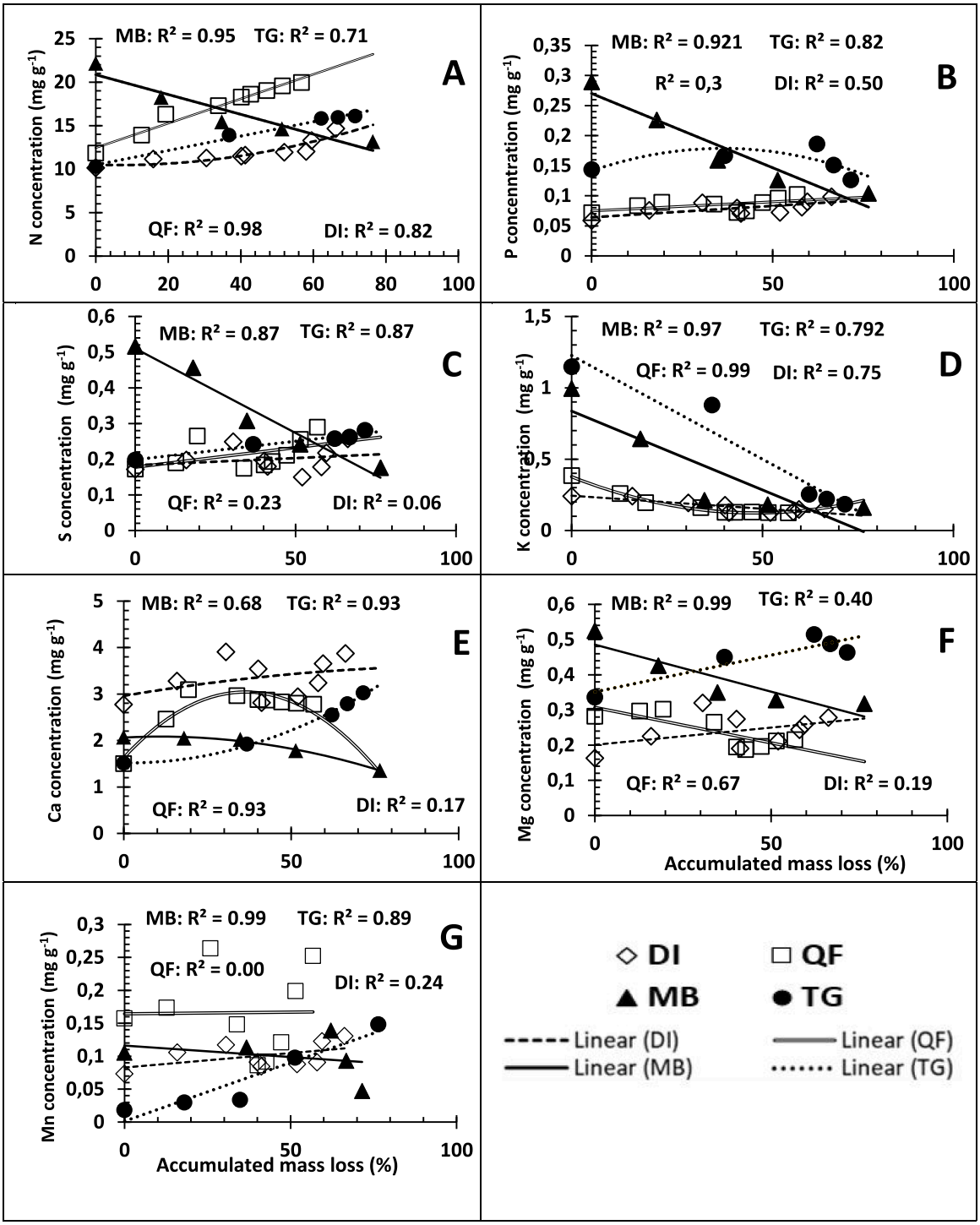

Fig. 4. Relationships between accumulated mass loss and concentrations of the main nutrients in decomposing leaf litter in a tropical and a sub-tropical forest in Mizoram, North-east India. For the tropical site: TG = *T. grandis*, MB = *M. baccifera*. For the sub-tropical site: QF = *Q. floribunda* and DI = *D. indica*. For slopes of linear relationships see also Table 3.

of *T. grandis* in which N, Mg and Ca had an initial immobilization followed by a steady release (Fig. 6). There was particularly notable uptake of Mn into *T. grandis* litter with the remaining Mn mass being >250 % of the initial litter Mn mass after 120 days (Fig. 6).

For all nutrients, there was a consistent decline in concentrations (excepting initial immobilisation in M1) and the release was slower at the STF site than the TF site (Fig. 7). The net release of K, S and Mn was extremely slow or stopped at around day 60.

3.7. Relationships between climatic and decomposition patterns

According to Pearson's correlation analyses, all the climatic and decomposition patterns of the different litter types showed positive correlations among the parameters. Significant relationships between the climatic parameters and the decomposition patterns of different litter types were observed with the exception of precipitation in TF which did not significantly correlate with the pattern of decomposition (Fig. 8).

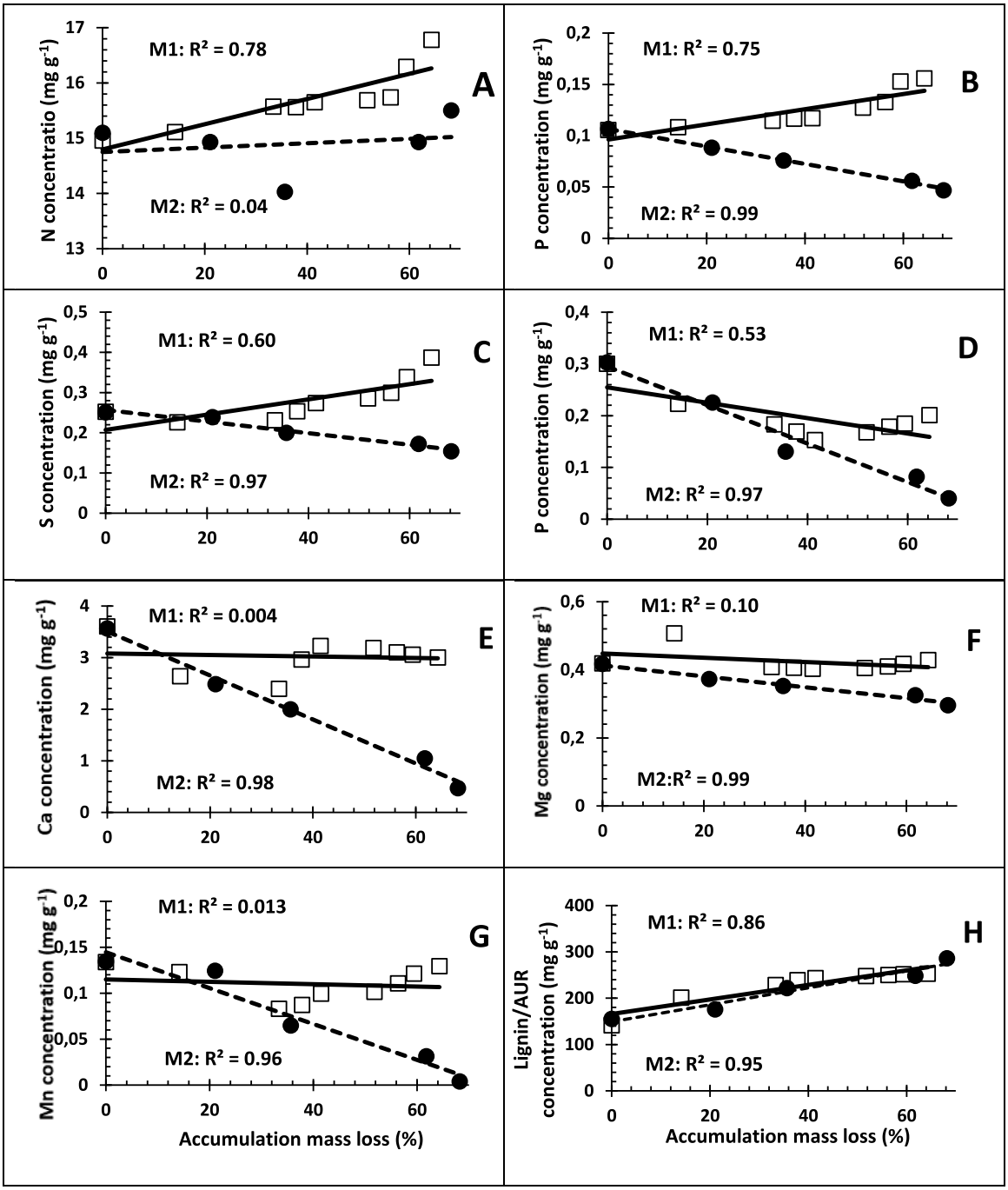

Fig. 5. Element and AUR concentrations in mixed decomposing leaf litter related to mass loss in a tropical and a sub-tropical forest in Mizoram, North-east India. Sub-tropical site = M1, tropical site = M2. For slopes see also Table 3.

4. Discussion

The accumulated mass loss pattern and chemical changes in the decomposing leaf litter varied between sites and litter types. That the *M. baccifera* litter lost AUR, N, P and S at such a high rate that their concentrations rapidly decreased (i.e. no initial immobilisation) may indicate decomposition by white-rot fungi (Yamada et al., 2005; Schilling et al. 2015;). A study by Osono et al. (2021) reported that gravimetric lignin was degraded at a rate fast enough to decrease its concentration when related to accumulated mass loss. For the other species, the concentrations of AUR, N, P and S increased. In boreal and temperate forests, as well as in sub-tropical forests, the increase in N and P concentrations versus accumulated mass loss appears to be a general phenomenon as is the increase in the concentration of AUR (Berg et al., 1997; Berg and McClaugherty, 2008). However, the initial immobilization of some nutrients, such as N, P, Ca, S, Mg, and Mn in *Q. floribunda* and *D. indica*, may be related to immobilization in the remaining litter microbial biomass and humic substances, since microbial absorption from the environment is a primary pathway for nutrient immobilization during litter decomposition (Lyngby and Brix, 1989; Yue et al., 2019).

In the TF site, decomposition rates were faster compared to rates in the STF site; this is most likely due to more favorable climatic conditions, such as high and consistent precipitation and hotter temperatures (Tripathi and Singh, 1992a,b; Osono and Takeda, 2001; Powers et al., 2009; Aas et al., 2024) However, with the biomes having different plant communities and litter chemistry, we also compared the decomposition

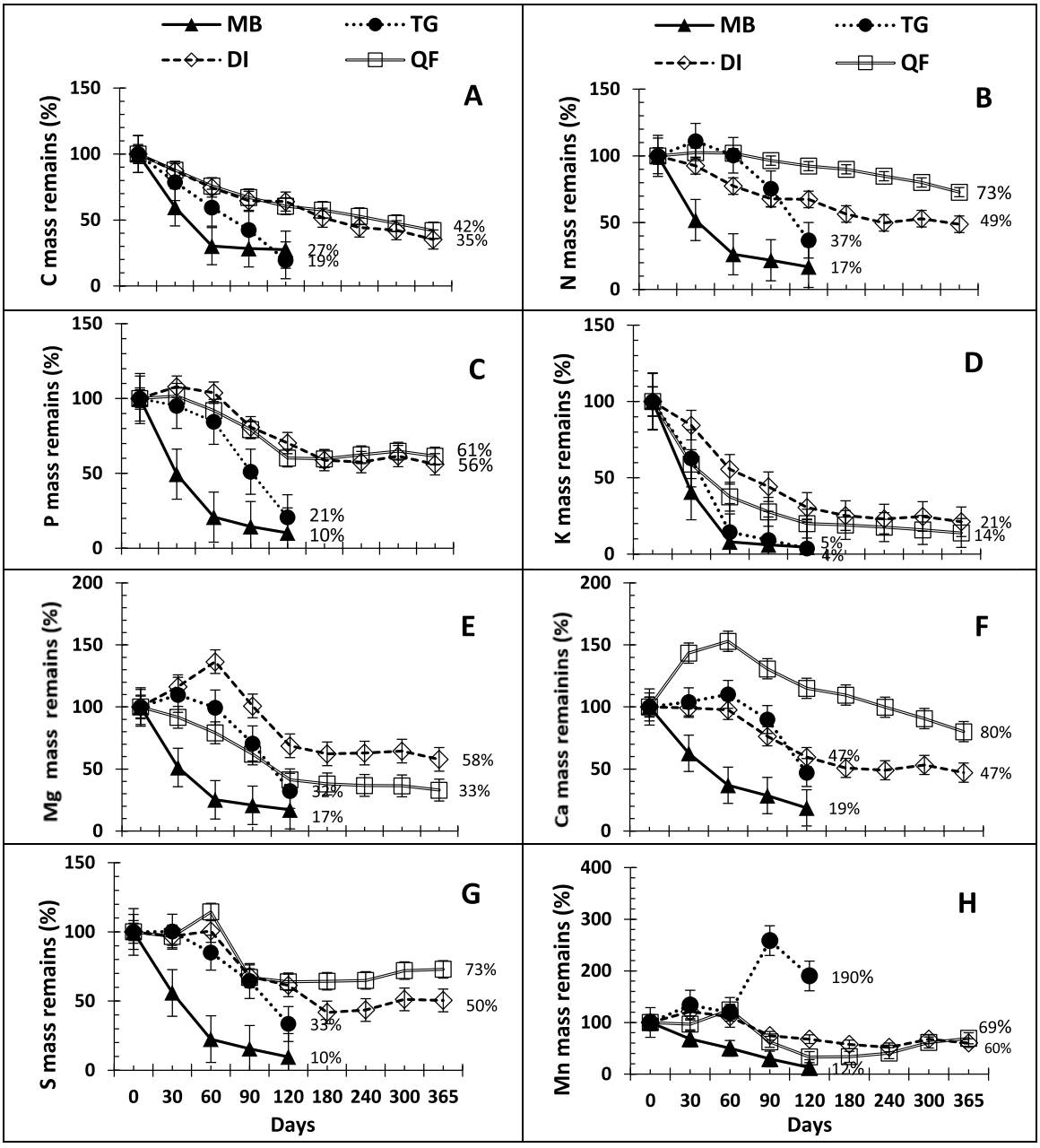

Fig. 6. Net release of mass of elements from decomposing leaf litter in a tropical and a sub-tropical forest in Mizoram, North-east India. Tropical site: TG indicates *T. grandis,* MB indicates *M. baccifera.* Sub-tropical site: QF indicated *Q. floribunda* and DI indicates *D. indica.* Percentages at the end of each line indicate the values remaining at the end of the incubations.

of a standard mixed litter. The decomposition rates for the mixed litter were also significantly different between the two sites, with both k_S and k_A values significantly greater for the TF than the STF. In addition, the decomposition patterns suggest that the single exponential (*ks*) (Olson, 1963) fitted the mass loss data better for the TF site. Also, the net loss of AUR (Fig. 2; Tables 2 and 3) were significantly faster in the TF than the STF. As the mixed litter was chemically identical, the different decomposition rates will be due to the two different environments. As the t_{95} value predicted that just 5 % of the litter mass in the TF was to remain after 365 days, it appears that essentially all the litter should be decomposed after one year. In contrast, for the STF, the pattern with a limit value indicated that the mixed litter had developed stabilized residues at a magnitude of c. 40 % of the initial mass. The different decomposition patterns of the mixed litter thus emphasized the contrast between sites. Limit values have so far not been related to climatic factors, but to litter properties, such as concentrations of N, Mn and AUR (Berg and McClaugherty, 2008; Osono and Takeda, 2001). With chemically identical litter, differences in limit values, and thus in decomposition patterns, may be ascribed to differences in climate and consequences of that difference, including contrasting populations of decomposer organisms, for example.

Annual decay constants (k_S) were 1.0 and 1.3 for *Q. floribunda* and *D. indica* litter, respectively, in the STF, and 3.2 and 4.9 for *T. grandis* and *M. baccifera* litter, respectively, in the TF. The two litter types in the TF site did not give any limit value (Table 2), but followed a constant decomposition rate, leading to complete decomposition. There are reports about similarly high rates in various species in agroforestry systems in North-east India, with decomposition completed within one year, e.g. Tangjang et al. (2015). In addition, Berg and Ekbohm (1993) identified a niche in the tropical biome for the foliar litter they reported

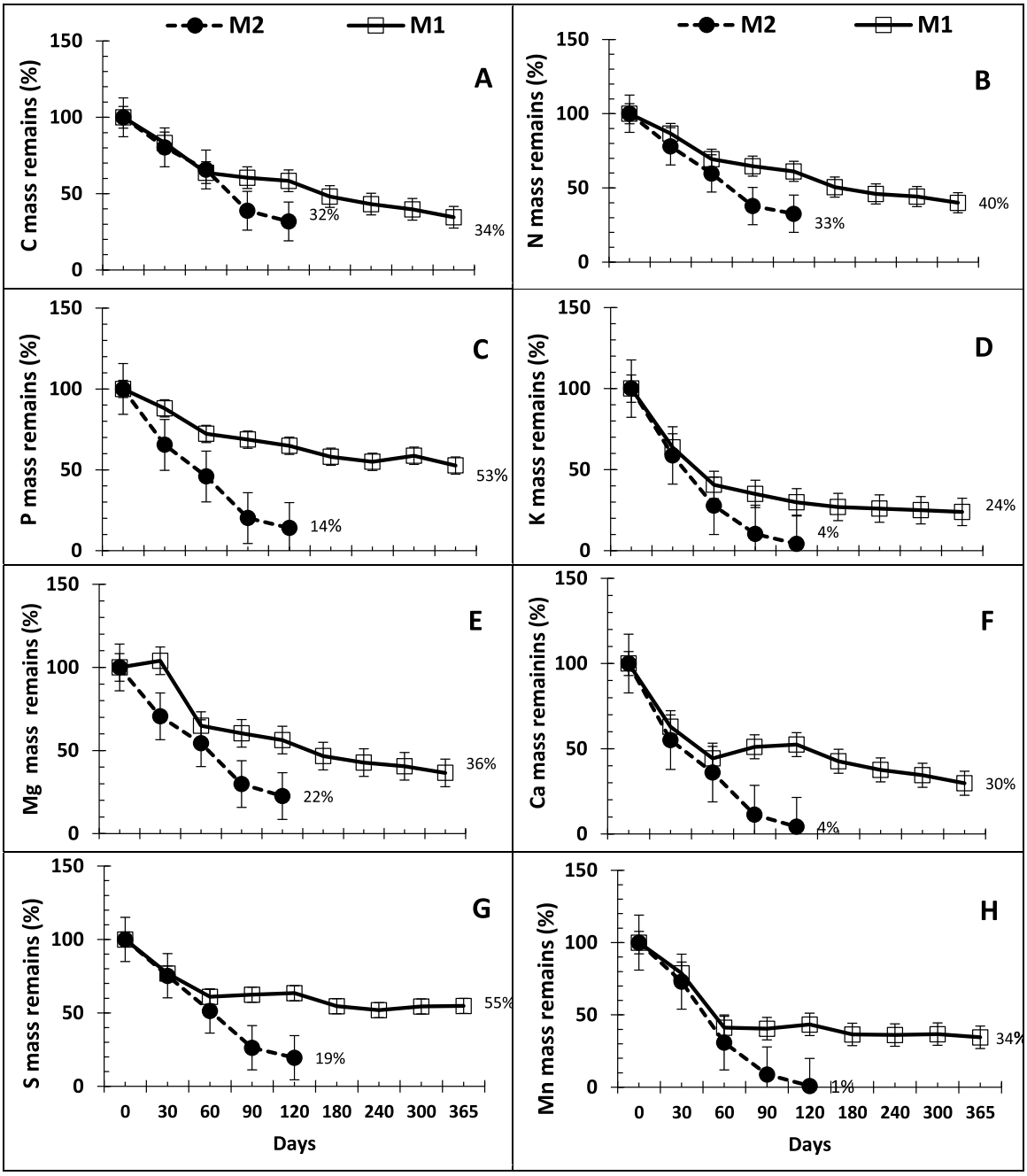

Fig. 7. Net release of mass of elements from mixed leaf litter incubated in a sub-tropical forest (M1) and a tropical forest (M2) in Mizoram, North-east India. Percentages at the end of each line indicate the values remaining at the end of the incubations.

to decompose completely, with MAT in the range from 14 to 28 °C and MAP from 1400 to 2800 mm. Further, AUR concentrations for those litter types ranged from 108 to 224 mg g^{-1} and N concentrations from 9.4 to 31 mg g^{-1}. We note that the two TF litters, as well as the mixed litter, fitted this provisional niche.

Although the local litter types were chemically different at the two sites, we did not find any specific pattern in the initial litter chemistry that may be related to the faster and complete decomposition in the TF. Still, both litter types in the TF were found to decompose completely, in contrast to those of the STF. Studies on boreal pine litter suggest that such a complete decomposition may be related to litter properties. Berg and Ekbohm (1993) compared limit values for decomposing needle litter of Scots pine (*Pinus sylvestris*: Pinaceae) and lodgepole pine (*Pinus contorta*) and noted average limit values of 85 % and close to 100 %, respectively. This difference was later related to the litter Mn concentration (Berg et al., 2010), which strongly influences the degradation of AUR (Hatakka, 2001). The Scots pine litter in that study had a range of Mn concentrations from 1.43 to 1.76 mg g^{-1} whereas for lodgepole pine the range was 2.17 to 3.07 mg g^{-1}. In the present study, the Mn concentrations in the local litter and the mixed litter were markedly lower and ranged from 0.02 to 0.16 mg g^{-1}. Therefore, it is concluded that the reason for different decomposition and AUR degradation patterns is not related to concentration of Mn but to other factors. Osono et al. (2021) described bleaching of six sub-tropical litter types due to the presence of white-rot fungal species. Therefore, in this study a rapid decomposition rate of AUR, which fits the observation for *M. baccifera* in the present study (Fig. S2), could be related to white-rot fungal species. Also, AUR loss from the *T. grandis* litter was more rapid than for the other two

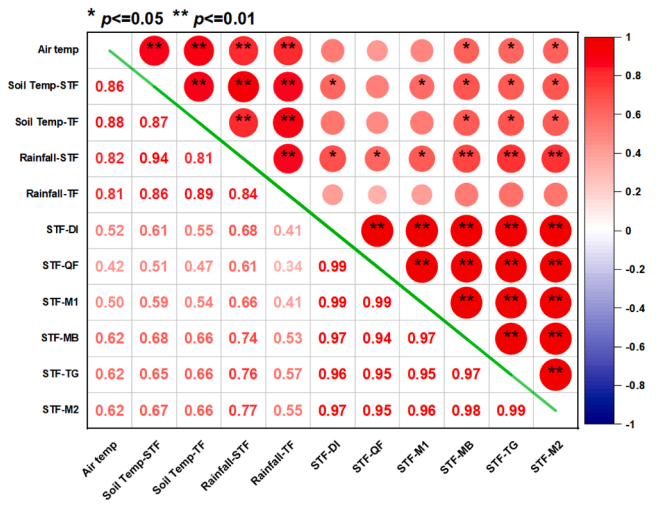

Fig. 8. Pearson's correlation among climate variables such as air temperature, rainfall, soil moisture, soil temperature, and litter decomposition patterns of different litter types in a tropical and a sub-tropical forest in Mizoram, North-east India. Where STF = subtropical forest, TF = tropical forest, DI = *D. indica*, QF = *Q. floribunda*, M1 = mixed litter, MB = *M. baccifera*, TG = *T.* grandis, and M2 = mixed litter.

litters in the STF site (Fig. S2). This finding is in direct contrast to the so far reported a linear increase in AUR concentrations with the accumulated mass loss (Berg and McClaugherty, 2008). The STF litter types fitted the more commonly described pattern with increasing AUR concentrations. We can also consider the role of soil organisms in influencing decomposition rates as other studies (Powers et al., 2009; Liu et al., 2024) found that soil mesofauna were important in tropical litter decomposition; mesofaunal populations may differ between the TF and STF sites in this study and should be the focus of further research.

At the TF site, litter mass disappeared within one year and thus the total nutrient mass released to the soil within a year indicating a rapid rate of nutrient cycling to support the new growth in TF. In contrast, at the STF site, litter mass and nutrients of the initial litter remained after one year were quite high indicating a slower release of nutrients to support STF productivity.

5. Conclusion

The two forests in North-east India showed contrasting different patterns of litter decomposition and nutrient release. For instance, the TF showed a complete release of nutrients within a year, in contrast to the STF, where a nutrient-rich residue persisted over the year, indicating the accumulation of soil organic matter and nutrients. However, in the TF, the absence of stable litter residue formation and organic layer influence the availability of soil nutrients. Consequently, the release of nutrients was at a much faster rate in TF than in the STF, which may thus affect plant growth and production. We conclude that the mechanisms driving complete decomposition in the TF compared to the STF is strongly influenced by environmental parameters such as temperature rather than any intrinsic factors.

CRediT authorship contribution statement

Ngangbam Somen Singh: Conceptualization, Methodology, Investigation, Writing – original draft, Writing – review & editing. **Francis Q Brearley:** Writing – review & editing, Supervision, Funding acquisition, Formal analysis. **Shri Kant Tripathi:** Conceptualization, Methodology, Writing – review & editing, Resources, Project administration, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare no conflict of Interest.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.envadv.2025.100634.

Data availability

Data will be made available on request.

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