ORIGINAL ARTICLE
Spatial variations of litterfall silicon flux and plant-available silicon in highly weathered soil in a lowland mixed dipterocarp forest of Lambir Hills National Park in Borneo

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ABSTRACT
Tropical forest trees take up silicon (Si) and return it to the forest floor via leaf litterfall. Our objective was to explore to what extent litter Si flux and Si availability from the soil are spatially coupled. We examined these relationships within a 4-ha area of lowland mixed dipterocarp forest of Lambir Hills National Park in Borneo. Using leaf litter samples collected with litter traps, we found that Si concentration and flux of leaf litter ranged 2–23 mg Si g⁻¹ and 0.8–13.1 g Si m⁻² yr⁻¹, respectively, whereas water-extractable Si from 0–10 cm deep soil ranged from 5.9 to 24.5 mg kg⁻¹ (0.7 to 3.0 g Si m⁻²) at 80 litter trap locations. There was no significant correlation among these three aspects of Si cycling via trees. Water-extractable soil Si from three 95 cm deep cores showed no significant change with depth, whereas in-situ measurements with six tension lysimeters showed higher soil-water Si concentration in the upper soil layer (0–5 cm depth). These results suggest that spatial variations of Si concentration and flux in leaf litter do not reflect those of soil Si availability, but are modulated by distribution of tree species that differ in Si uptake. Si returned to the soil via leaf litter did not show strong spatial signals probably because solubility of Si from dead leaves differs among species. At the stand level, our results are consistent with the perspective that litter Si input enriches plant-available Si pool in the upper soil horizons in tropical forests.

Key words: biogenic silicon, Lambir, phytolith, tropical rainforest, Ultisols

INTRODUCTION
Silicon (Si) is a beneficial element for many higher plants (Ma and Takahashi 2002), some of which apparently benefit from accumulation of Si in their bodies by enhancing defense against herbivores and pathogens (Ma and Takahashi 2002; Korndörfer and Del-Claro 2006; Cooke and Leishman 2011). On the other hand, many plant species have evolved to avoid entry of Si into xylem water streams (Ma and Takahashi 2002). Whereas previous comparative studies on leaf Si concentrations were heavily biased to plant species in temperate regions (Hodson et al. 2005), increasing number of studies demonstrate wide variations among lowland tropical tree species (e.g. 0.4–126 mg Si g⁻¹ from a lowland dipterocarp forest, Ishizawa et al. 2019). Perhaps due to presence of high Si accumulating species in lowland tropical forests, at the forest stand level, Si flux via litterfall is higher in tropical forests (Lucas et al. 1993; Alexandre et al. 1997; Ishizawa et al. 2019) than in temperate forests (e.g. Cornelis et al. 2010). Furthermore, forests at lower elevation contain more tree species that accumulate high concentration of Si in leaves than forests at higher elevation on Mt. Kinabalu in Borneo, and consequently the former exhibits higher Si concentration in leaf litter at the community-level (Nakamura et al. 2019). Yet, how spatial distribution of tree species that differ in Si uptake and accumulation affects Si cycles within a tropical forest has just begun to be explored (Ishizawa et al. 2019).

Si cycling via plants is a significant component in biogeochemical models of Si cycles (Cornelis and Delvaux 2016). Plants take up monosilicic acid (H₄SiO₄) in soil water that is dissolved through mineral weathering (Epstein 1994) or dissolution of biogenic silica from dead bodies of plants and microbes (Cornelis and Delvaux 2016). Once absorbed by plants, Si is transported along transpiration stream from roots to leaves (Raven 1983) and continues to accumulate mostly in leaves as biogenic Si until leaf abscission (Honaine et al. 2019). Subsequently, Si contained in dead leaf litter is expected to be returned to the forest floor and influences the size and quality of plant-available Si pool in upper soils (Cornelis et al. 2011; Ishizawa et al. 2019).
Local variations in edaphic conditions and tree species distributions may influence litter Si flux within a forest stand. A recent study by Ishizawa et al. (2019) evaluated this possibility within a 2-ha area of a lowland tropical forest in Peninsular Malaysia. They found no significant spatial correlations between soil Si availability and Si concentration and flux of leaf litter. Hence, litter Si concentration does not simply reflect spatial variations of soil Si availability, probably because tree species exert active control over their Si uptake and accumulation. But, the results from their study may not be extendable to other lowland tropical forests, which differ in soil types and species composition. In particular, negligible Si dissolution from sand particles (quartz) (Dove and Elston 1992; Quigley et al. 2016) may mean that the contribution of biogenic Si to plant-available Si pool relative to mineral weathering is higher in forests on sandy soil (Frayse et al. 2009).

To understand how biogenic Si input via leaf litter may be spatially associated with variations in soil Si availability, our study examined litterfall Si flux components from a lowland tropical forest in Borneo with higher sand content compared to the peninsula Malaysia site studied by Ishizawa et al. (2019). We analyzed litter collected monthly from traps throughout nine months, rather than litter collected at a small number of specific collection times as reported in other recent studies of litter Si flux in SE Asian tropical forests (Ishizawa et al. 2019; Nakamura et al. 2019). More specifically, we tested two hypotheses: (i) spatial variation of Si availability from the soil is positively associated with variations in Si concentration and flux in leaf litter within a 4-ha area of forest, and (ii) litter Si flux results in enrichment of soluble Si pool in upper soil horizons. These are based on a null-expectation of no difference among tree species in their Si uptake or Si solubility from leaf litter.

**MATERIALS AND METHODS**

**Study site**

This study was carried out in a lowland mixed dipterocarp forest within the 4-ha plot (200 m × 200 m in size) centered around an 85-m tall canopy-access crane at Lambir Hills National Park (4°12’ N, 114°02’ E, 150–200 m above sea level), Sarawak, Malaysia. The forests of Lambir are known for their high tree diversity. As many as 1,182 tree species are recorded in the 52-ha forest dynamics plot approximately 3 km away from the 4-ha plot (Tan et al. 2009). Density and basal area of trees (dbh > 10 cm) were 592 and 39.3 m² ha⁻¹ within the 4-ha plot in old-growth stand in 2001, and it has experienced no major mortality during the past 18 years (Nakagawa et al. 2019). The mean annual temperature was 25.8°C, and mean annual precipitation was 2,620 mm from 2001 to 2016 (Nakagawa et al. 2019). The soil is classified as Ultisols (Soil Survey Staff 1999) with high sand content (62–72%), high porosity (54–68%) and low pH (4.0–4.3) (Ishizuka et al. 1998; Sakurai 1999). Monthly monitoring of litterfall has been conducted within the 4-ha plot since 2001, using 80 litter traps (0.5 m² each, circular frame covered with 1 mm nylon mesh) (Nakagawa et al. 2019). Over 16 years of monitoring, the litterfall exhibits steady 12-month cycles with slight trend of increasing annual litter production over years, averaging 7.02 Mg ha⁻¹ yr⁻¹, of which 67.9% was leaf litter (Nakagawa et al. 2019).

**Litter sampling**

We used leaf litter sampled monthly for the above-mentioned litter monitoring study for a total of nine months from October 2015 to June 2016, which represents 42.8% of total leaf-litter production from January 2015 to December 2016, i.e., 85% of the mean annual leaf litter collection. Litter had been separated to leaves, branches, and reproductive parts, and only leaf litter samples were stored for the subsequent procedure. After re-drying for 72 hours at 50°C, we homogenized leaf litter from each trap at a given sampling occasion by crashing by hand to ca. 2 cm size, and subsampled ca. 10 g for later analysis for Si concentrations. Each sample was ground to powder with a mill (Cyclotec 1093, Foss, Sweden). We randomly selected 10 litter traps to analyze temporal variations of leaf Si concentration at each litter trap. They show positive correlations, indicating that a trap that showed lower Si concentration tended to show lower Si concentration in other collection months (Fig. S1 in Appendix). Because our objective was to estimate the mean Si concentration over a long term, in order to conduct laboratory analysis efficiently, we created a composite sample by combining ground leaf-litter samples from different collection times to follow the abundance-weighted ratios, i.e., the proportion of sample mass from a given month in the combined sample of a given litter trap equaled the leaf-litter mass of that month relative to the total leaf-litter mass from October 2015 to June 2016 in that trap. To calculate leaf-litter Si flux at each trap, we used the average value of annual leaf-litter production from 2015 and 2016 (Nakagawa et al. 2019).
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Soil and soil water sampling

We collected soil from the top 10-cm layer corresponding to A-horizon within a radius of 1 m from each litter trap in March 2016, using a stainless steel sampler (4.8 cm diameter) after removing O-layer. In this forest, trees may take up Si mainly from top 10-cm mineral soil because most of fine roots occur at this depth (Katayama et al. 2009). The soil samples were air-dried for a week and kept in airtight plastic bags until further analysis.

Additionally, soil was sampled with a wider core sampler (5.3 cm diameter) from different depths (0–5, 10–15, 20–25, 30–35, 60–65 and 90–95 cm) of three pits in the adjacent area of the plot in August 2017. These soil samples were weighed and divided into two sets of subsamples. The first set was air-dried for a week and stored in plastic bags for further analysis. Another set was oven-dried at 105°C for a week to calculate bulk density.

Soil water was sampled from six locations randomly selected within the 4-ha plot, with porous tension-cup lysimeters set at four depths (0–5, 30–35, 60–65 and 90–95 cm). Sampling was done for seven days at the end of February 2018 and for three days in the middle of July 2018. The suction force was regulated to a constant pressure (~48 kPa). Soil water was taken into a 30-ml polycarbonate bottle every day and stored separately by sampling date in a cool and dark condition until Si analysis. For the analysis of Si concentrations, 1 ml subsample was taken from each sample bottle.

Si extraction and measurements

For Si extraction, about 30 mg of ground sample was precisely weighed and placed in a 60-ml polycarbonate bottle, to which 20 ml of 1% Na₂CO₃ was added for extraction overnight by shaking at 85°C following Conley and Schelske (1993). After cooling down, 1 ml subsample of extract solution was used for determination of Si concentration. To measure water-extractable Si concentration in the soil, 3 g of air-dried soil was placed in a 50 ml centrifuge tube with 20 ml of distilled water and shaken for 20 hours at 25°C (ca. 180 oscillations per minute). The suspension was centrifuged at 10,000 rpm (ca. 12,000 g) for 10 minutes, and 1 ml of supernatant was taken for determination of Si concentration. All determination of Si concentration in extract and soil-water solutions was done with the molybdate blue colorimetry (Sauer et al. 2006).

Statistical analysis

In order to understand the spatial autocorrelations for leaf-litter Si concentration and water-extractable Si from the soil in the 4-ha plot, Moran’s I index (Huo et al. 2012) was calculated with the “ncf” R-package (Bjornstad 2015). For water-extractable Si and characteristics of soil along profiles, Tukey’s multiple comparison test was used to test the differences among soil depths. We examined whether soil-water Si concentration in the 0–5 cm deep soil differs from that from deeper soils, using a linear mixed model analysis in which soil depth (as a categorical variable) was a fixed effect and sampling location, date and investigation season (February or July) were random effects. Soil-water Si concentration was log-transformed to improve normality before the analysis. The correlations between measurement variables were tested with a simple linear regression. Elevation data at the 4-ha plot was obtained elsewhere (Nakagawa et al. 2019). All data analyses were performed with R software Ver. 3.1.3. (R Core Team 2016).

RESULTS

Si concentration of leaf litter and Si flux via leaf litter

Leaf-litter Si concentration varied from 2.0 to 22.5 mg Si g⁻¹ (Fig. 1a), and litter Si flux ranged from 0.8 to 13.1 g Si m⁻² yr⁻¹, among the 80 sets of litter trap samples. The mean annual leaf-litter production from 2015 to 2016 was not correlated with leaf-litter Si concentration ($R^2 = 0.002, P = 0.72$). A significantly positive spatial autocorrelation of leaf-litter Si concentration was observed up to approximately 34.1-m distance interval ($P<0.05$) with correlation above 0.10 (Fig. 2a).

Spatial pattern of water-extractable Si from soil

Water-extractable Si from the soil varied up to four folds among 80 locations (6~24 mg kg⁻¹) within the 4-ha plot (Fig. 1b). This spatial variation was not associated with elevation ($R^2 = 0.02, P = 0.24$). A significantly positive spatial autocorrelation of water-extractable Si from soil was observed up to 20-m distance interval (correlation coefficient = 0.16, $P<0.05$), above which the spatial autocorrelation was not significant except at 50-m interval (correlation coefficient = −0.13, $P<0.05$, Fig. 2b). Across the 80 spatial sampling points at 20 m intervals, leaf-litter Si concentration was not correlated with water-extractable Si from soil.
within the 4 ha-plot (Fig. 3a). Similarly, water-extractable Si from soil was not correlated with litterfall Si flux (Fig. 3b).

**DISCUSSION**

Our first hypothesis on the positive association of spatial variation in soil Si availability with that of litter Si concentration and flux was based on a null expectation of the lack of tree species difference in their Si uptake and litter Si solubility. If all tree species passively uptake and accumulate Si, the expectation is that spatial variations in soil Si availability should have a positive effect on leaf-litter Si concentration and flux. Likewise, a positive spatial association is expected if spatial variations in leaf-litter Si flux have a simple effect on soil Si availability. We did not find such spatial associations (Fig. 3), similarly to the findings by Ishizawa et al. (2019) who studied another lowland dipterocarp forest. Finding the same conclusion again, this time with greater temporal coverage of litter collection, favors the generality of the findings from the two studies. The rejection of our first hypothesis likely indicates that tree species are not equal in their effects on forest Si cycles. As the studies with herbaceous plants (e.g. Liang et al. 2006) report that Si accumulation rate is not merely transpiration-dependent, but also regulated by active uptake by roots, high Si accumulating tropical trees should compensate for low Si availability from the soil with high sand content. Previous studies have shown that active regulation of Si uptake overrides differences in Si availability from soils at regional scales (Cooke and Leishman 2012; Quigley et al. 2016; Schaller et al. 2018; Nakamura et
We also recognize that horizontal spreads of roots and scattering of leaf litter may also weaken spatial correlation between leaf-litter Si concentration and soil Si availability (Fig. 3a).

There are multiple potential reasons why high litter Si flux at a given location may not increase soil Si availability at given spot. Water-extractable Si from soil was positively autocorrelated until 20-m distance (Figs. 1b and 2b) similarly to the report by Ishizawa et al. (2019). This level of spatial grain can reflect not only distribution of tree species (Figs. 1a and 2a) but also fine scale variations in topography and soil characteristics (e.g. soil particle distribution). Interestingly, litter Si concentration exhibited spatial autocorrelation up to 37 m. Spread and mixing of leaf litter on the forest floor, as well as differences among tree species in Si solubility from dead leaves (Nakamura et al. 2020) modulates the spatial signature of biogenic Si input via leaf litter.

There was a significant support for our second hypothesis that litter Si flux should result in enrichment of soluble Si pool in upper soil horizons. Higher Si concentration in soil water in the upper soil horizon (Table 1) likely represents a significant contribution of litter Si flux on plant-available Si pool in soil at a stand level (Lucas et al. 1993; Lucas 2001). We failed to detect the same pattern for water-extractable Si from the soil partly owing to insufficient sample size (n’<3) for the variable that exhibits a large variation among samples (Fig. 1b).

For better understanding of Si dynamics in soil water, future study should measure Si concentration in soil water at frequent intervals on a longer-term (e.g. Gewirtzman et al. 2019) in relation to litter decomposition and rainfall patterns.

Leaf-litter Si flux of our study site (4.9 g Si m⁻² yr⁻¹)
was within the same range as reported from other tropical forests, higher than a lowland Amazonian forest (3.3 g Si m\(^{-2}\) yr\(^{-1}\), Lucas et al. 1993), montane forests (0.1–4.4 g Si m\(^{-2}\) yr\(^{-1}\), Nakamura et al. 2019) and a lowland forest on La Reunion Island (0.7 g Si m\(^{-2}\) yr\(^{-1}\), Meunier et al. 2010), but lower than another dipterocarp forest in Peninsular Malaysia (8.5 g Si m\(^{-2}\) yr\(^{-1}\), Ishizawa et al. 2019). If we calculate the Si that becomes soluble by water-shaking from the 1-m deep soil column (based on Table 1), it is 19.5 g Si m\(^{-2}\). Intact soil structures are unlikely to release this much Si over much longer duration. Thus, leaf litter Si flux is substantial compared to soil Si availability. Pasoh and Lambir were similar both in terms of the mean leaf-litter Si concentration (9.9 vs. 10.7 mg Si g\(^{-1}\)) as well as their spatial variation (CV among litter traps). Hence, we expect a large variation of live-leaf Si concentration among dominant trees at a lowland mixed dipterocarp forest of Lambir as in Pasoh (e.g. up to 315 folds, Ishizawa et al. 2019). For revealing variations of litter Si flux and Si uptake by trees in tropical forests and their proximate factors, future investigation on ecosystem Si cycling is required to be conducted in a wide range of tropical forest ecosystems at different spatial scales.

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APPENDIX

Fig. S1. Correlations of leaf litter Si concentration between different collection months. (a) December 2015 – January 2016 (vertical axis) vs. October – November 2015 (horizontal axis), (b) June 2016 vs. December 2015 – January 2016, (c) October – November 2015 vs. June 2016.