EFFECTS OF SELECTIVE LOGGING AND APPLICATION OF PHOSPHORUS AND NITROGEN ON FLUXES OF CO_2, CH_4 AND N_2O IN LOWLAND TROPICAL RAINFORESTS OF BORNEO

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We compared fluxes of carbon dioxide (CO_2), nitrous oxide (N_2O) and methane (CH_4) in a primary forest and a secondary forest that has experienced selective logging more than 14 years ago. Effects of phosphorus (P) and nitrogen (N) application were also reported. We observed lower CO_2 fluxes in the logged forest (2.0–2.4 g carbon (C) m^{-2} day^{-1}) than the primary forest (2.4–3.5 g C m^{-2} day^{-1}). The lower fluxes were probably because root respiration and heterotrophic respiration were lower in the logged forest. Smaller amounts of microbial biomass C (840–985 and 589–641 µg C g $soil^{-1}$ in the primary and secondary forests respectively) and N (109–143 and 106–117 µg N g $soil^{-1}$) in the secondary forest than the primary forest suggested that there were less substrate inputs such as leaf and root litters, soil organic matters and root exudates in the former which produced less microbial population with lower heterotrophic respiration. Application of P increased CO_2 emission (from 2.0–2.7 to 2.2–3.5 g C m^{-2} day^{-1}) and microbial biomass N (from 106–115 to 110–143 µg N g $soil^{-1}$), suggesting that the belowground ecosystems of both forests were limited by availability of P as reported in other tropical forests. Fluxes of CH_4 showed no differences between forests or manipulation of nutrient because of the high variability of fluxes. Logging operation and nutrient application did not influence N_2O fluxes. The invariable N_2O fluxes occurred because water content was low during sampling and emission of N_2O was restricted by water availability, which might have masked the effects of logging or nutrient application on N_2O emission.

Keywords: Logged forest, primary forest, secondary forest, microbial biomass

INTRODUCTION

A large part of the remaining forests in South-East Asia consists of degraded or logged over forests due to clear cutting or selective logging (ITTO 2006). In Malaysia, for example, more than 10.7 million ha of forests are classified as production forests (ITTO 2011), which account for more than half of its total forest area. Logging causes extensive forest degradation and negative impacts on ecosystem services such as carbon (C) storage, protection of hill slopes and moderation of microclimate. Efforts have been made to reduce logging intensity and collateral damages on ecological functions (Putz et al. 2008, ITTO 2011, Kitayama 2013).

Logging has great impacts on fluxes of greenhouse gases, namely, carbon dioxide (CO_2), nitrous oxide (N_2O) and methane (CH_4) (Tate et al. 2006, Yashiro et al. 2008, Page et al. 2011). Logging can either enhance or reduce CO_2 emission (Hendrickson & Robinson 1984, Nakane et al. 1986, Lavoie et al. 2013, Zerva & Mencuccini 2005, Köster et al. 2011, Goutal et al. 2012). In contrast, N_2O and CH_4 fluxes are usually enhanced by logging operation (Yashiro et al. 2008, Page et al. 2011). Factors that control fluxes after logging include soil/air temperature, moisture, organic matter inputs and soil nitrogen (N) cycling (Ishizuka et al. 2002, Zerva & Mencuccini 2005, Yashiro et al. 2008, Page et al. 2011). The fluxes gradually return to background levels within a few months to a few years after logging (Tang et al. 2005, Page et al. 2011), but observations of more than 10 years after logging of tropical forests are still rare.

Primary productivity in many tropical forests is limited by phosphorus (P) shortage (Vitousek & Sanford 1986, Elser et al. 2007) in contrast to that of temperate forests which are usually limited

by N. Soil microbial activities in tropical forests are also believed to be limited by availability of P, because soil heterotrophic microbial respiration (Cleveland et al. 2002, Ilstedt et al. 2003, Cleveland & Townsend 2006, Liu et al. 2012, Mori et al. 2013c) or biomass (Liu et al. 2012, 2015, Mori et al. 2016) is increased by addition of P. Since CH_4 and N_2O exchange between the atmosphere and soil is also derived from soil microbial activities, P availability may also control CH_4 uptake and N_2O emission in P-limited tropical forest soil (Mori et al. 2010b). Application of P in a natural tropical forest stimulates root N uptake and reduces N inhibition on CH_4 oxidation, increasing the CH_4 uptake rates (Zhang et al. 2011). In a series of studies in a tropical leguminous tree plantation, P application reduced N_2O emission by stimulating root uptake of N resources (Mori et al. 2014) or soil water (Mori et al. 2013b) but stimulated the emission in laboratory by accelerating microbial nitrification and denitrification (Mori et al. 2010a, 2013d). However, studies of the effects of P addition on fluxes of CH_4 and N_2O are biased to plantations (Mori et al. 2013a, Zhang et al. 2014), laboratory (Mori et al. 2010a), paddy fields (Adhya et al. 1997, Lu et al. 1999) or secondary forests (Wang et al. 2014). Very few studies have tested the effects of P addition in natural tropical lowland forests.

In 2011, a nutrient application experiment was carried out using P and N in two types of mixed dipterocarp tropical rainforests (one is primary forest and the other is secondary forest which has experienced selective logging more than 14 years ago) in Sabah, Malaysia. These experimental sites provided a chance to test the effects of logging (long-term influence) and nutrient (P and N) application on greenhouse gas fluxes. In this study, we tested the effects of selective logging and nutrient application on fluxes of CO_2, CH_4 and N_2O in tropical lowland forests in Sabah.

MATERIALS AND METHODS

Study sites

Study sites are located in a primary forest in Deramakot Forest Reserve (551 km^2) and in a selectively logged forest in Tangkulap Forest Reserve (275 km^2) in Sabah, Malaysia (5° 14–30' N, 117° 11–36' E) (Imai et al. 2010). The climate is humid equatorial. Mean annual temperature was 25.2 °C with annual precipitation of 3098 mm for the period 2008–2010 (Ong et al. 2013). Both forests are mixed dipterocarp tropical rainforests located adjacent to each other (Imai et al. 2012). Logging in Tangkulap started in 1970s, thereafter the forest was damaged due to repeated conventional logging until 2001 (Imai et al. 2009).

Fertilisation experiment

Twelve 0.12-ha (30 m × 40 m) plots were established in each forest and experimental nutrient manipulations were conducted in both forests. Treatments included control (without P or N application), P-application, N-application, and PN-application (n = 3 for each treatment). In December 2011, triple super phosphate and urea were applied by hand at a rate of 50 kg P ha^{-1} and 100 kg N ha^{-1} respectively. To ensure uniform application, fertiliser was scattered over 12 areas, each measuring 10 m × 10 m (0.12-ha plot divided into 12 parts). Thereafter, nutrient application was conducted at the same rate once a year.

Gas flux measurements

In March 2015, CO_2, CH_4 and N_2O fluxes were measured using static chamber method (Ishizuka et al. 2002). We set four PVC chambers (7.7 cm diameter, 15 cm height) in each plot (n = 12 for each treatment). The chambers were covered with lids equipped with sampling ports in the middle and silicone seats at adhesive surfaces. Chambers and the lids were attached using four eyeball clips so as not to release air. During daytime, 15-mL gas samples were taken at 0 and 30 min after the closure of the lids and transferred into 10-mL pre-evacuated glass vials equipped with butyl rubber stoppers. Due to time, physical and labour constraints in taking many samples, only two gas samples (0 and 30 min) were taken for each flux measurement. This might have underestimated gas fluxes if gas concentration inside the chamber did not change linearly over time due to high fluxes exceeding maximum measurement. Since changes in gas concentrations were linear for the first 30 min even when the range of fluxes was larger than the present study (Konda et al. 2008), we believed that the gas fluxes were properly determined. Gas concentrations were analysed

using gas chromatograph equipped with thermal conductivity detector for CO_2, flame ionisation detector for CH_4 and electron capture detector for N_2O. Gas fluxes were calculated as follows:

$$F = \rho \times (V/A) \times (\Delta c/\Delta t) \times [273/(T + 273)] \quad (1)$$

where F = gas flux (mg m^{-2} $hour^{-1}$), ρ = density of gas (kg m^{-3}), V = volume of the chamber (m^3), A = base area of the chamber (m^2), $\Delta c/\Delta t$ = change of concentration with time (ppmv $hour^{-1}$) and T = temperature (°C) in the chamber.

Soil analyses

Two soil cores were taken at a depth of 0–5 cm approximately 50 cm apart from each chamber using a soil sampling core (3.4 cm diameter) to make a composite (in total 12 composite samples in each treatment). After roots and organic matters were removed, soil samples were passed through a 2-mm sieve. Water-filled pore space (WFPS) was calculated as follows:

$$WFPS\ (\%) = \omega \times BD/(1 - BD/PD) \quad (2)$$

where ω = gravimetric water content of soil (g g^{-1}), BD = bulk density (mg cm^{-3}) and PD = particle density (2.65 mg cm^{-3}, a generally used typical value (Rossi et al. 2008)). Inorganic N (NH_4 and NO_3^-) and dissolved organic C in the soil were extracted by shaking 1 fresh soil: 5 K_2SO_4 (0.5 M) for 30 min using electric shaker NH_4^+ was determined by indophenol blue absorptiometry and NO_3^- by the naphthyl ethylenediamine method using flow-injection analyser. Dissolved organic C was analysed using total organic C analyser. Soil microbial biomass C and N were determined using chloroform fumigation extraction method (Vance & Jenkinson 1987).

Statistical analysis

Three-way ANOVA followed by Tukey's hoc test (primary forest vs logged forest, without N vs N, without P vs P) was used for comparing each gas type and soil chemical data, assuming the normality of data. If interactions were significant, simple main effect analyses (Tukey) were performed. We assumed N_2O fluxes were higher than zero, thus replaced data lower than zero with zero. All statistical analyses were performed by Excel 2013 with statistical add-in software (SSRI).

Results

During the present research, water-filled pore space was low in every site (Table 1). CO_2 fluxes were significantly lower in the logged forest (mean daily fluxes of 2.0, 2.2, 2.3 and 2.6 g C m^{-2} day^{-1} in control, P-, N- and PN-applied plots respectively, Figure 1a) than the primary forest (2.7, 3.1, 2.4, 3.5 g C m^{-2} day^{-1} respectively). Application of P significantly increased CO_2 emission without any interaction with logging nor N application, while N application did not influence CO_2 emission (Figure 1a). N_2O and CH_4 fluxes were not influenced by logging operation, P nor N application (Figure 1b and c). Microbial biomass C and N values were significantly higher in the primary forest than in the logged forest (Figure 2). Application of P significantly increased microbial biomass N, but not microbial biomass C. Microbial biomass C and N values were not affected by addition of N. Logging operation and nutrient application affected properties of soil C and N. Dissolved organic C contents were higher in the primary forest than the logged forest, but not influenced by nutrient application (Table 2). Soil NH_4^+ contents were increased by N but not affected by logging nor P application (Table 2). Logging and nutrient application significantly influenced soil NO_3^- contents (Table 2). Applications of N and P increased NO_3^- contents only in the primary forest (Table 2).

DISCUSSION

Effects of logging on CO_2 emission

CO_2 fluxes from the primary forest ranged from 2.4 to 3.5 g C m^{-2} day^{-1}, which were comparative with other tropical lowland forests (1.4–4.4 g m^{-2} day^{-1}) (Fernandes et al. 2002, Ishizuka et al. 2002, Kiese & Butterbach-Bahl 2002, Schwendenmann et al. 2003, Dalal & Allen 2008, Yashiro et al. 2008). Logging can either increase or decrease CO_2 emission in forests. Emission of CO_2 is increased when soil/air temperature (Yashiro et al. 2008), soil moisture (Page et al. 2011) and organic matters (e.g. logging slash and dead roots) (Tate et al. 2006) increase. On the other hand, decrease in root respiration, substrate inputs (such as leaf and root litters) and microbial population can reduce CO_2 emission (Hendrickson & Robinson 1984, Schilling et al. 1999, Zerva & Mencuccini 2005, Page et al. 2011). Time after logging has

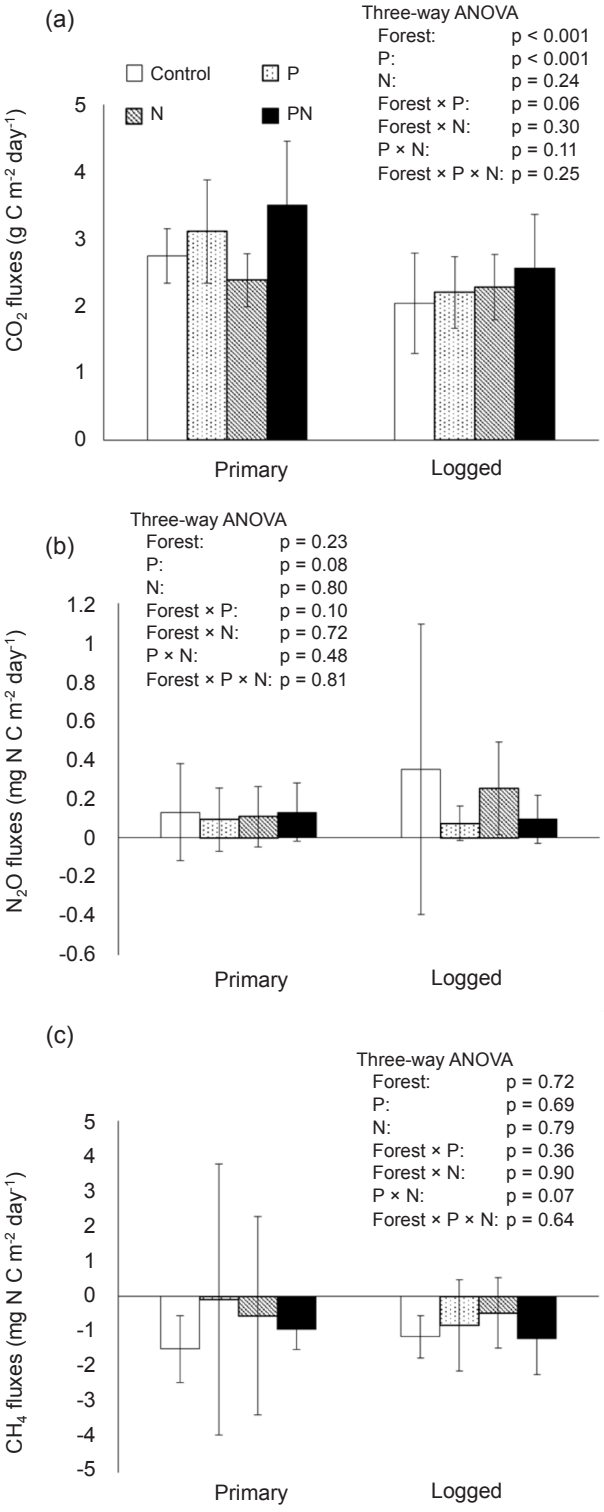

Figure 1 Fluxes of (a) CO_2, (b) N_2O, and (c) CH_4 under different treatment in a primary forest and a logged forest; P = phosphorus, N = nitrogen; data are illustrated as means and error bars represent 1 standard deviation, n = 12 (n = 11 in CO_2 and CH_4 fluxes at PN treatment in the primary forest, and n = 11 in CO_2 fluxes at PN treatment in the logged forest because of the experimental failure)

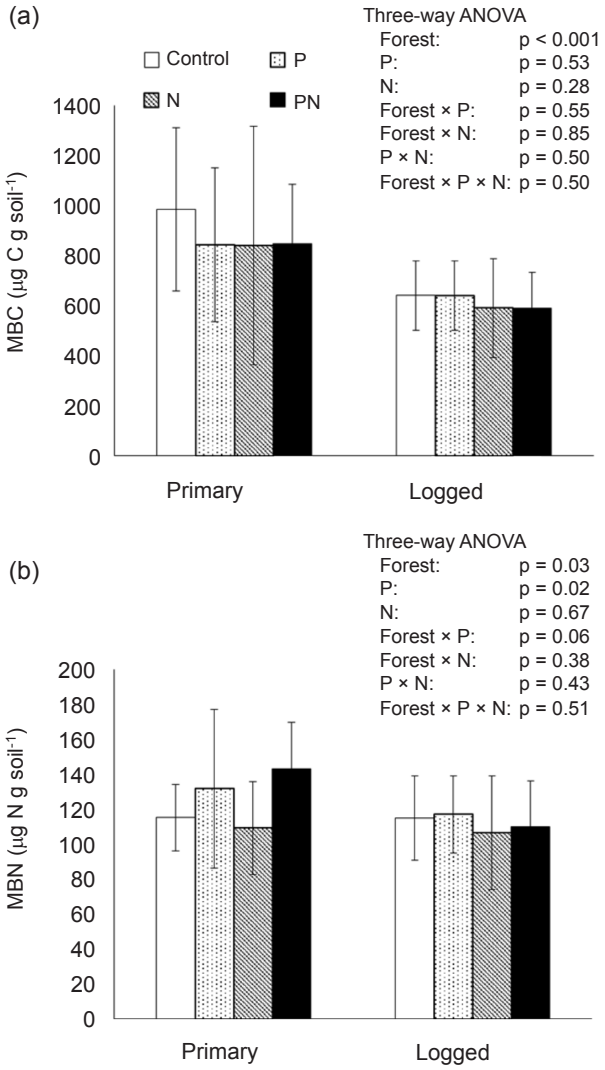

Figure 2 Microbial biomass (a) carbon and (b) nitrogen under different treatment in a primary forest and a logged forest; P = phosphorus, N = nitrogen, MBC = microbial biomass carbon, MBN = microbial biomass nitrogen; data are illustrated as means, and error bars represent 1 standard deviation, n = 12

great impacts on soil respiratory response (CO_2 emission) with an initial increase in CO_2 emission due to increased substrate availability through harvest slash inputs followed by gradual decrease as tree roots gradually die and stop respiring (Guo et al. 2010, Page et al. 2011). Lower CO_2 emission observed in the logged forest (2.0–2.6 g C m^{-2} day^{-1}; Figure 1a) compared with the primary forest (2.4–3.5 g C m^{-2} day^{-1}, Figure 1a) are in accordance with previous findings, because the stimulatory effects of logging operation on CO_2 emission have disappeared after 14 years. Lower CO_2 emission in the logged forest could

Table 1 Environmental parameters during sampling

Forest type		Air temperature (°C)		Soil temperature (°C)		WFPS (%)	
		Average	SD	Average	SD	Average	SD
Primary forest	Control	26.0	1.7	24.7	0.4	25.3	2.4
	N	25.7	0.7	24.5	0.2	24.6	4.1
	P	26.3	0.7	24.5	0.2	30.9	8.5
	NP	26.0	1.1	24.8	0.3	28.5	4.1
Logged forest	Control	25.8	1.3	25.0	0.3	36.3	7.8
	N	27.5	0.4	25.4	0.3	30.1	5.2
	P	26.6	2.2	25.1	0.3	30.1	4.0
	NP	26.9	1.6	25.3	0.3	33.7	4.3

SD = standard deviation; WFPS = water filled pore space, P = phosphorus, N = nitrogen

be attributed to lower root respiration and substrates for heterotrophic respiration such as leaf and root litters, soil organic matters and root exudates. Microbial biomass C and N were lower in the logged forest than in the primary forest (Figure 2). Decrease in substrate inputs into the soil could have reduced microbial population (Schilling et al. 1999, Zerva & Mencuccini 2005), decreasing heterotrophic respiration (CO_2 emission). In contrast with microbial biomass, dissolved organic C contents were higher in the logged forest than in the primary forest (Table 2). Although dissolved organic C is thought to be a substrate for microbial respiration, the rate of its production rather than its concentration was suggested to be the limiting factor for soil respiration rates (Bengtson & Bengtsson 2007). It is assumed that the turnover of dissolved organic C is faster in primary than in logged forests.

Effects of logging on fluxes of CH_4 and N_2O

The CH_4 flux values were comparable with other tropical rainforests (Potter et al. 1996 (0.78 mg C m^{-2} day^{-1}), Dalal & Allen 2008 (1.1 mg C m^{-2} day^{-1})). Logging causes reduction in CH_4 uptake due to soil compaction and increase in soil moisture, temperature or accelerated N cycles (Zerva & Mencuccini 2005). On the contrary, this study demonstrated that CH_4 fluxes in the forest logged more than 14 years ago showed no significant differences with those in the primary forest. The negative effects of logging on CH_4 uptake might have disappeared as the forests and CH_4-oxidising microbes therein recovered.

Emission rates of N_2O (Figure 1b) in the logged and primary forests were at the lower end of the tropical forest average (0.23–3.5 mg N m^{-2} day^{-1}; Dalal & Allen 2008), most possibly due to lower water-filled pore spaces (Table 1). The fact that higher inorganic N in N-applied plots did not result in higher N_2O fluxes supported this idea (Figure 1, Table 2). Another possible reason is that tropical forests in Asia have fewer legumes (Primack & Corlett 2005) (also in our study site) compared with neotropical (Steege et al. 2000) and African tropical (Schulze et al. 1991) forests and N cycling is slower (Arai et al. 2008). Emission of N_2O from Asian tropical forests was lower than from the other areas (Ishizuka et al. 2002).

Although logging operation generally stimulated N_2O emission through increases in N cycling (Tate et al. 2006, Page et al. 2011), this was not observed in this study. There were no differences in N_2O emission between logged and primary forests (Table 2). Inorganic N pools were also not affected by logging operation. The impact of logging on N_2O emission may have disappeared during the long term of recovery. However, it is also possible that low water-filled pore space, one of the most important factor controlling N_2O emission, has masked the impact of logging on N_2O emission.

Effects of nutrient addition on greenhouse gas emission

Application of P significantly increased CO_2 emission (Figure 1a), suggesting that P availability limited the belowground ecosystems in tropical

Table 2 Labile carbon and nitrogen contents under different nutrient treatments in primary and logged forests

Forest type		DOC µg C g soil^{-1}		NH_4^+ µg N g soil^{-1}		NO_3^- µg N g soil^{-1}	
		Average	SD	Average	SD	Average	SD
Primary forest	Control	205	29	22	6.4	2.2	1.7
	N	207	40	117	151	9.7	7.6
	P	211	33	22	6.6	8.1	5.0
	NP	212	35	151	185	16	5.9
Logged forest	Con.	238	58	19	3.4	7.7	4.4
	N	246	39	117	135	11	9.0
	P	225	23	19	3.6	3.7	2.2
	NP	217	26	74	70	4.6	3.6
Significant factors ($p < 0.05$, three-way ANOVA)		Forest		N		Forest N Forest × P Forest × N	

DOC = dissolved organic carbon, P = phosphorus, N = nitrogen, C = carbon; SD = standard deviation

forests (Cleveland et al. 2002, Cleveland & Townsend 2006, Liu et al. 2012). Shortage of P in belowground was relieved by P application, leading to stimulated root respiration (Mori et al. 2013e) and accelerated decomposition of organic matters by heterotrophic microbes (Cleveland et al. 2002, Ilstedt et al. 2003). On the other hand, P application did not change the amount of microbial biomass C, although microbial biomass N was increased by P application (Table 2). This could be due to the microbial community shift affected by P application in P-limited soils (Liu et al. 2012). Higher emission of CO_2 and microbial biomass N contents might be partly affected by higher water-filled pore space condition in P-applied plots in the primary forest (Table 1). Although N addition did not change CO_2 emission (Figure 1a), we cannot conclude that the ecosystem was not limited by N. This is because when N is limited, its addition reduces decomposition of organic matters, which is known as N-mining (Moorhead & Sinsabaugh 2006).

The effects of P application on CH_4 fluxes have been well studied in laboratory experiments, paddy fields and plantations but the results are inconsistent. Phosphorus influences microbial methanotrophic and methanogenesis activity directly or indirectly through changing the amount of root exudates and root uptake of water and N (Lu et al. 1999, Zhang et al. 2011). Very few reports have investigated the effects of P on CH_4 fluxes in natural tropical forests. Application of P stimulated root N uptake and mitigated N inhibition on CH_4 uptake in a natural tropical forest in China (Zhang et al. 2011). However, we did not observe any differences between sites with or without P application. Application of N inhibits CH_4 oxidation through enzyme inhibition by NH_4^+, NO_2^- toxicity and osmotic stress (Schnell & King 1994, Kravchenko et al. 2002, Baggs & Blum 2004, Bodelier & Laanbroek 2004). However, this was not the case in the present study. Application of N did not affect CH_4 fluxes.

Application of P suppressed N_2O emission through stimulating N uptake of roots and reduced resources (N) producing N_2O in P-limited maize cropland (Baral et al. 2014), tropical monoculture plantation (Mori et al. 2013b, 2014) and N-saturated natural forest (Chen et al. 2015). Phosphorus application stimulated N_2O emission if vegetation was excluded (Mori et al. 2010a, 2013d). Thus, P application in P-limited ecosystem influences emission of N_2O. However, in the present study, P application had no significant effect on N_2O emission probably because of low water-filled pore space. Similarly, N application, which generally increased N_2O emission in most

other studies (Liu & Greaver 2009), was also not significant in the present study (Figure 1), suggesting that water (and not N resources) limited N_2O production. Dry conditions may have masked the effects of P and N application on N_2O emission in the present study.

CONCLUSIONS

The effects of logging on the emission of soil CO_2 were still discernible 14 years after the operation has ceased, but fluxes of N_2O and CH_4 were not affected. Availability of P limited belowground ecosystem including root respiration and microbial activities. In contrast to the hypothesis that P application influenced N_2O and CH_4 fluxes in P-limited tropical forests, significant effects of P application were not observed in the present study.

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REFERENCES

Adhya TK, Pattnaik P, Satpathy SN, Kumaraswamy S & Sethunathan N. 1997. Influence of phosphorus application on methane emission and production in flooded paddy soils. *Soil Biology and Biochemistry* 30: 177–181.

Arai S, Ishizuka S, Ohta S et al. 2008. Potential N_2O emission from leguminous tree plantation soils in the humid tropics. *Global Biogeochemical Cycles*. doi:10.1029/2007GB002965.

Baggs EM & Blum H. 2004. CH_4 oxidation and emission of CH_4 and N_2O from *Lolium perenne* swards under elevated atmospheric CO_2. *Soil Biology and Biochemistry* 36: 713–723.

Baral BR, Kuyper TW & Van Groenigen JW. 2014. Liebig's law of the minimum applied to a greenhouse gas: alleviation of P-limitation reduces soil N_2O emission. *Plant and Soil* 374: 539–548.

Bengtson P & Bengtsson G. 2007. Rapid turnover of DOC in temperate forests accounts for increased CO_2 production at elevated temperatures. *Ecology Letters* 10: 783–790.

Bodelier PLE & Laanbroek HJ. 2004. Nitrogen as a regulatory factor of methane oxidation in soils and sediments. *FEMS Microbiology Ecology* 47: 265–277.

Chen H, Gurmesa GA, Zhang W et al. 2015. Nitrogen saturation in humid tropical forests after 6 years of nitrogen and phosphorus addition: hypothesis testing. *Functional Ecology* 30: 305–313.

Cleveland C, Townsend A & Schmidt S. 2002. Phosphorus limitation of microbial processes in moist tropical forests: evidence from short-term laboratory incubations and field studies. *Ecosystems* 5: 680–691.

Cleveland CC & Townsend AR. 2006. Nutrient additions to a tropical rainforest drive substantial soil carbon dioxide losses to the atmosphere. *Proceedings of the National Academy of Sciences of the United States of America* 103: 10316–10321.

Dalal RC & Allen DE. 2008. Greenhouse gas fluxes from natural ecosystems. *Australian Journal of Botany* 56: 369–407.

Elser JJ, Bracken MES, Cleland EE et al. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters* 10: 1135–1142.

Fernandes SAP, Bernoux M, Cerri CC, Feigl BJ & Piccolo MC. 2002. Seasonal variation of soil chemical properties and CO_2 and CH_4 fluxes in unfertilised and P-fertilised pastures in an Ultisol of the Brazilian Amazon. *Geoderma* 107: 227–241.

Goutal N, Parent F, Bonnaud P et al. 2012. Soil CO_2 concentration and efflux as affected by heavy traffic in forest in northeast France. *European Journal of Soil Science* 63: 261–271.

Guo J, Yang Y, Chen G, Xie J, Gao R & Qian W. 2010. Effects of clear-cutting and slash burning on soil respiration in Chinese fir and evergreen broadleaved forests in mid-subtropical China. *Plant and Soil* 333: 249–261.

Hendrickson OQ & Robinson JB. 1984. Effects of roots and litter on mineralization processes in forest soil. *Plant and Soil* 80: 391–405.

Ilstedt U, Giesler R, Nordgren A & Malmer A. 2003. Changes in soil chemical and microbial properties after a wildfire in a tropical rainforest in Sabah, Malaysia. *Soil Biology and Biochemistry* 35: 1071–1078.

Imai N, Kitayama K & Titin J. 2010. Distribution of phosphorus in an above-to-below-ground profile in a Bornean tropical rainforest. *Journal of Tropical Ecology* 26: 627–636.

Imai N, Kitayama K & Titin J. 2012. Effects of logging on phosphorus pools in a tropical rainforest of Borneo. *Journal of Tropical Forest Science* 24: 5–17.

Imai N, Samejima H, Langner A et al. 2009. Co-benefits of sustainable forest management in biodiversity conservation and carbon sequestration. *PLoS ONE* 4. doi.org/10.1371/journal.pone.0008267.

Ishizuka S, Tsuruta H & Murdiyarso D. 2002. An intensive field study on CO_2, CH_4 and N_2O emission from soils at four land-use types in Sumatra, Indonesia. *Global Biogeochemical Cycles* 16. doi:10.1029/2001GB001614.

ITTO (International Tropical Timber Organization). 2006. *Status of Tropical Forest Management 2005*. ITTO, Yokohama.

ITTO. 2011. *Status of Tropical Forest Management 2011*. ITTO, Yokohama.

Kiese R & Butterbach-Bahl K. 2002. N_2O and CO_2 emission from three different tropical forest sites in the wet tropics of Queensland, Australia. *Soil Biology and Biochemistry* 34: 975–987.

Konda R, Ohta S, Ishizuka S et al. 2008. Soil biology and biochemistry spatial structures of N_2O, CO_2 and CH_4 fluxes from *Acacia mangium* plantation soils during a relatively dry season in Indonesia. *Soil Biology and Biochemistry* 40: 3021–3030.

Köster K, Püttsepp Ü & Pumpanen J. 2011. Comparison of soil CO_2 flux between uncleared and cleared windthrow areas in Estonia and Latvia. *Forest Ecology and Management* 262: 65–70.

Kravchenko I, Boeckx P, Galchenko V & Van Cleemput O. 2002. Short- and medium-term effects of $NH4^+$ on CH_4 and N_2O fluxes in arable soils with a different texture. *Soil Biology and Biochemistry* 34: 669–678.

Kitayama K. 2013. *Co-benefits of Sustainable Forestry: Ecological Studies of a Certified Bornean Tropical Rain Forest*. Ecological Research Monographs. Springer, Berlin.

Lavoie M, Kellman L & Risk D. 2013. The effects of clear-cutting on soil CO_2, CH_4, and N_2O flux, storage and concentration in two Atlantic temperate forests in Nova Scotia, Canada. *Forest Ecology and Management* 304: 355–369.

Liu L & Greaver TL. 2009. A review of nitrogen enrichment effects on three biogenic GHGs: the CO_2 sink may be largely offset by stimulated N_2O and CH_4 emission. *Ecology Letters* 12: 1103–1117.

Liu L, Gundersen P, Zhang T & Mo J. 2012. Effects of phosphorus addition on soil microbial biomass and community composition in three forest types in tropical China. *Soil Biology and Biochemistry* 44: 31–38.

Liu L, Gundersen P, Zhang W, Zhang T, Chen H & Mo J. 2015. Effects of nitrogen and phosphorus additions on soil microbial biomass and community structure in two reforested tropical forests. *Scientific Reports* 5: 14378.

Lu Y, Wassmann R, Neue HU & Huang C. 1999. Impact of phosphorus supply on root exudation, aerenchyma formation and methane emission of rice plants. *Biogeochemistry* 47: 203–218.

Moorhead D, Sinsabaugh R. 2006. A theoretical model of litter decay and microbial interaction. *Ecological Monographs* 76: 151–174.

Mori T, Ohta S, Ishizuka S, Konda R, Wicaksono A, Heriyanto J & Hardjono A. 2010a. Effects of phosphorus addition on N_2O and NO emission from soils of an *Acacia mangium* plantation. *Soil Science and Plant Nutrition* 56: 782–788.

Mori T, Ohta S, Konda R, Ishizuka S & Wicaksono A. 2010b. Phosphorus limitation on CO_2, N_2O, and NO emission from a tropical humid forest soil of South Sumatra, Indonesia. Pp 18–21 in Saji B & Yang D (eds) *2010 International Conference on Environmental Engineering and Applications*. 10–12 September 2010, Singapore.

Mori T, Ohta S, Ishizuka S, Konda R, Wicaksono A & Heriyanto J. 2013a. Effects of phosphorus application on CH_4 fluxes in an *Acacia mangium* plantation with and without root exclusion. *Tropics* 22: 13–17.

Mori T, Ohta S, Ishizuka S et al. 2013b. Soil greenhouse gas fluxes and C stocks as affected by phosphorus addition in a newly established *Acacia mangium* plantation in Indonesia. *Forest Ecology and Management* 310: 643–651.

Mori T, Ohta S, Ishizuka S et al. 2013c. Effects of phosphorus and nitrogen addition on heterotrophic respiration in an *Acacia mangium* plantation soil in South Sumatra, Indonesia. *Tropics* 22: 83–87.

Mori T, Ohta S, Ishizuka S et al. 2013d. Effects of phosphorus addition with and without ammonium, nitrate, or glucose on N_2O and NO emission from soil sampled under *Acacia mangium* plantation and incubated at 100% of the water-filled pore space. *Biology and Fertility of Soils* 49: 13–21.

Mori T, Ohta S, Ishizuka S et al. 2013e. Effects of phosphorus application on root respiration and heterotrophic microbial respiration in *Acacia mangium* plantation soil. *Tropics* 22: 113–118.

Mori T, Ohta S, Ishizuka S, Konda R, Wicaksono A & Heriyanto J. 2014. Phosphorus application reduces N_2O emission from tropical leguminous plantation soil when phosphorus uptake is occurring. *Biology and Fertility of Soils* 50: 45–51.

Mori T, Yokoyama D & Kitayama K. 2016. Contrasting effects of exogenous phosphorus application on N_2O emission from two tropical forest soils with contrasting phosphorus availability. *Springer Plus* 5: 1–8.

Nakane K, Tsubota H & Yamamoto M. 1986. Cycling of soil carbon in a Japanese red pine forest II: changes occurring in the first year after a clear-felling. *Ecological Research* 1: 47–58.

Ong RC, Langner A, Imai N & Kitayama K. 2013. Management history of the study sites: the Deramakot and Tangkulap Forest Reserves. Pp 1–21 in Kitayama K (ed) *Co-benefits of Sustainable Forestry: Ecological Studies of a Certified Bornean Tropical Rainforest*. Ecological Research Monographs. Springer, Japan.

Page KL, Dalal RC & Raison RJ. 2011. The impact of harvesting native forests on vegetation and soil C stocks, and soil CO_2, N_2O and CH_4 fluxes. *Australian Journal of Botany* 59: 654–669.

Potter CS, Davidson EA & Verchot LV. 1996. Estimation of global biogeochemical controls and seasonality in soil methane consumption. *Chemosphere* 32: 2219–2246.

Primack R & Corlett. 2005. *Tropical Rainforests—An Ecological and Biogeographical Comparison*. Blackwell, Malden.

Putz FE, Sist P, Fredericksen T & Dykstra D. 2008. Reduced-impact logging: challenges and opportunities. *Forest Ecology and Management* 256: 1427–1433.

Rossi AM, Hirmas DR, Graham RC & Sternberg PD. 2008. Bulk density determination by automated three-dimensional laser scanning. *Soil Science Society of America Journal* 72: 1591–1953.

Schilling EB, Lockaby BG & Rummer R. 1999. Belowground nutrient dynamics following three harvest intensities on the Pearl River floodplain, Mississippi. *Soil Science Society of America Journal* 63: 1856–1868.

Schnell S & King GM. 1994. Mechanistic analysis of ammonium inhibition of atmospheric methane consumption in forest soils. *Applied and Environmental Microbiology* 60: 3514–3521.

Schulze ED, Gebauer G, Ziegler H & Lange OL. 1991. Estimates of nitrogen fixation by trees on an aridity gradient in Namibia. *Oecologia* 88: 451–455.

Schwendenmann L, Veldkamp E, Brenes T, O'Brien JJ & Mackensen J. 2003. Spatial and temporal variation in soil CO_2 efflux in an old-growth neotropical

rainforest, La Selva, Costa Rica. *Biogeochemistry* 64: 111–128.

Steege TH, Sabatier D, Castellanos H et al. 2000. Analysis of the floristic composition and diversity of Amazonian forests including those of the Guiana Shield. *Journal of Tropical Ecology* 16: 801–828.

Tang J, Qi Y, Xu M, Misson L & Goldstein AH. 2005. Forest thinning and soil respiration in a ponderosa pine plantation in the Sierra Nevada. *Tree Physiology* 25: 57–66.

Tate KR, Ross DJ, Scott NA, Rodda NJ & Townsend JA & Arnold GC. 2006. Post-harvest patterns of carbon dioxide production, methane uptake and nitrous oxide production in a *Pinus radiata* D. Don plantation. *Forest Ecology and Management* 228: 40–50.

Vance ED & Jenkinson DS. 1987. Microbial biomass measurement in forest soils: the use of the chloroform fumigation-incubation method in strongly acid soils. *Soil Biology and Biochemistry* 19: 697–702.

Vitousek PM & Sanford RL. 1986. Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics* 17: 137–167.

Wang F, Li J, Wang X, Zhang W, Zou B, Neher Da & Li Z. 2014. Nitrogen and phosphorus addition impact soil N_2O emission in a secondary tropical forest of South China. *Scientific Reports* 4: 5615. doi:10.1038/srep05615

Yashiro Y, Kadir WR, Okuda T & Koizumi H. 2008. The effects of logging on soil greenhouse gas: CO_2, CH_4, N_2O. flux in a tropical rainforest, Peninsular Malaysia. *Agricultural and Forest Meteorology* 148: 799–806.

Zerva A & Mencuccini M. 2005. Short-term effects of clearfelling on soil CO_2, CH_4, and N_2O fluxes in a Sitka spruce plantation. *Soil Biology and Biochemistry* 37: 2025–2036.

Zhang T, Zhu W, Mo J, Liu L & Dong S. 2011. Increased phosphorus availability mitigates the inhibition of nitrogen deposition on CH_4 uptake in an old-growth tropical forest, southern China. *Biogeosciences* 8: 2805–2813.

Zhang W, Zhu X, Luo Y, Rafique R, Chen H, Huang J & Mo J. 2014. Responses of nitrous oxide emission to nitrogen and phosphorus additions in two tropical plantations with N-fixing vs non-N-fixing tree species. *Biogeosciences Discussions* 11: 1413–1442.

