Biogeochemistry
https://doi.org/10.1007/s10533-024-01137-z

Drought-induced turnover of soil microbial biomass increases nutrient subsidies for the reproduction of tropical forest

Kazumichi Fujii · Chie Hayakawa · Sukartiningsih

Received: 17 September 2023 / Accepted: 14 March 2024

Abstract El Niño-induced drought, which is intensified by climate change, can have huge impacts on soil microbial biomass and plant productivity in tropical forests. We tested whether drought-induced turnover of soil microbial biomass can be a potential source of phosphorus (P), the limiting nutrient, for the reproduction of tropical forest trees (mast fruiting). We measured the seasonal variations in soil microbial biomass P and soil solution P concentrations including the periods before and after drought in a dipterocarp forest in Indonesia. Drought resulted in a decrease in soil microbial biomass C, N, and P, followed by a recovery after re-wetting. There was a sharp peak of soil solution P concentrations during the drought. The significant difference between soil microbial biomass P before and after drought amounted to 2.0 kg P ha^{-1}. The potential P release from microbial turnover is not negligible compared to the additional P demand for fruit production (1.0 kg P ha^{-1}) as well as the annual demand for litter production (2.5 kg P ha^{-1} $year^{-1}$). In addition to the accumulation of nutrients for several non-fruiting years and their re-distribution in tree biomass, drought-induced microbial turnover can be nutrient subsidies for dipterocarp reproduction in highly-weathered soils.

Keywords Dipterocarp · Drought · Microbial biomass · Stoichiometry · Tropical forests

Responsible Editor: Marie-Anne de Graaff

K. Fujii (✉)
Forestry and Forest Products Research Institute, 1 Matsunosato, Tsukuba, Ibaraki 305-8687, Japan
e-mail: fjkazumichi@gmail.com

C. Hayakawa
Faculty of Agriculture, Utsunomiya University, Utsunomiya 321-8505, Japan

Sukartiningsih
Tropical Rainforest Research Center, Mulawarman University, Samarinda 75123, Indonesia

Introduction

Soil microbes function as decomposers in forest ecosystems, but the microbial biomass could be a potential sink/source of nutrients such as nitrogen (N) and phosphorus (P) in soil (Singh et al. 1989). The nutrient concentrations vary between phylogenetic groups (bacteria and fungi) within soil microbial community, but N and P could be released along with the release of microbial biomass carbon (C) at atomic C:N:P ratios of 60:7 (5 for fungi to 10 for bacteria):1 (Cleveland and Liptzin 2007; Strickland and Rousk 2010). The microbial biomass depends roughly on soil C concentration (Inubushi et al. 2005; Xu et al. 2013). However, the size of microbial biomass could fluctuate seasonally depending on soil microclimate and substrate availability (Diaz-Ravina et al. 1995; Wardle 1998). Tropical forests in humid tropics are characterized by narrow seasonal variations in soil

Published online: 17 April 2024

temperature, but drought (El Niño) or wet-dry cycles have potentially large impacts on soil microbial biomass and plant productivity (Singh et al. 1989).

Supra-annual production of fruits at the community level is characteristic of dipterocarp forests in Southeast Asia (Janzen 1974). The massive flowering and mass fruiting have been hypothesized to be triggered by periodic climatic events such as low temperatures and droughts related to El Niño (Ashton et al. 1988; Sakai et al. 2006). Reproduction can be limited by slow P accumulation in the tree biomass due to low P availability in highly-weathered tropical soils (Ichie et al. 2005; Ichie and Nakagawa 2013), where P availability can be reduced through incorporation of P into humus or sorption onto clays (Fujii 2014; Fujii et al. 2018). Trees need to acquire P as well as N on the highly-weathered soils to allocate nutrients for reproduction as well as annual litter cycles.

Drought generally reduces the microbial activity of organic matter decomposition (Fujii et al. 2010), but drought-induced changes in microbial biomass could be one of the potential sources of P in soils. Based on the stoichiometry of microbial biomass constituents, seasonal fluctuation in soil microbial biomass could release P and N through cell lysis or mineralization of microbial necromass (Cleveland and Liptzin 2007).

We hypothesized that the drought-induced changes in microbial biomass can increase soil P availability in a dipterocarp forest. We also assess the impact of the potential nutrient release associated with drought-induced microbial turnover relative to nutrient demands of trees for reproduction quantitatively.

Materials and methods

Descriptions of experimental plots

The dipterocarp forest plots were located in the 9 ha plots (100 m × 100 m) of the Experimental Forest of the Tropical Rainforest Research Center, Mulawarman University, Bukit Soeharto, East Kalimantan Province, Indonesia (S0°51′, E117°06′; 99 m a. s. l.). The mean annual air temperature and annual precipitation were recorded as 26.8 °C and 1977 mm year^{-1}, respectively. The vegetation was dominated by *Shorea laevis* and *Dipterocarpus cornutus*. Soils were derived from sedimentary rocks and classified as Typic Paleudults (Soil Survey Staff 2022). The detailed information was given in Fujii et al. (2021a, b).

Monitoring temperature and volumetric water content in soils

Volumetric water contents (L L^{-1}) of soils at a depth of 5 cm were measured with amplitude domain reflectometry probes (Theta probe, ML2x, Delta T Devices), while air temperature and soil temperature at a depth of 5 cm were also measured using temperature loggers (Thermochron, SL type). Both soil temperature and moisture were recorded at 1-h intervals during the study. In this study, we define drought as the period of soil volumetric water content less than 0.17 L L^{-1}, which corresponded to volumetric water content of wilting point (pF 4.5) of the studied soil.

Soil physicochemical properties

Soil samples were collected from three pits in each plot once per 3 months. The distance between each pit was 10 m. Three composite samples (surface mineral soil; 0–5 cm depth) were taken using a spoon (ca. 200 mL) from each plot (3 samples per plot). The field-moist, unsieved soils were used for microbial biomass measurement without eliminating fine roots. For chemical analysis of soils, subsamples were air-dried and sieved (<2 mm) to eliminate litter, roots, and pebbles.

Using the air-dried and sieved soil samples, soil pH was measured using a soil-to-solution (H_2O) ratio of 1:5 (w/v) after shaking for 1 h. Total C and N concentrations were determined using a CN analyzer (Vario Max CN, Elementar Analysensystem GmbH). The amounts of total and available P were measured using hydrofluoric–sulfuric acid digestion (Jackson 1958) and the Bray 2 extraction method (Bray and Kurtz 1945), respectively. Particle size distribution was determined by the pipette method. The microbial biomass C, N, and P were determined in triplicate by the chloroform fumigation-extraction method (Vance et al. 1987). The soluble C and N of the fumigated and non-fumigated soil samples were extracted with 0.5 M K_2SO_4 (soil-to-solution ratio of 1:5) and were determined using a total organic C analyzer (TOC-V CSH, Shimadzu, Japan). The soluble P of the fumigated and non-fumigated soil samples were extracted with Bray-1 (0.03 M NH_4F–0.025 M HCl) solution

(Wu et al. 2000). To calculate microbial biomass-C, -N, and -P, the conversion factors used in this study were 0.45 for C (Wu et al. 1990), 0.54 for N (Jenkinson 1988), and 0.4 for P (Jenkinson et al. 2004), respectively. The turnover rate ($year^{-1}$) of microbial biomass was estimated according to McGill et al. (1986) by dividing the total measured losses in microbial biomass at different sampling times by the average microbial biomass throughout the year.

Phosphorus and nitrogen concentration in litterfall and fruits

Circular litter traps of 1 m diameter were used to collect litterfall, in five replications per plot. Plant samples were oven-dried at 70 °C for 48 h, weighed and milled. Biomass [leaves, fruits (seeds and wings)] was collected. The C and N concentrations were measured with a CN analyzer (Vario Max CN, Elementar Analysensystem GmbH). The P concentrations in plant materials were measured with an Autoanalyzer (SWAAT, BL-TEC Inc., Japan) after nitric-sulfuric acid digestion. Dry mass/N concentration and dry mass/P concentration in litterfall were used as indicators of N and P use efficiency (NUE and PUE), respectively (Vitousek 1984).

Phosphorus concentration in soil solution

Soil solution samples were collected using a tension-free lysimeter in five replications beneath the O, A, and Bt horizons (0, 5, and 30 cm depths from the boundary between organic and mineral soil layers). The lysimeters were installed horizontally in the small soil pits by inserting the plates of 200 cm^2 in area into the precut opening with a decline of approximately 5% towards the pit and connected with tubing to the collecting bottles. Samples were taken once per month from 2014 to 2015 May. Sample solutions were filtered through a 0.45 μm PTFE syringe filter (Advantec DISMIC-13HP, Toyo Roshi Kaisha, Ltd., Tokyo, Japan), and stored at 1 °C in the dark prior to analyses. The solution pH was determined with a glass electrode and the concentrations of DOC and TDN in the solution were determined using a total organic carbon analyzer (TOC-V_{CSH}, Shimadzu, Japan). The concentrations of NH_4^+ and NO_3^- in solution were determined by high-performance liquid chromatography (HPLC; ion chromatograph HIC-6A, Shimadzu; shim-pack IC-C3 for NH_4^+, shim-pack IC-A1 for NO_3^-, conductivity detector CDD-6A). DON concentrations were calculated by subtracting NH_4^+ and NO_3^- from TDN concentrations ($DON = TDN - NH_4^+ - NO_3^-$). The concentrations of inorganic P ($H_2PO_4^-$ and HPO_4^{2-}) in soil solution were measured with an auto-analyzer (SWAAT, BL-TEC Inc., Japan).

Statistics

The data are expressed as the mean ± standard error (SE), using combined SEs in three replicates, unless otherwise stated. The significance of differences in MBC, MBN, and MBP between sampling periods was assessed using analysis of variance (ANOVA). Pearson's correlation coefficients were calculated to examine the relationships between soil properties. All statistical analyses were performed using SigmaPlot 14.5 software (Systat Software, San Jose, CA, USA), with the significance level set at $P < 0.05$ (unless otherwise stated).

Results

Physicochemical properties and microbial biomass in soil

The average soil pH and C concentrations of the soil samples were presented (Table 1), as no significant differences were found between soil pH and C concentrations in the soil samples collected at four sampling periods. There was a sharp decline in volumetric water contents in September 2014, followed by an increase at the end of November 2014 (Fig. 1a). When we compared the average soil temperatures during drought (September 9th to November 21st, 2014) and those before and after drought (June 18th to September 8th and November 22th to June 10th, 2015, respectively), soil temperatures during drought and after drought (28.0 °C and 28.1 °C, respectively) were higher than soil temperature before drought (26.2 °C).

MBC varied from 0.7% to 1.2% of total soil C (Table 2). The MBC in the soil sample collected during the drought was significantly lower than MBC values during the other three periods (Table 2; Fig. 1b). MBN and MBP accounted for 1.4–2.2% of

Table 1 Chemical properties of the dipterocarp forest soil

Horizon	Depth (cm)	Bulk density (g cm^{-3})	Total C[a] (g kg^{-1})	Total N[a] (g kg^{-1})	Soil P[a]		pH		Particle size distribution[b]		
					Total (mg P kg^{-1})	Bray-2 (mg P kg^{-1})	H_2O	KCl	Clay (%)	Silt (%)	Sand (%)
A	0–5	1.1	22.9	1.6	132	10	4.0	3.9	23	25	52
BA	5–25	1.4	4.2	0.5	100	n.d	3.8	3.8	24	27	49
B1	25–40	1.5	3.5	0.5	95	n.d	4.0	3.8	27	30	43
Bt	40+	1.5	2.5	0.4	96	n.d	4.3	3.8	31	35	34

[a]Oven dried basis

[b]Clay (<0.002 mm); Silt (0.002–0.05 mm); Sand (0.050–2 mm)

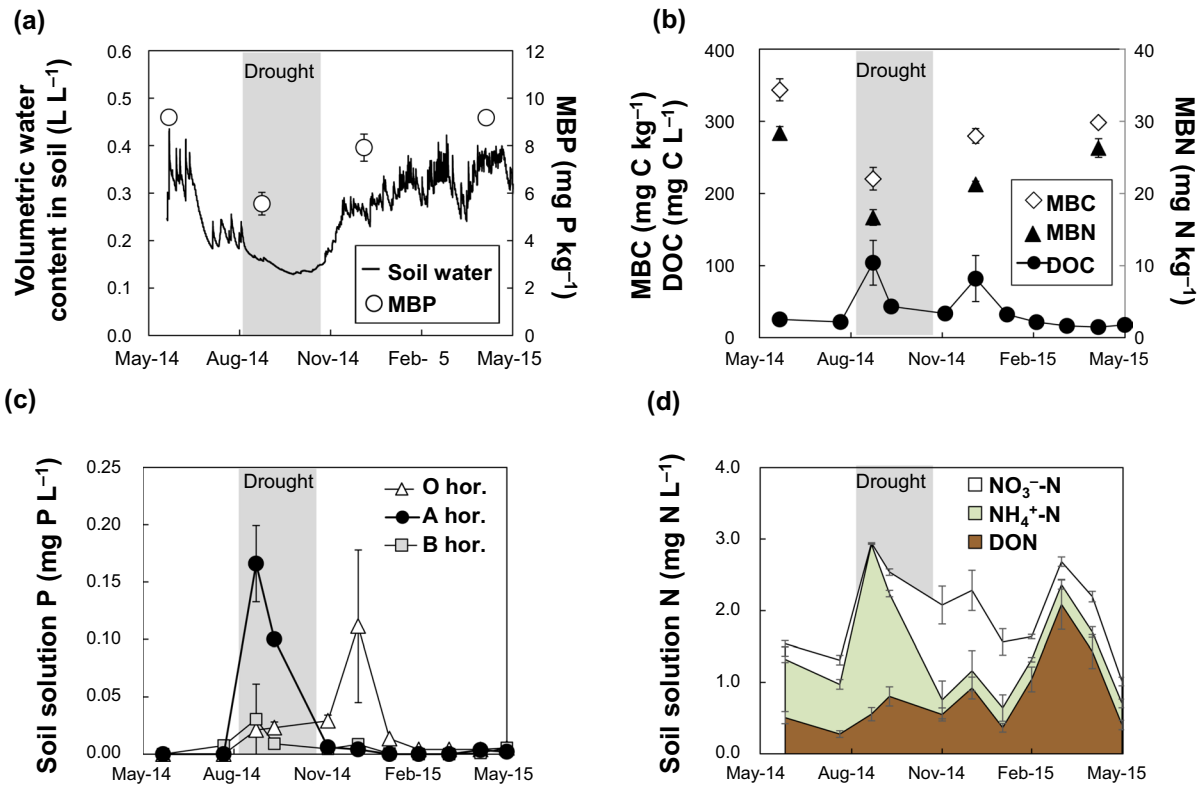

Fig. 1 Fluctuation in volumetric water content and microbial biomass P in the surface soil (0–5 cm) (**a**), dissolved organic carbon (DOC) in soil solution (5 cm depth) and microbial biomass C (MBC) and N (MBN) (**b**), P concentration in soil solutions percolating from the bottom of the organic horizon, the A horizon (5 cm), and the B horizon (30 cm depth) (**c**), and soil solution N concentration (5 cm depth) (**d**). Bars indicate standard errors ($N = 3$–5). The shaded period corresponded to drought

total N and 4.0–6.9% of total P in the soil (Table 2). MBC:MBN ratio varied from 8.8 to 10.2, while MBN:MBP ratio varied from 7.4 to 9.1 (Table 2). The average C:N:P ratio of microbial biomass was 76:7.4:1 in our study. The turnover rate of microbial biomass was estimated to be 0.50, 0.43, and 0.45 for C, N, and P, respectively. Using bulk density and soil depth (5 cm) and MBC, MBN, and MBP changes

Table 2 Soil microbial biomass carbon (MBC), nitrogen (MBN), and phosphorus (P) and their ratios

	Unit	Sampling date					
		Wet season 2014/6/25	Drought 2014/9/20	Wet season 2014/12/30	Wet season 2015/4/30		Nutrient release in drought (kg ha^{-1})
MBC	(mg C kg^{-1})	283.6 ± 9.1A	166.9 ± 10.9C	214.9 ± 4.2B	259.5 ± 12.9A		64.2
MBN	(mg N kg^{-1})	34.4 ± 1.5a	22.1 ± 1.6b	28.2 ± 1.0a	29.5 ± 0.8a		6.8
MBP	(mg P kg^{-1})	9.2 ± 0.3A	5.6 ± 0.5B	8.0 ± 0.6A	9.1 ± 0.1A		2.0
MBC	(% in total C)	1.2	0.7	0.9	1.1	Av.	1.1
MBN	(% in total N)	2.2	1.4	1.8	1.9	Av.	1.9
MBP	(% in total P)	6.9	4.2	6.0	6.9	Av.	6.9
C:N	(molar)	9.6	8.8	8.9	10.2	Av.	10.2
N:P	(molar)	8.5	9.1	8.1	7.4	Av.	7.4

Mean ± standard errors (SE). Within each column, values denoted by the same capital or lower-case letters do not differ significantly between soil texture classes ($P > 0.05$)

between wet season and drought, the C, N, and P release from microbial turnover was estimated to be 64.2 kg C ha^{-1}, 6.8 kg N ha^{-1}, and 2.0 kg P ha^{-1}, respectively (Table 2).

Plant N and P demand for reproductive organs

Nutrient concentration and flux in reproductive organs, which consist of flowers and fruits (seed and wing), and litterfall from our study and those from the published sources were presented in Table 3. The measured N and P concentrations of the reproductive organs were higher than in litterfall (leaf and twig) in our study (Table 3). The N demand for reproductive organ production corresponded to 15% of litterfall N flux (Table 3), while the P demand for reproductive organ production corresponded to 40% of litterfall P flux (Table 3).

Soil solution N and P fluctuation

The seasonal variation of soil solution concentration in the surface mineral soil (5 cm depth) varied between N and P (Fig. 1c, d). When the CV was calculated to compare seasonal variations of soil solution concentrations between P and N, the CV of soil solution P concentration was much higher (2.10) than the CV of soil solution N concentration (0.31) (Fig. 1c, d). Soil solution P at the depth of 5 cm (A horizon) exhibited the maximum concentration during the drought (Fig. 1c). The peak of P concentration in the A horizon was followed by the O horizon due to the litterfall inputs of flowers and seeds into the O horizon (Fig. 1c). NH_4^+ concentrations increased during the drought, followed by an increase in NO_3^- after rewetting (Fig. 1d).

Discussion

Effects of drought on microbial biomass and its turnover

Nutrients, especially P, can be primarily supplied from organic matter decomposition in the highly-weathered tropical soils poor in weatherable minerals (Turner and Engelbrecht 2011; Fujii 2014). Based on our previous study on seasonal fluctuations of microbial respiration rates, nutrient release from organic matter decomposition must be limited in dry seasons (Fujii et al. 2009). This is the reason why nutrient supply from microbial biomass turnover can be relatively important during drought in dipterocarp forests. MBC, MBN, and MBP accounted for 1.1% of total C, 1.9% of total N, and 6.9% of total P in the soil studied (Table 2). This is close to the global average, where soil microbial biomass accounts for 1.2%, 2.6%, and 8.0% of soil C, N, and P, respectively (Xu et al. 2013). This implies that microbial biomass plays a small role in soil C, N, and P pools in tropical forests (Table 2; Turner and Wright 2014). Further, based on the facts that soil microbial biomass depends primarily on SOC concentrations (Xu et al. 2013) and that topsoil C concentrations in humid tropical forests

Table 3 Allocation of nitrogen and phosphorus to reproductive organs of lowland dipterocarp forests in Borneo

Site		Organic matter production (Mg ha^{-1} $year^{-1}$)	Concentration			Flux			NUE	PUE	Data source
			C (mg g^{-1})	N (mg g^{-1})	P (mg g^{-1})	C (kg ha^{-1} $year^{-1}$)	N (kg ha^{-1} $year^{-1}$)	P (kg ha^{-1} $year^{-1}$)			
Indonesia											
Bukit Soeharto	Flower	0.3	477.4	12.9	1.4	158.5	6.3	0.5			This study
	Seed	0.8	480.0		10.1	0.5	384.0	8.1	0.4		
	Wing	0.2	514.1	8.9	0.7	82.3	1.4	0.1			
	Litterfall	10.0	519.2	10.3	0.2	5214.7	103.8	2.5	97	4069	
Bukit Soeharto	Litterfall	8.3	492.7	12.2	0.3	4100.0	101.1	2.5	82	3275	Fujii et al. (2009)
Buki Bankirai	Litterfall	6.8	532.4	13.7	0.4	3620.0	93.5	3.0	73	2258	Fujii et al. (2010)
Malaysia											
Sarawak	Flower	0.3	491.6	8.6	1.7	163.2	2.9	0.6			Ichie and Nakagawa (2013), Ichie et al. (2005)
	Fruit	1.1	506.2	8.0	0.7	555.3	8.8	0.8			
	Litterfall	8.9		11.2	0.3	4450.0	100	2.8	89	3179	Lim (1978)
Kinabalu	Flower/seed	0.7–1.4		8.0–18.0	0.5–1.1		12.8–23.8	0.7–1.4			Kitayama et al. (2015)
	Litterfall	8.8–9.1		7.0–14.0	0.1–0.5		114.0–115.6	3.3–3.7	77–79	2459–2667	

are low (Table 1), pool size of nutrients in microbial biomass has been assumed to be smaller compared to the soils in temperate or tropical dry regions (McGill et al. 1986; Singh et al. 1989). These assumptions would underestimate the potential importance of microbes by overlooking fluctuations in microbial biomass. Severe drought related to El Niño causes a large fluctuation in microbial biomass and associated nutrient storage in the studied soil (Fig. 1a, b). This supports the roles of soil microbial biomass for potential nutrient sources even in humid tropical forest ecosystems.

Nutrient release from microbial turnover and potential impacts on reproduction

The massive flowering and mass fruiting, which are characterized by large flower and seed production once in several years, have been explained by sharing pollinator hypothesis and the predator-satiation hypothesis (Sakai et al. 2005) and were also hypothesized to be triggered by periodic climatic events such as low temperatures and droughts (Ashton et al. 1988; Sakai et al. 2006). On the other hand, the resource budget model assumes that reproduction is limited by the accumulation rates of resources (photosynthate or soil nutrients) in the tree body and triggered by saturation of the demand for the limited nutrients (Han et al. 2014). Climatic regulation and resource limitation hypotheses are not inconsistent, because drought may stimulate nutrient transfer from soil to plants through soil microbes.

The higher P use efficiency than N use efficiency suggests that tropical forest in our study is limited by P, rather than N (Table 3), as also reported by Vitousek (1984). In addition, P demand for reproductive organs (40% of litterfall-P flux) is much higher than N demand (15% of litterfall-N flux) (Table 3). Severe P limitation for the production of reproductive organs has also been confirmed in the dipterocarp forest in Sarawak (Malaysia) (Table 3). The potential P release from microbial turnover (2.0 kg P ha^{-1}; Table 2) is comparable to the plant P demand for reproduction in our study (1.0 kg P ha^{-1}; Table 3). Note that P released from microbial turnover is primarily consumed by sorption onto clays (Turner and Engelbrecht 2011). Despite this, high P concentrations were observed in soil solution collected during the drought (Fig. 1c). The background level of soil solution P is supplied from organic matter decomposition, which is limited in dry season (Fujii et al. 2009). Annual P supply from organic matter decomposition is assumed to be almost equal to annual P supply from litterfall (2.5 kg P ha^{-1}; Table 3). However, El Niño-induced drought in 2014 lasted for longer period (73 days), compared to the drought (15 days) in 2005 (Fujii et al. 2009). According to the relationship between microbial respiration and relative water content (Yan et al. 2018), microbial activities drop to <40% of organic matter decomposition during drought with low relative soil water content [<30% water saturation of soil porosity (0.46 L L^{-1}; from Fujii et al. 2009)]. Using these data, the prolonged drought in 2014 was estimated to decrease P supply from organic matter decomposition by at least 0.25 kg P ha^{-1}, 10% of annual P supply in 2005.

In addition to the limited P supply from organic matter decomposition mentioned above, P release associated with microbial biomass turnover can be another important source of soil solution P (Fig. 1a, c). Soil solution P is considered to be temporarily available to plants even in mass flow through P release from microbial biomass that exceeds sorption (Fig. 1c). The coexistence of high concentrations of DOC limits sorption by competition of sorption sites by organic acids and phosphate (Guppy et al. 2005). P mobility can be enhanced by low molecular weight organic acids (citric acid, oxalic acid, and malic acid) exuded from roots or rhizosphere microbes (Fujii et al. 2021a, b; Turner et al. 2007). However, the P flux from the A horizon, where root density is maximum (Fujii et al. 2009), is still minor (0.04 kg P ha^{-1} dry $period^{-1}$), considering the limited water flux (39 mm) during the drought. In addition, ectomycorrhizal fungi and dipterocarp association develops stronger drought tolerance, compared to saprotrophic fungi, and facilitates nutrient uptake even under dry conditions (Condit et al. 2013). These facts support the potential importance of microbial turnover in the supply of P for reproduction and survival during drought (drought tolerance) and the dominance of dipterocarp trees in tropical forests, which has been under debate (e.g., Corrales et al. 2016).

Acknowledgements This work was supported by a Japan Society for the Promotion of Science (JSPS) Grant No. 20KK0149 and JST Fusion Oriented Research for destructive Science and Technology (FOREST) Grant No. 20351100.

Author contributions All authors contributed to the study conception and design. Site preparation, sample collection, experiments, and analysis were performed by KF, CH, and S. The first draft of the manuscript was written by KF and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability The datasets analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

References

Ashton PS, Givnish TJ, Appanah S (1988) Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. Am Nat 132(1):44–66

Bray RH, Kurtz LT (1945) Determination of total, organic, and available forms of phosphorus in soils. Soil Sci 59(1):39–46

Cleveland CC, Liptzin D (2007) C:N:P stoichiometry in soil: is there a "Redfield ratio" for the microbial biomass? Biogeochemistry 85:235–252

Condit R, Engelbrecht BM, Pino D, Pérez R, Turner BL (2013) Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. Proc Natl Acad Sci 110(13):5064–5068

Corrales A, Mangan SA, Turner BL, Dalling JW (2016) An ectomycorrhizal nitrogen economy facilitates monodominance in a neotropical forest. Ecol Lett 19:383–392

Diaz-Ravina M, Acea MJ, Carballas T (1995) Seasonal changes in microbial biomass and nutrient flush in forest soils. Biol Fertil Soils 19:220–226

Fujii K (2014) Soil acidification and adaptations of plants and microorganisms in Bornean tropical forests. Ecol Res 29:371–381

Fujii K, Uemura M, Funakawa S, Hayakawa C, Sukartiningsih, Kosaki T, Ohta S (2009) Fluxes of dissolved organic carbon in two tropical forest ecosystems of East Kalimantan, Indonesia. Geoderma 152:127–136

Fujii K, Hartono A, Funakawa S, Uemura M, Sukartiningsih, Kosaki T (2010) Acidification of tropical forest soils derived from serpentine and sedimentary rocks in East Kalimantan, Indonesia. Geoderma 160:311–323

Fujii K, Shibata M, Kitajima K, Ichie T, Kitayama K, Turner BL (2018) Plant–soil interactions maintain biodiversity and functions of tropical forest ecosystems. Ecol Res 33:149–160

Fujii K, Hayakawa C, Sukartiningsih (2021a) Root exudation and biodegradation of organic acids in a tropical forest soil under dipterocarp and pioneer trees. Plant Soil 469(1):213–226

Fujii K, Toma T, Sukartiningsih (2021b) Comparison of soil acidification rates under different land uses in Indonesia. Plant Soil 465(1–2):1–17

Guppy CN, Menzies NW, Moody PW, Blamey FPC (2005) Competitive sorption reactions between phosphorus and organic matter in soil: a review. Soil Res 43(2):189–202

Han Q, Kabeya D, Iio A, Inagaki Y, Kakubari Y (2014) Nitrogen storage dynamics are affected by masting events in *Fagus crenata*. Oecologia 174:679–687

Ichie T, Nakagawa M (2013) Dynamics of mineral nutrient storage for mast reproduction in the tropical emergent tree *Dryobalanops aromatica*. Ecol Res 28:151–158

Ichie T, Kenta T, Nakagawa M, Sato K, Nakashizuka T (2005) Resource allocation to reproductive organs during masting in the tropical emergent tree, *Dipterocarpus tempehes*. J Trop Ecol 21(2):237–241

Inubushi K, Sakamoto K, Sawamoto T (2005) Properties of microbial biomass in acid soils and their turnover. Soil Sci Plant Nutr 51:605–608

Jackson ML (1958) Soil chemical analysis. Prentice-Hall Inc, Englewood Cliffs, NJ

Janzen DH (1974) Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. Biotropica 6:69–103

Jenkinson DS (1988) Determination of microbial biomass carbon and nitrogen in soil. In: Wilson JR (ed) Advances in nitrogen cycling in agricultural ecosystems. CAB International, Wallingford, UK, pp 368–386

Jenkinson DS, Brookes PC, Powlson DS (2004) Measuring soil microbial biomass. Soil Biol Biochem 36:5–7

Kitayama K, Tsujii Y, Aoyagi R, Aiba SI (2015) Long-term C, N and P allocation to reproduction in Bornean tropical rain forests. J Ecol 103(3):606–615

Lim MT (1978) Litterfall and mineral nutrient content of litter in Pasoh forest reserve. Malay Nat J 30:375–380

McGill WB, Cannon KR, Robertson JA, Cook FD (1986) Dynamics of soil microbial biomass and water-soluble organic C in Breton L after 50 years of cropping to two rotations. Can J Soil Sci 66(1):1–19

Sakai S, Momose K, Yumoto T, Nagamitsu T, Nagamasu H, Hamid Karim AA, Nakashizuka T, Inoue T (2005) Plant reproductive phenology and general flowering in a mixed dipterocarp forest. In: Roubik DW, Sakai S, Hamid Karim AA (eds) Pollination ecology and the rain forest: Sarawak studies. Springer, New York, pp 35–50

Sakai S, Harrison RD, Momose K, Kuraji K, Nagamasu H, Yusunari T, Chong L, Nakashizuka T (2006) Irregular

droughts trigger mass flowering in aseasonal tropical forests in Asia. Am J Bot 93:1134–1139
Singh JS, Raghubanshi AS, Singh RS, Srivastava SC (1989) Microbial biomass acts as a source of plant nutrients in dry tropical forest and savanna. Nature 338:499–500
Soil Survey Staff (2022) Keys to soil taxonomy, 13th ed. USDA-Natural Resources Conservation Service. Illustrated Guide to Soil Taxonomy
Strickland MS, Rousk J (2010) Considering fungal: bacterial dominance in soils—methods, controls, and ecosystem implications. Soil Biol Biochem 42(9):1385–1395
Turner BL, Engelbrecht BM (2011) Soil organic phosphorus in lowland tropical rain forests. Biogeochemistry 103:297–315
Turner BL, Wright SJ (2014) The response of microbial biomass and hydrolytic enzyme activities to a decade of nitrogen, phosphorus, and potassium addition in a lowland tropical rain forest. Biogeochemistry 117:115–130
Turner BL, Condron LM, Richardson SJ, Peltzer DA, Allison VJ (2007) Soil organic phosphorus transformations during pedogenesis. Ecosystems 10:1166–1181
Vance ED, Brookes PC, Jenkinson DS (1987) An extraction method for measuring soil microbial biomass C. Soil Biol Biochem 19:703–707
Vitousek PM (1984) Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology 65(1):285–298
Wardle DA (1998) Controls of temporal variability of the soil microbial biomass: a global-scale synthesis. Soil Biol Biochem 30(13):1627–1637
Wu J, Joergensen RG, Pommerening B, Chaussod R, Brookes PC (1990) Measurement of soil microbial biomass C by fumigation extraction—an automated procedure. Soil Biol Biochem 22:1167–1169
Wu J, He ZL, Wei WX, O'donnell AG, Syers JK (2000) Quantifying microbial biomass phosphorus in acid soils. Biol Fert Soils 32:500–507
Xu X, Thornton PE, Post WM (2013) A global analysis of soil microbial biomass carbon, nitrogen and phosphorus in terrestrial ecosystems. Glob Ecol Biogeogr 22:737–749
Yan Z, Bond-Lamberty B, Todd-Brown KE et al (2018) A moisture function of soil heterotrophic respiration that incorporates microscale processes. Nat Commun 9:2562