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REGULAR ARTICLE

Effects of land use change on turnover and storage of soil organic matter in a tropical forest

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Abstract
Aims Land-use change of tropical forests causes loss of soil organic matter and plant productivity. Effects of fallow or plantation vegetation on soil organic matter storage need to be clarified to optimize land-use that maximizes soil organic matter storage and plant productivity.
Methods We compared 30-year changes in soil carbon stocks and litter decomposition under different land-uses (primary dipterocarp forest, *Macaranga* forest, *Imperata* grassland, transition of *Imperata* grassland to *Acacia* plantation, transition of *Imperata* grassland to oil palm plantation) in Indonesia.
Results The *Imperata* grassland maximizes soil carbon stocks for up to 10 years due to considerable root litter inputs, but additional organic matter storage is limited over the following 20 years, due to high grass litter decomposability in the less acidified soil. The conversion of *Imperata* grassland to oil palm plantation causes greatest loss of soil organic matter, whereas *Acacia* plantation on *Imperata* grassland or the *Macaranga* forest maximizes soil carbon stocks due to input of recalcitrant forest litters and reduced microbial activities in the acidified soils.
Conclusion Farmers could adopt short-term (<10 years) grass fallow or longer-term (>10 years) fallow under *Acacia* plantation on *Imperata* grassland or *Macaranga* regeneration forest to maximize soil organic matter storage. The optimum and feasible land-use strategies should be selected based on the length of fallow period and the original acidity of soil.

Keywords Agroforestry · Fallow system · Soil acidification · Soil organic matter · Tropical forest

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Introduction

Tropical forests have been exposed to drastic land-use changes in the past 50 years (Don et al. 2011; Gibson et al. 2011). The change from traditional shifting cultivation to continuous cropping or oil palm plantations leads to a loss of soil organic matter (SOM) and a rapid decline in plant productivity in some tropical regions (Kimetu et al. 2008). The limited availability of fertilizers and organic resources (e.g., manure) induces land abandonment and further deforestation for small-holder farmers in low-input agriculture settings (Lal 2004,

2006; Smith 2008). Land-use strategies, including fallow systems, need to be optimized to maintain levels of SOM in tropical agroecosystems, considering the availability of resources for farmers.

Carbon (C) cycle in tropical forest soils are characterized by large C fluxes via litterfall and microbial decomposition (Vitousek and Sanford Jr 1986; Fujii et al. 2018). Continuous cropping usually results in a rapid loss of soil organic carbon (SOC) stocks (Fujii et al. 2009a), whereas both gains and losses in SOC stocks under natural grassland and secondary forests or human-induced pastures and plantations have been reported (Veldkamp 1994; Yonekura et al. 2012; Sang et al. 2013). The effects of land-use changes on SOC stocks are inconsistent and variable, depending on the stage of cropping or fallow system and the extent of disturbance or management practice (e.g., fires and tillage) (Don et al. 2011), but both natural and disturbed ecosystems share similarity that SOC dynamics are driven by plant and soil microbial processes (Veldkamp 1994; Hooper and Vitousek 1998). By extracting the dominant plant traits and soil properties regulating turnover and storage of organic matter in these ecosystems, the effects of fallow grassland or forest on SOC stocks can be evaluated.

Vegetation changes could influence SOC stocks directly through litter quantity and quality and indirectly through effects on soil chemical and biological properties (Fujii et al. 2018). Field incubation of standard substrates (litter bag or cellulose test) have shown that litters with high lignin to nitrogen (N) ratios decompose relatively slowly (Berg and MacClaugherty 2003) and that SOM of C4 plant (e.g., *Imperata* grass) origin can decompose faster than SOM of C3 plant (e.g., trees) origin (Wynn and Bird 2007). Organic matter turnover could also be affected by soil properties that are changeable under different vegetation covers (Yamashita et al. 2008). For example, soil acidification under tropical forests (e.g., *Acacia* plantation) can reduce microbial activity and retard organic matter decomposition (Hayakawa et al. 2014). The stability of organic matter derived from forest and grassland can be traced using the difference in their litter ^{13}C isotopic signature and the potential importance of grassland in SOM storage has been reported by several studies (Yonekura et al. 2012). Combination of litter bag tests of standard substrates and ^{13}C isotopic signature analysis allow us to extract the effects of plant traits and soil properties on SOC dynamics by tracing the SOC stocks of individual plant origins.

Fires that occurred in 1982–83 and 1997–1998 in East Kalimantan, Indonesia, resulted in land-use changes from primary dipterocarp forest to cropland, *Imperata* grassland, oil palm or leguminous tree (*Acacia mangium*) plantation on *Imperata* grassland, and natural secondary forests regenerated by pioneer species *Macaranga* spp. (Ohta et al. 2000). We monitored 30-year changes in SOC stocks and analyzed the factors regulating organic matter turnover and storage using litter bag tests and ^{13}C natural abundances. Based on preceding studies (Fujii et al. 2011, Yonekura et al. 2013), we hypothesized that (1) grassland can contribute to initial increase in SOC stocks, but secondary forest or *Acacia* plantation maximize the long-term gain in SOC stocks due to inputs of lignin-rich litter; and (2) soil acidification in *Acacia* plantation on *Imperata* grassland would reduce microbial decomposition of grassland-derived SOC and increase total SOC stocks, compared with continuous *Imperata* grassland or oil palm plantation. Based on SOC stocks and nutrient availability, we also attempt to propose an optimal fallow system for agroecosystems transformed from dipterocarp forests.

Materials and methods

Site description and sampling design

Experiments were carried out in tropical forests and agroecosystems in Bukit Soeharto (S0°51′, E117°06′; 99 m a. s. l., average inclination 15°), East Kalimantan Province, Indonesia (Fig. 1). The mean annual air temperature was 26.8 °C, and the mean annual precipitation was recorded as 2187 mm yr^{-1}. Soils were derived from sedimentary rocks and classified as Typic Paleudults (Soil Survey Staff 2014). Soil pH is low throughout the profile (3.8–4.3) and clay contents increase with depth (23–31%). The detailed information of soil physicochemical properties was given in Fujii et al. (Fujii et al. 2009a, b). After the fires in 1982–1983, we establish plots of vegetation cover change sequences: continuous primary dipterocarp forest (PF plots), the vegetation cover changed from primary dipterocarp forest to natural secondary forests of the pioneer species *Macaranga gigantea* regeneration (*Macaranga* forest; MF plots), and *Imperata cylindrical* grassland (IG plots). The adjacent *Imperata cylindrica* grassland of IG plots were further changed to oil palm (*Elaeis guineensis* L.) plantation (OP plots) during the period

2004–2015 and *Acacia mangium* plantation (*Acacia* forest; AF plots) during the period 1992–2015. Each land-use sequence composed of three plots (20 m × 20 m), composite soil samples were collected from three pits at each plot. The distance between each pit was 10 m. Our study is based on two assumptions that (1) initial soil properties of five sites are similar to those obtained from the pristine dipterocarp forest site in 1983 and (2) the soil properties of AF and OP plots before land-use change was same with the those in grassland plots at the time of conversion (IG plots). We monitored changes in SOC stocks from 1986 to 2015 and compared litter decomposition rates using litter bag tests for five sites under vegetation change sequences in 2015.

Physicochemical and microbiological properties of soils

All the soil samples were collected, kept in plastic bags at 4 °C prior to analysis, and sieved (<2 mm) to eliminate litter, roots, and stones. For the soil samples collected from the PF, MF, AF, IG, OP sites in 2015, a subsample of field-moist soil was used for measurements of microbiological properties, and another subsample was air dried and used for measurements of physicochemical properties.

The concentrations of total C and N in soils were measured using a CN analyzer (Vario Max CN; Elementar Analysensystem GmbH). Soil pH was measured using a soil to solution (water) ratio of 1:5 (*w*/*v*) after shaking for 1 h. The particle size distribution was determined by the pipette method (Gee and Bouder 1986). The concentrations of exchangeable potassium (K^+) were measured using batch extraction with ammonium acetate (1 M, pH 7.0) and flame photometry. The concentrations of inorganic N (NH_4^+ and NO_3^-) in the field-moist soils were measured by extraction with 2 M KCl for 30 min using a soil to solution (H_2O) ratio of 1:5 (*w*/*v*) (Mulvaney 1996; Rhine et al. 1998). Available phosphorus (P) concentrations were estimated using the Bray 2 extraction method (Blakemore et al. 1987). The microbial biomasses C (MBC) at the start of litter bag field incubation was determined using the chloroform fumigation-extraction method (Vance et al., 1987) with conversion factor of 0.45 (Wu et al. 1990). The soluble C in the fumigated and non-fumigated soil samples were extracted with 0.5 M K_2SO_4 (soil to solution ratio of 1:5) and measured using a total organic C analyzer (TOC-V CSH; Shimadzu, Japan).

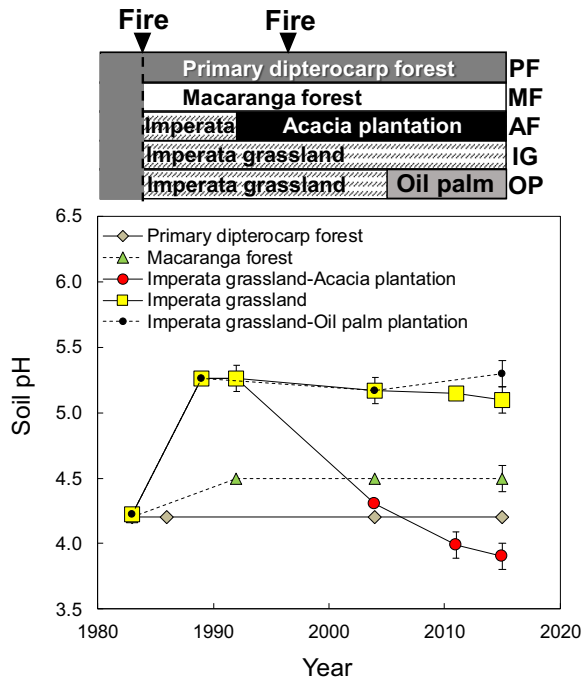

Fig. 1 Changes in soil pH (0–5 cm) under different land-uses. Bars represent standard errors ($N = 3$)

Soil carbon stocks and calculation of grass and forest origins using ^{13}C natural abundance

The organic horizons were sampled in 30 × 30-cm quadrates in three replicates per plot, oven dried (48 h, 70 °C), and individually weighed. For the mineral soil horizons (<200 g C kg^{-1}), the bulk density (g cm^{-3}) was measured using a 0.1-L core in three replicates per plot. The SOC stocks in each soil horizon were calculated by multiplying the soil C concentrations, the bulk density, and individual depths as follows:

$$\begin{aligned} &\textit{Soil C stock}\ \left(\text{kg } C\ m^{-2}\right) \\ &\quad = \text{Soil } C \text{ concentration}\ \left(g\ C\ kg^{-1}\right) \\ &\qquad \times \text{Soil horizon depth}\ (m) \\ &\qquad \times \text{Bulk density}\ \left(\text{Mg}\ m^{-3}\right) \end{aligned} \quad (1)$$

The SOC stocks at each site were calculated by summing up to the mineral soil depth of 40 cm. A sample (1 mg litter and 10 mg soil) was weighed into a tin capsule, and $\delta^{13}C$ was measured with an on-line C analyzer (NC 2500; Thermo Fishe Scientific) coupled with an isotope ratio mass spectrometer (MAT252; Thermo Electron, Bremen, Germany). All $\delta^{13}C$ values

were expressed relative to the Vienna Pee Dee Belemnite (VPDB) international standard:

$$\delta^{13}C = \frac{\frac{^{13}C}{^{12}C}(\text{sample})}{\frac{^{13}C}{^{12}C}(\text{VPDB})} - 1 \quad (2)$$

The standard deviation for four replicate combustions of the same standard within a sequence was 0.02%.

Assuming that the soil $\delta^{13}C$ profiles in primary dipterocarp forests at the sampling periods are identical to those in 1983 and those unaffected by *Imperata* grass before and after the fires, grassland-derived and forest-derived C concentrations (mg C kg^{-1} soil) were estimated using the following equations, respectively (Veldkamp 1994):

$$\text{Grassland derived C}\left(\text{mg kg}^{-1}\right) = \frac{\delta^{13}C(\text{grassland soil sample}) - \delta^{13}C(\text{forest soil})}{\delta^{13}C(\text{grass litter}) - \delta^{13}C(\text{forest soil})} \times \text{Soil C}\left(\text{mg kg}^{-1}\right) \quad (3)$$

$$\text{Forest derived C}\left(\text{mg kg}^{-1}\right) = \text{Soil C}\left(\text{mg kg}^{-1}\right) - \text{Grassland derived C}\left(\text{mg kg}^{-1}\right) \quad (4)$$

where *Imperata* leaf biomass $\delta^{13}C$ (−12.3‰) was used for $\delta^{13}C$ (grass litter). The calculation was made at each corresponding depth and scaled up to the soil profiles.

Similarly, to examine the effects of *Imperata* grassland conversion to *Acacia* or oil palm plantation on SOC storage, *Acacia*-derived and grassland and primary forest–derived C concentrations (mg C kg^{-1} soil) were estimated for the *Acacia* plantation (AF site) and oil palm plantation (OP site) using the following equations, respectively:

$$\text{Acacia derived C}\left(\text{mg kg}^{-1}\right) = \frac{\delta^{13}C(\text{Acacia soil sample}) - \delta^{13}C(\text{grassland soil})}{\delta^{13}C(\text{Acacia litter}) - \delta^{13}C(\text{grassland soil})} \times \{\text{Soil C} - \text{Forest derived C}\}\ \left(\text{mg kg}^{-1}\right) \quad (5)$$

$$\text{Grassland derived C}\left(\text{mg kg}^{-1}\right) = \text{Soil C}\left(\text{mg kg}^{-1}\right) - \text{Forest derived C}\left(\text{mg kg}^{-1}\right) - \text{Acacia derived C}\left(\text{mg kg}^{-1}\right) \quad (6)$$

where forest-derived C concentration in AF site was assumed to be equal to the value obtained in the continuous *Imperata* grassland (IG site) for each sampling year. *Acacia* leaf litter $\delta^{13}C$ (−32.7%) was used for $\delta^{13}C$ (*Acacia* litter). The same calculation was conducted for the oil palm plantation (OP site) using the oil palm leaf litter $\delta^{13}C$ (−30.9%). The changes in forest-derived and grassland-derived SOC stocks were plotted respectively against time after vegetation change (yr). The data were fitted to a single exponential decay function using the least-squares technique in SigmaPlot 11.0 (SYSTAT Software Inc., Point Richmond, CA, USA):

$$R_r = R_i e^{-kt} \quad (7)$$

where R_r is the remaining proportion of the substrate (%), R_i is the initial proportion of the substrate (i.e., 100%), k is the decomposition rate constant (yr^{-1}), and t is time (yr) since conversion. The mean residence times were estimated from $1/k$, assuming a steady state.

Litterfall carbon input, organic layer carbon stock, and litter decomposition rate factor

Litterfall was collected using circular litter traps (60 cm diameter) between June 2015 and June 2016. The organic layers and fine root (diameter < 2 mm) biomass were collected in the 30 cm × 30 cm quadrats. Fine root biomass in the mineral soil (0–40 cm) was estimated by collecting the roots in 5 cm depth intervals in cores of 0.1 L volume. Roots were rinsed in distilled water to remove soil materials. Five replicates were used for these measurements.

The litterfall, organic layer, and fine root samples were oven dried at 70 °C for 48 h, weighed, and milled. The Klason lignin concentrations in the leaf and root litter samples were determined by digestion with sulfuric acid (Allen et al. 1974). The P and K concentrations in the fresh litter samples were determined using inductively coupled plasma atomic emission spectrometry (ICP-AES; SPS1500; Seiko Instruments Inc.) after nitric-sulfuric acid wet digestion.

Assuming that the organic layer C stock reaches a steady state, the organic C turnover rate (yr^{-1}) in the organic layer was calculated by dividing litterfall C input (Mg C ha^{-1} yr^{-1}) by the organic layer C stock (Mg C ha^{-1}) (Olson 1963). The lignin (%) to N (%) ratio was calculated and used as an indicator of litter recalcitrance (Aerts 1997).

Measurement of litter and cellulose decomposition rates under field conditions

To examine whether litter decomposition rates depend simply on litter quality, or whether it is also affected by the soil environment, decomposition rates of the standard substrate (cellulose filter paper and leaf and root litters) were also compared. Cellulose is a major constituent of plant materials [10–87% from Berg and McClaugherty 2003] and decomposition rates of cellulose can be a rough indicator of soil microbial activities involved in litter decomposition (Hayakawa et al. 2014). As a standard substrate, the decomposability of *Macaranga* root litter was compared between PF and MF soils, while the decomposability of *Imperata* grass root litter was compared between IG and AF soils.

The leaf litter bags were buried at the boundary between the organic horizon and the mineral soil, while root litter bags were buried into surface mineral soil (A horizon, 5-cm depth). Cellulose filter paper (Advantec no. 6, 55-mm diameter) was buried into surface mineral soil (5-cm depth) (Hayakawa et al. 2014). All substrates were packed in the nylon mesh bags (65 × 65 mm, 100-μm mesh pore size) to keep out insects and worms. The fallen leaves collected by litter traps (10 × 10 mm) and fine roots (diameter < 2 mm; length, 10 mm) collected from the surface mineral soil were used for litter bag tests after oven drying at 70 °C for 24 h. In PF plots, leaf litters were composed of *Shorea laevis* litters (60%) and *Dipterocarpus cornutus* litters (30%), and others (10%). We used *Shorea laevis* litters as a representative litters of the PF plots for litter bag test. At each site, five mesh bags of litter or cellulose filter paper were collected at each sampling interval (3 months and 1 month, respectively). The substrate remaining in the mesh bag was dried (70 °C, 24 h) and weighed after soil particles had been carefully removed. The remaining weight of substrates was calculated on an ash-free basis by subtracting the weight of the soil adhering to the substrates, which was estimated by dry combustion (600 °C, 4 h).

To obtain the decomposition rate constant k (yr^{-1}) for litter and cellulose decomposition using Eq. 7, the remaining proportion of substrate (leaf litter, root litter, or cellulose filter paper) (%) relative to the initial weight of the substrates (i.e., 100%) was plotted against time (yr) and fitted to a single exponential decay function (Sparrow et al. 1992).

Measurement of fine root production rates

To estimate root litter input, annual production of fine root (diameter < 2 mm) was measured using the root mesh method (Hirano et al. 2009) at forest sites (PF, MF, AF) in five replicates. A net sheet (width 20 cm × depth 20 cm) with 2-mm openings was inserted vertically into the mineral soil to a depth of 20 cm. After 1 year of incubation, a soil block (width 20 cm × depth 20 cm × thickness 2 cm) containing the net sheet was collected to measure the biomass of fine roots that had grown through the net sheet. Due to the occurrence of fires at the IG site (October 2015), annual fine root production at this site was measured based on the net increase in fine root biomass between October 2015 and October 2016. It should be noted that both methods risk underestimating fine root production due to decomposition of dead fine roots between sampling intervals.

Monitoring of soil temperature and volumetric water content

To determine the effects of soil temperature and moisture on litter and cellulose decomposition rates, we monitored soil hydrothermal conditions at each site. The volumetric water contents of the soils (5-cm depth) were measured in three replicates with amplitude-domain reflectometry probes (Theta probe, ML2x; Delta T Devices). The air and soil temperatures at each depth were measured in three replicates using temperature loggers (Thermochron, SL type). Seasonal fluctuations in soil temperature (5-cm depth) and soil moisture were monitored, with recording at 30-min intervals.

Statistical analyses

All data were expressed as means ± standard errors (SEs), with combined SEs from three to six replicates (Taylor 1997; Zar 1999). The significance of differences in rate constants, k, for litter and cellulose decomposition between sites and substrate types was tested using the F-test and the Tukey method modified for comparison of regression slopes (Zar 1999). The significance of differences in SOC stocks between sites and sampling periods was analyzed using one-way ANOVA and the Tukey method for multiple comparisons. Pearson's correlation coefficients were calculated to examine relationships between the rate constants and soil properties.

All statistics were performed using Sigmaplot 11.0 (SYSTAT Software Inc., CA, USA) and tested at significance level of 0.05, unless otherwise stated.

Results

Chemical and biological properties of surface soils

Soil pH values were significantly lower at the three forest sites (PF, MF, AF) than at the IG and OP sites (Table 1). Thirty-year soil monitoring showed that pH increased after the change from primary dipterocarp forest to *Imperata* grassland and oil palm plantation due to ash or lime inputs, and decreased by *Acacia* plantation on *Imperata* grassland (Fig. 1). The soil C and N concentrations (0–5-cm depth) were significantly lower at the OP site than at the other four sites (Table 1). The microbial biomass C in the OP and IG soils were significantly ($P < 0.05$) lower than the forest soils (Table 1). Soil nutrient (N, P, K) availability differed among potential fallow vegetation sites (MF, AF, and IG; Table 1). Soil exchangeable K concentrations were significantly lower in MF than in AF and IG. Soil available P concentrations were significantly lower in AF than in MF and IG (Table 1). Soil inorganic N (mainly NH_4^+) concentrations were significantly lower in IG than in AF and MF (Table 1).

Changes in soil organic carbon stocks under land use changes

Thirty-year soil monitoring revealed a net increase in SOC stocks within the initial 10 years following the fire-induced change from primary dipterocarp forest to *Imperata* grassland (Fig. 2). No increase in SOC stocks was found at the continuous *Imperata* grassland (IG site) between 1992 and 2015, whereas conversion of *Imperata* grassland to *Acacia* plantation (AF site) and *Macaranga* forest (MF site) resulted in continuous increases in SOC stocks until 2010 or 2015 (Fig. 2). A net decrease in SOC stocks was observed within the initial 10 years after conversion of *Imperata* grassland to oil palm plantation (2005–2015; Fig. 2).

The $\delta^{13}C$ values of *Imperata* grass litter differed significantly from those of forest and oil palm litters (Table 2). The change of primary dipterocarp forest to continuous *Imperata* grassland consistently resulted in the significantly higher soil $\delta^{13}C$ values between 0 and 40 cm depth, with higher $\delta^{13}C$ values at shallower depths of grassland soil samples (Fig. 3a). In the continuous *Imperata* grassland (IG site), grassland-derived C rose rapidly to 12–48% between 1983 and 1992, and reached 59% in 2015 (Fig. 4a). Conversion of *Imperata* grassland to *Acacia* or oil palm plantation resulted in a decrease in soil $\delta^{13}C$ (Fig. 3b) due to the input of litter with higher $\delta^{13}C$ values (Table 2). The forest-derived soil C stocks in the continuous *Imperata* grassland decreased by 9.8 Mg C ha^{-1} over 32 years (1983–2015; Fig. 4a). The grassland-derived soil C stocks increased by 16.2 Mg C ha^{-1} over 32 years with SOC accumulation rate of 0.5 Mg C ha^{-1} yr^{-1} (Fig. 4a). The conversion of *Imperata* grassland to *Acacia* plantation increased SOC stocks by 28.5 Mg C ha^{-1} over 23 years at the expense of 2.0 Mg C ha^{-1} loss of grassland-derived SOC (Fig. 4b). The conversion of *Imperata* grassland to oil palm plantation resulted in a loss of 10.1 Mg C ha^{-1} grassland-derived SOC over 11 years

Table 1 Mean ($N = 3$) chemical and biological properties of soil samples (0–5 cm)

Site	Vegetation	Soil pH	Soil C[a]	Soil N[a]	C/N	Available[a] P	Exchangeable[a] K	Inorganic N[a]		MBC[a]
			(mg kg^{-1})			(mg P kg^{-1})	($cmol_c$ kg^{-1})	NH_4-N (mg N kg^{-1})	NO_3-N	(mg C kg^{-1})
PF	Primary dipterocarp forest	4.1 c	26.5 c	1.9 b	14	9 c	1.6 b	207 a	7 b	207 a
MF	*Macaranga* forest	4.4 b	31.7 b	2.0 b	16	20 a	1.2 c	179 b	2 c	179 b
AF	*Acacia* forest	3.9 c	47.7 a	3.6 a	13	12 c	1.7 b	165 b	14 a	165 b
IG	*Imperata* grassland	5.1 a	27.4 c	1.7 b	16	19 a	2.5 a	135 c	1 c	135 c
OP	Oil palm	5.3 a	12.0 d	1.1 c	11	15 b	1.2 c	82 d	2 c	82 d

[a] Oven-dry basis. Data of the soil samples colelcted in 2015 are presented

Within each column, different letters indicate that values are significantly ($P < 0.05$) different

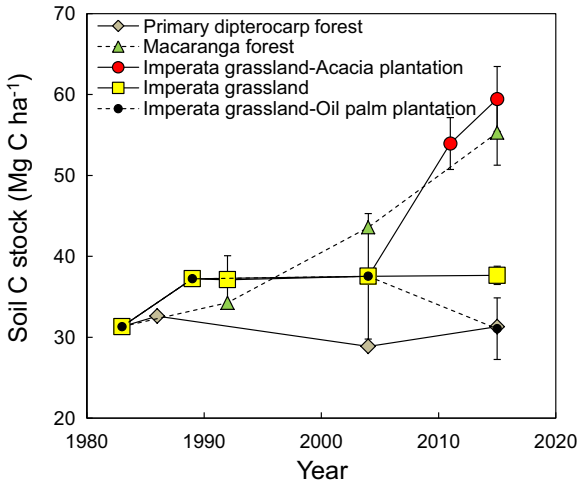

Fig. 2 Changes in soil carbon stocks (0–40 cm) under different land-uses. The C stock in the organic horizon was not counted. Bars represent standard errors ($N = 3$)

with SOC loss rate of −0.92 Mg C ha^{-1} yr^{-1} (Fig. 4c). Compared to the SOC stocks in primary dipterocarp forest, net increase in SOC stocks in *Macaranga* regeneration forest after the fires was 23.9 Mg C ha^{-1} over 30 years, with an average SOC accumulation rate of 0.8 Mg C ha^{-1} yr^{-1} (Fig. 5). The accumulation rate of *Acacia*-derived SOC remains high (1.2 Mg C ha^{-1} yr^{-1}) for 23 years, while the initial accumulation rate of grassland-derived SOC dropped from 1.6 Mg C ha^{-1} yr^{-1} to an average SOC accumulation rate of 0.2 Mg C ha^{-1} yr^{-1} for 32 years (Fig. 5). The grassland-derived SOC in *Acacia* plantation was decomposed at slower rates, compared to grassland-derived SOC in oil palm plantation and forest-derived SOC in *Imperata* grassland (Table 3).

The SOC stocks in the deeper soil horizons (40 to 100 cm depth) amounted to 16.3 ± 1.1 Mg C ha^{-1} under primary dipterocarp forests. However, grassland-derived SOC accounted for <20% of SOC stocks (40–100 cm; 18.5 ± 0.5 Mg C ha^{-1}) and continuous grassland resulted in a gain of 3.7 Mg C ha^{-1} SOC stocks (40–100 cm) for 32 years, which was far smaller than a gain of 16.0 Mg C ha^{-1} SOC stocks (0–40 cm; Fig. 5). There were no significant changes in SOC stocks (40–100 cm) and their soil δ^{13}C between primary dipterocarp and *Macaranga* forests (Fig. 3a), while *Acacia* plantation increased SOC stocks (40–100 cm; 24.3 ± 1.0 Mg C ha^{-1}) and lead to an increase in soil δ^{13}C (Fig. 3b) and a gain of 8.0 Mg C ha^{-1} SOC stocks (40–100 cm) for 23 years, which was also smaller than a gain of 28.5 Mg C ha^{-1} SOC stocks (0–40 cm; Fig. 5).

Decomposition rates of leaf and root litters and cellulose paper

Lignin concentrations were significantly higher in forest litters (PF, MF, AF) than in grass and oil palm litters ($P < 0.05$; Table 2). The *Acacia*, *Macaranga*, and *Imperata* grass leaf litters were rich in N, P, and K, respectively (Table 2). The C/N ratio of *Imperata* grass leaf litter was highest among the plant samples, but its lignin to N ratio was lower than those in the PF, MF, and AF litters (Table 2). The decomposition rate factors of C in the organic layer in MF and AF were significantly lower than in OP, IG, and PF (Table 4).

The litter bag tests showed that the rates of mass loss differed markedly between substrates (Fig. 6). The coefficient of determination (R^2) for fitting to the Eq. 7

Table 2 Chemical properties of leaf and root litter samples

Site	Vegetation	Dominant species		C (%)	N	C/N ratio	δ^{13}C (‰)	Lignin (%)	Lignin/N	P (mg g^{-1})	K (mg g^{-1})
PF	Primary forest	*Shorea laevis*	Leaf	49.2	1.1	46	−27.4	23	22	0.2	12.0
			Root	46.8	0.7	64	−29.1	24	33	0.4	
MF	*Macaranga* forest	*Macaranga gigantea*	Leaf	47.8	1.0	49	−28.1	24	25	0.7	10.5
			Root	46.0	1.0	44	−29.3	19	18	0.5	
AF	*Acacia* forest	*Acacia mangium*	Leaf	52.9	1.7	31	−32.7	32	19	0.3	10.5
			Root	47.1	1.4	33	−32.7	22	16	0.2	
IG	*Imperata* grassland	*Imperata cylindrica*	Leaf	47.3	0.5	103	−12.3	8	17	0.2	26.0
			Root	43.9	1.0	46	−12.5	7	8	0.4	
OP	Oil palm	*Elaeis guineensis*	Leaf	45.0	1.0	44	−30.9	8	7	0.5	14.3
			Root	45.0	1.2	38	−30.9	5	4	0.4	

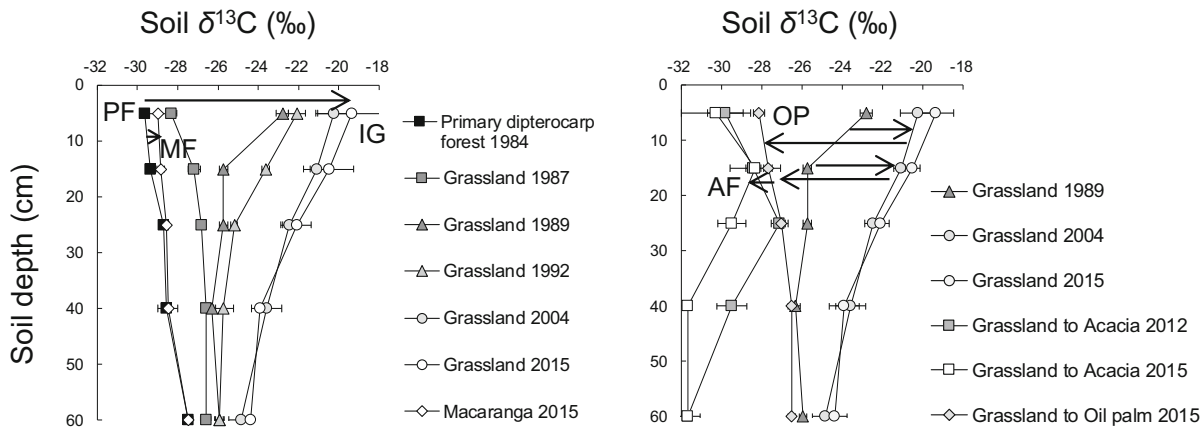

Fig. 3 Changes in soil ^{13}C natural abundance in forest change to *Imperata* grassland and *Macaranga* forest (**a**) and *Acacia* or oil palm plantation on *Imperata* grassland (**b**). Bars represent standard errors ($N = 3$)

ranged from 0.85 to 0.98, and rate constants (k) of litter decomposition were significant ($P < 0.05$; Table 4). The k values of oil palm litter decomposition were lowest among the five sites, followed by those for *Imperata* grass and forest litters (Table 4). The results were consistent for leaf and root litters (Table 4), as shown by a positive correlation between the k values of leaf litter and root litter decomposition (Fig. 7). Among forest

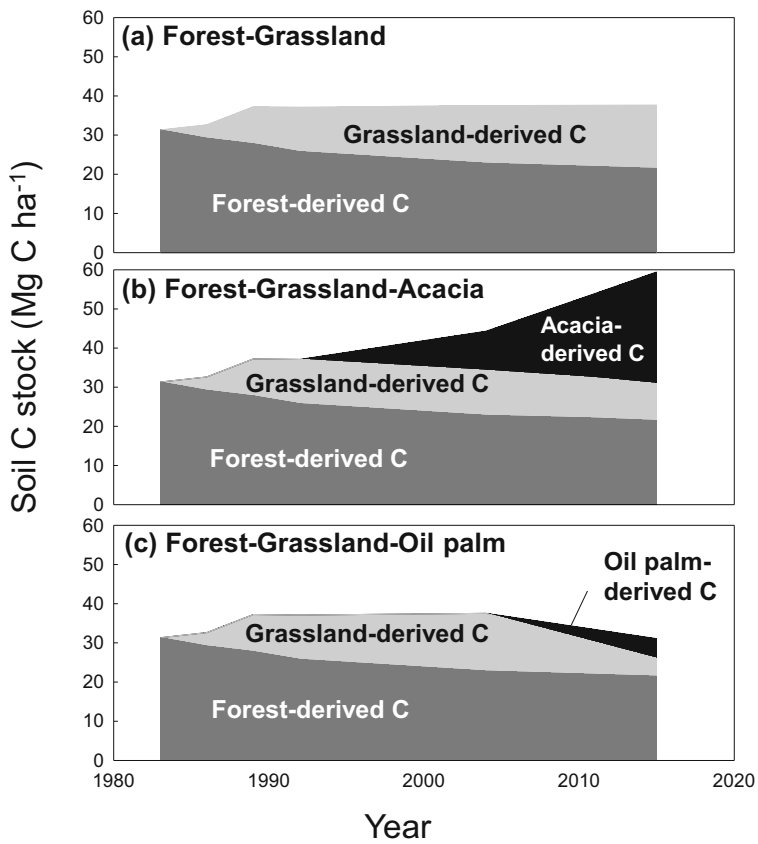

Fig. 4 Changes in soil carbon stocks (0–40 cm) under different land-uses. Changes from primary dipterocarp forest to the grassland (**a**), primary dipterocarp forest to grassland, followed by *Acacia* plantation (**b**), and primary dipterocarp forest to grassland, and to oil palm plantation (**c**)

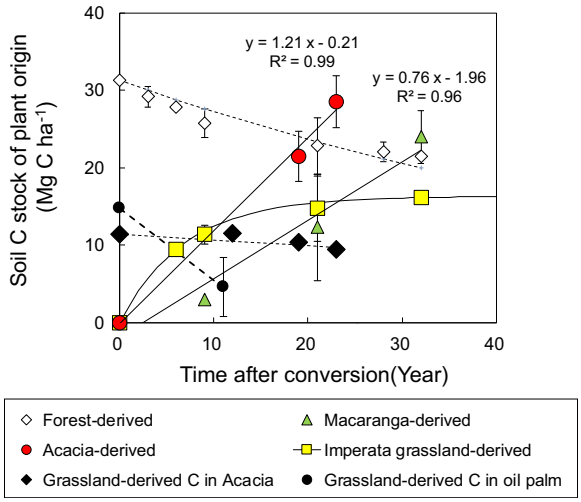

Fig. 5 Changes in soil carbon stocks derived from primary dipterocarp forest under *Imperata* grassland, changes in soil carbon stocks derived from grassland under *Acacia* or oil palm plantation, and soil carbon gain under *Imperata* grassland, *Macaranga*, and *Acacia*

litters, the *k* values for *Macaranga* leaf and root litter decomposition were lower than those for the other two sites (Table 4). The *k* values for leaf and root litter decomposition were correlated negatively with litter lignin to N ratios ($R = -0.76$, $P < 0.05$, $N = 10$; Fig. 8a), but not with litter C/N ratios (Table 2) nor with microbial biomass C (Table 1). There was no significant difference between the *k* values of root and leaf litter decomposition for respective plant species, but the slope of linear regression between them significantly higher than the slope of 1:1 line (Fig. 7).

The *k* values of cellulose decomposition for the IG and OP sites were significantly higher than those for the forest sites (Table 4). The *k* values of cellulose decomposition were correlated positively with soil pH (Fig. 8b). Due to the small variation in mean annual soil temperature at 5 cm depth (27 to 28 °C) in five sites, the *k* values of cellulose decomposition were independent of cumulative soil temperatures. The *k* value of *Imperata* grass root litter decomposition was significantly higher in the IG soil than in the AF soil ($P < 0.05$; Table 5). In contrast, the *k* values of *Macaranga* root litter decomposition did not differ significantly between the PF and MF soils (Table 5).

Fine root biomass and annual litter input

Fine root biomass and annual production were significantly higher at the IG site than at the three forest sites ($P < 0.05$; Table 6). Among the forest sites, there was no significant difference in litterfall C inputs (Table 6). Similarly, there was no significant difference in fine root production between the forest sites (Table 6). Using the changes in SOC stocks under the present fallow or plantation vegetation (Fig. 2), the annual SOC budgets under the present vegetation ranged from −0.6 to 1.2 Mg C ha^{-1} yr^{-1} (Table 6). The average proportion of annual SOC gain relative to annual C inputs (litterfall + fine root production) varied from −11.9 to 25.2% (Table 6). Among the four fallow or plantation systems, the proportion of annual SOC gain relative to annual C input was negatively correlated with soil pH (Fig. 9) or the *k* values of root litter decomposition obtained under the current vegetation, respectively.

Discussion

Effects of plant traits on litter decomposability under different land uses

Changes in vegetation types influence SOC stocks through effects on litter input and microbial litter decomposition (Stockmann et al. 2013). Microbial litter decomposition increases with decreasing litter recalcitrance or lignin/N ratios (Taylor et al. 1989). Thus, we hypothesize that the changes from primary dipterocarp forest to lignin-poor grassland or oil palm and N-rich *Acacia*

Table 3 Decomposition rates of grassland-derived and forest-derived soil organic matter under different land use

Vegetation	Substrate	Decomposition rate constant *k* (yr^{-1})	Mean residence time (yr)
Imperata grassland-*Acacia* (AF)	Grassland-derived SOC	0.007 ± 0.001 c	147
Imperata grassland-Oil palm (OP)	Grasland-derived SOC	0.107 ± 0.012 a	9
Imperata grassland (IG)	Forest-derived SOC	0.014 ± 0.002 b	71

Mean ± standard errors ($N = 3$). Within each group, different letters indicate that values are significantly ($P < 0.05$) different. Mean residence time was calculated from 1/*k*

Table 4 Litter turnover and decomposition rates of cellulose paper, leaf litter, and root litter

Site	Vegetation	Litterfall C	Organic layer C stock	Organic C[b] turnover rate (yr^{-1})	Decomposition rate constant k (yr^{-1})		
		($Mg\ C\ ha^{-1}\ yr^{-1}$)	($Mg\ C\ ha^{-1}$)		Cellulose	Leaf litter	Root litter
PF	*Shorea*	4.9 ± 0.3 a	3.0 ± 0.2 c	1.6 ± 0.1 b	7.8 e	2.0 c	1.5 d
MF	*Macaranga*	4.8 ± 0.4 a	5.1 ± 0.3 b	0.9 ± 0.1 c	18.8 c	1.5 d	1.1 e
AF	*Acacia*	4.2 ± 0.2 a	6.1 ± 0.5 a	0.7 ± 0.1 c	15.7 d	2.3 c	1.9 c
IG	*Imperata* grass	2.4 ± 0.3 b	1.1 ± 0.1 e	2.1 ± 0.3 a	26.2 b	4.1 b	3.4 b
OP	Oil palm	2.8[a]	1.9 ± 0.3 d	1.5 ± 0.2 b	34.3 a	8.5 a	7.3 a

Mean ± standard errors ($N = 3$). Within each column, different letters indicate that values are significantly ($P < 0.05$) different

[a] Litterfall mass of the oil palm site was cited from Kotowska et al. (2016)

[b] Organic C turnover rate was calculated by dividing litterfall C by organic layer C stock

plantations could accelerate microbial litter decomposition and a loss of SOC stocks. The positive correlation between leaf and root litter decomposition suggests that plant traits strongly influence litter decomposition in both of the organic and mineral soil layers (Fig. 7). The negative correlation between litter decomposability and lignin/N ratios (Fig. 8a) supports the principle that low N availability, as well as lignin abundance, reduces litter decomposition (Taylor et al. 1989; Prieto et al. 2016), and that the lignin/N ratio could be a rough predictor of litter decomposability across major plants in the tropical forests and agroecosystems (Fig. 8a).

The lower decomposability of root litter than of leaf litter (Fig. 7) is consistent with the results of five tree species in temperate forest (Makita and Fujii 2015). The larger contributions of recalcitrant root litters to soil C storage have also been suggested by Uselman et al. (2007), but the decomposability of root litters in our study is lower than leaf litters despite lower recalcitrance or lignin/N ratios of root litters at all sites except for PF (Fig. 8a). Considering the limited physical protection of root litters in the litter bag tests (e.g., soil aggregates), the reduced microbial or enzyme activities due to the increased acidity (Fig. 8b), rather than litter recalcitrance, can contribute to the lower root litter decomposability in the mineral soil (Fig. 7).

In addition to leaf and root decomposability, the differences in pathways of litter supply to the mineral soil can affect SOC storages in forests and grasslands (Qualls 2000). In the forests, majority of aboveground litterfall-C is respired and a proportion of dissolved organic matters [e.g., 30% of litterfall-C from Fujii et al. 2009b] are supplied into the mineral soil. The dissolved organic C fluxes leaching from the organic horizon into the mineral soil [ca. 0.5 $Mg\ C\ ha^{-1}\ yr^{-1}$ from Fujii et al. 2009b] are smaller than root litter inputs or fine root production in the *Imperata* grassland soil (2.6 $Mg\ C\ ha^{-1}\ yr^{-1}$; Table 6). The direct and greater

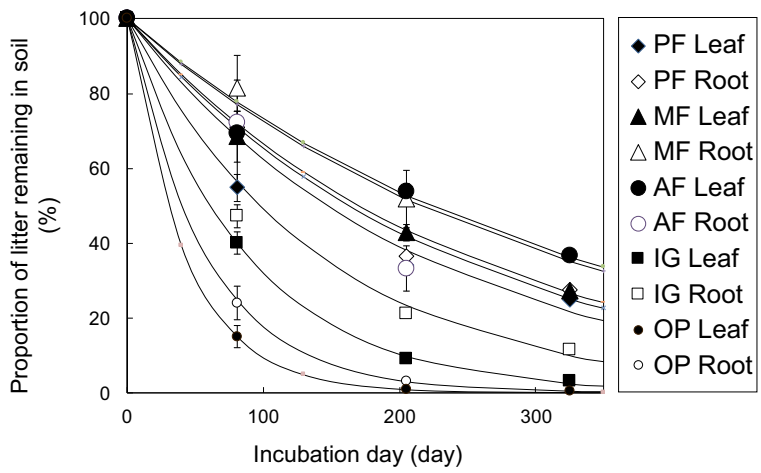

Fig. 6 Proportion of litter remaining relative to the initial litter mass in litter bag field incubation. Note that leaf and root litter bags were buried in the organic layer and the surface soil, respectively. Bars represent standard errors ($N = 3$)

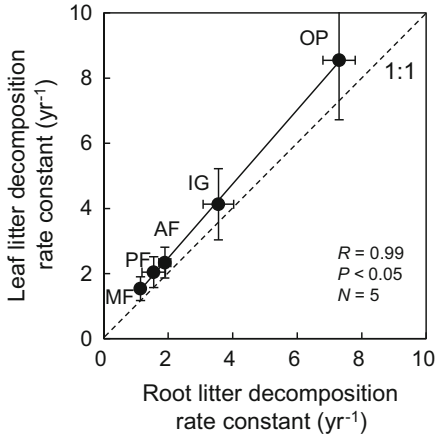

Fig. 7 Relationship between rate constants of leaf litter decomposition in the organic layers and root litter decomposition in the surface soil (0–5 cm). Bars represent standard errors ($N = 3$)

inputs of fine root litter in *Imperata* grassland (Table 6) can contribute to the greater initial SOC gain (Figs. 3 and 4a), compared to three forest sites, where the annual C input is dominated by aboveground litterfall (Table 6).

Effects of soil acidity on litter decomposability under different land uses

The positive correlations between cellulose decomposition rate constants and soil pH (Fig. 8b) support the hypothesis that soil acidity, as well as litter quality (lignin/N ratio; Fig. 8a), affect litter decomposition rates. The limited decomposition of grass litters and preservation of grassland-derived SOC under *Acacia* plantation (Tables 3, 5 and Fig. 5) is consistent with the limited microbial activities of litter decomposition at low pH (Fig. 8b). This can be explained by (1) the decreased litter-degrading enzyme activities at low pH and (2) the increased Al toxicity to microorganisms (Illmer and Mutschlechner 2004) and deactivation of enzymes by Al (Scheel et al. 2008). Especially, degrading enzyme activities of cellulose, major constituent of plant litters, are sensitive to soil acidification (Fig. 3b) and reduce at pH < 5.5 (optimal pH) (Criquet 2002; Hayakawa et al. 2014). This could retard overall litter decomposition in the PF, MF, and AF forests. Drastic soil acidification due to nitrification of the N fixed by leguminous *Acacia* trees (Fig. 1) contributes to SOC accumulation by limiting microbial activities of grassland-derived SOC decomposition (Fig. 8b; Table 3). This result contrasts with the lack of difference in *Macaranga* root litter decomposition rates between primary dipterocarp and *Macaranga* forest sites (Table 5), where the change in soil pH was smaller (Fig. 1) and the decomposition of lignin-rich substrates were less sensitive to soil acidification, compared to cellulose-rich grass root litters (Table 2). Our previous study also supports that ligninolytic enzyme activities are not reduced under acidic condition (Fujii et al. 2012). The sensitivity of litter decomposition to soil pH change could depend on plant quality (lignin/N) and the magnitude of soil acidification (Fig. 8a,b).

Effects of land-use change on soil organic matter storage

Changes in vegetation cover or land use could cause an increase or a decrease in SOC stocks (Veldkamp 1994; Cerri et al. 2004). The vegetation cover that maximizes soil C stocks within the initial 10 years is *Imperata* grassland; thereafter, *Acacia* plantation and *Macaranga* forest maximize soil C stocks (Fig. 2). Initial increases of grassland-derived SOC [1.3 Mg C ha^{-1} yr^{-1} (1983–1992); Fig. 5] are consistent with the reports in tropical grasslands or pastures (Cerri et al. 2004; Yonekura et al. 2013). The relatively high SOC accumulation rates

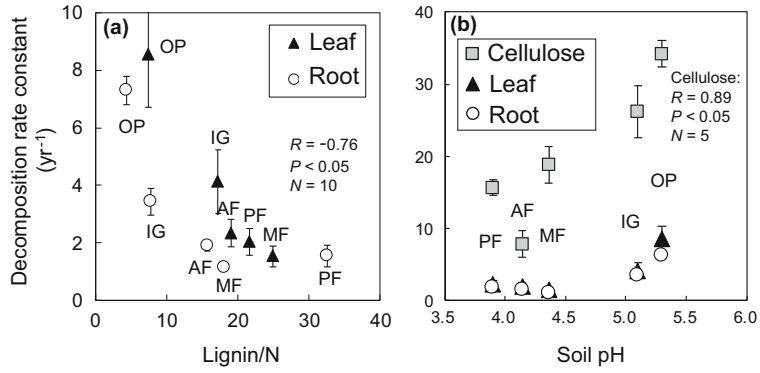

Fig. 8 Relationship between rate constants of leaf and root litter decomposition and litter lignin to nitrogen ratio (**a**) and relationship between rate constants of leaf and root litter and cellulose paper (**b**). Bars represent standard errors ($N = 3$)

Table 5 Decomposition rates of *Macaranga* or *Imperata* root litters in the soils under different vegetation

Vegetation & Soil	Substrate	Decomposition rate constant k (yr^{-1})	Mean residence time (yr)
Macaranga forest (MF)	*Macaranga* root litter	1.0 ± 0.1 a	1.0
Primary forest (PF)	*Macaranga* root litter	1.1 ± 0.1 a	0.9
Primary forest (PF)	*Shorea* root litter	1.5 ± 0.4 a	0.6
Imperata grassland (IG)	*Imperata* grass root litter	3.4 ± 0.4 a	0.3
Acacia (AF)	*Imperata* grass root litter	2.5 ± 0.1 b	0.4
Acacia (AF)	*Acacia* root litter	1.9 ± 0.2 c	0.5

Mean ± standard errors ($N = 3$). Within each group, different letters indicate that values are significantly ($P < 0.05$) different

[0.6 Mg C ha^{-1} yr^{-1} (1983–1992); Fig. 2], compared to the global average after land use changes [ca. 0.3 Mg C ha^{-1} yr^{-1} from Post and Kwon 2000], could be related to the following *Imperata* grassland characteristics: rapid colonization after frequent fires (Kiyono 2000), high primary productivity (Hartemink 2001), and large C inputs from root litter (Table 6; Astapati and Das 2010). The saturation of grassland-derived SOC stocks (Fig. 5) is explained by the efficient stabilization of initial grass-derived C in aggregates or at sorption sites with limited capacity (Hayakawa et al. 2014), but additional C inputs are not fully protected in aggregates or sorption sites already occupied by forest-derived or grassland-derived SOC (Fig. 5). The variation in mean residence times of grassland-derived SOC and *Imperata* root litters in *Acacia* and oil palm plantation (Tables 3 and 5) suggest that decomposition of grassland-derived organic matter can be accelerated by land-use change to oil palm plantation (Table 3 and Fig. 8a). In addition to intrinsic nature of lignin-poor grass litters and high biodegradability of C4 plant (Table 2; Wynn and Bird 2007), higher soil pH compared with forest sites (Fig. 1 and Table 1) are favorable for rapid mineralization of litter and SOM by microbes (Fig. 8b). The SOC accumulation rates in the *Imperata* grassland–*Acacia* sequence or *Macaranga* forest (0.8 to 1.2 Mg C ha^{-1} yr^{-1}; Fig. 5 and Table 6) are close to the upper limit reported of global dataset (Post and Kwon 2000) and are supported by the low decomposability of forest litters (Fig. 7 and Table 4) and reduced microbial decomposition activities in acidified soils (Table 5 and Fig. 8b). Soil acidification, which is accelerated by nitrification of the fixed N under *Acacia* plantation (Fig. 1), and input of recalcitrant litter reduce microbial decomposition (Fig. 8a) and contributes to an increase in soil C stocks (Fig. 2 and Table 3). The high rates of SOC accumulation in *Macaranga* forests (Fig. 5) compared with primary dipterocarp forests (Fig. 2) are caused by inputs of coarse woody debris derived from the fires (Toma et al. 2017) and higher litter recalcitrance (Table 4). Non-myrmecophytic *Macaranga gigantea* could produce lignin-rich litters compared with the other *Macaranga* species with ant defense system (Eck et al. 2001; Table 2). In addition to litter recalcitrance (Fig. 8a), the greater SOC gain in the soils with lower pH (Fig. 9) suggests the role of soil acidification in the retardation of

Table 6 Aboveground and fine root biomass, annual litter production, and proportion of soil organic carbon gain relative to carbon input

Site	Vegetation	Aboveground biomass (Mg C ha^{-1})	Fine root biomass	Litterfall (Mg C ha^{-1} yr^{-1})	Fine root production (Mg C ha^{-1} yr^{-1})	Annual C input (A)[b] (Mg C ha^{-1} yr^{-1})	Annual SOC budget (B)[c]	Annual SOC gain (B) /Annual C input (A) (%)
PF	*Shorea*	143.2	2.1	4.9 ± 0.3 a	0.8 ± 0.1 b	5.7 ± 0.3		
MF	*Macaranga*	23.6	1.3	4.8 ± 0.4 a	0.8 ± 0.3 b	5.6 ± 0.4	0.7 ± 0.1	13.5 ± 2.8
AF	*Acacia*	121.1	1.0	4.2 ± 0.2a	0.6 ± 0.1 b	4.9 ± 0.2	1.2 ± 0.1	25.2 ± 2.1
IG	*Imperata* grass	6.0	3.7	2.4 ± 0.3 b	2.6 ± 0.3 a	5.0 ± 0.4	0.2 ± 0.1	3.9 ± 1.2
OP	Oil palm	n.d.	1.3	2.8 [a]	2.6 [a]	5.4 [a]	−0.6 ± 0.1	−11.9 ± 1.1

[a] Litterfall and fine root production of the oil palm site was cited from Kotowska et al. (2016)

[b] Sum of litterfall and fine root production

[c] Annual SOC budget (gain) was calculated by dividing total SOC increase by the period under the present vegetation (Fig. 2)

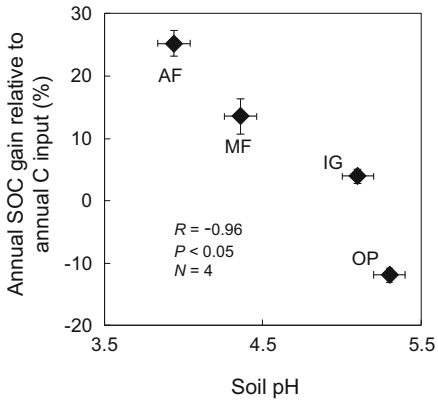

Fig. 9 Relationship between soil pH and the proportion of annual gain in soil organic carbon stocks relative to annual carbon input under land use change. Data sources are Tables 4 and 6. Bars represent standard errors ($N = 3$)

microbial decomposition and SOC preservation under fallow and plantation vegetation (Fig. 8b and Table 3).

Fallow systems to maximize soil carbon storage and implications for fertility improvement

The roles of grass fallow and *Acacia* plantation in restoration of soil organic matter has been recognized (Islam and Weil 2000; Yonekura et al. 2012), while we found that the optimum and feasible land-use strategies could vary depending on the length of fallow period, available resources, and the original acidity of soil. In a short-term (<10 years) fallow system, SOC stocks can be maximized by continuous *Imperata* grassland, rather than natural secondary *Macaranga* forest (Fig. 5). The potential importance of grassland or pasture for SOC accumulation has been confirmed in several tropical regions (Cerri et al. 2004; Yonekura et al. 2012; Sugihara et al. 2019), but one of our novel findings is saturation of SOC storage in short-term grassland fallow (Fig. 5). In a relatively long-term (>10 years) fallow system, SOC stocks can be maximized by the *Imperata* grassland–*Acacia* sequence or *Macaranga* forest (Fig. 5). Regarding essential macronutrients (N, P, K) for plants, *Imperata* grass leaf input leads to high C/N ratios (Table 1). *Imperata* grass and *Macaranga* have been regarded as common and notorious weeds or bush by people native to this region, and *Acacia* trees have invasive, despite commercial merits in plantation, in natural dipterocarp forests in Southeast Asia (Ohta et al. 2000). The high availability of these three litter resources and the difference in nutrient availability among them could allow small-holder farmers to supply NPK in low-input agriculture (Table 2). For example, the amendment of N-rich *Acacia* leaf litters into N-poor *Imperata* grassland soil, amendment of P-rich *Macaranga* leaf litters into P-poor *Acacia* forest soil, and amendment of K-rich *Imperata* leaf litters into *Macaranga* forest could increase soil fertility without high fertilizer costs in tropical low-input agriculture (Table 1). Fallow systems that combine three vegetation covers could be one of land-use strategies that increase soil productivity and potentially reduce deforestation pressure in tropical forests.

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