SOIL ORGANIC MATTER DYNAMICS UPON SECONDARY SUCCESSION IN IMPERATA GRASSLAND, EAST KALIMANTAN, INDONESIA

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SOIL ORGANIC MATTER DYNAMICS UPON SECONDARY SUCCESSION IN IMPERATA GRASSLAND, EAST KALIMANTAN, INDONESIA. Soil organic matter (SOM) dynamics upon secondary succession in Imperata grassland was studied by stable carbon isotope analysis. The data of litter and soil samples of twenty plots in four different stages of successions were compared. These different stages were represented by plots that were; (1) burnt 3 years before sampling/observation (Imperata grassland), (2) burnt 9 years before sampling /observation, (3) secondary forest (≥15 years) and (4) primary forest. The results showed that isotopic signatures of all soil horizons of the regeneration stages were statistically different from those of the primary forest. The A-horizon under the 3-years Imperata plot still contained 23% forest (C3) carbon, and this fraction increased to 51% in the-B-horizon. In the 9-years plot and in the secondary forest, the C3 carbon in the A-horizon increased to 51% and 96%, respectively. In the topsoil, the loss of C4-C between the 3-years and the 9-years plot was significant, while it appeared negligible in the AB-horizon. The strong decay in the topsoil under Imperata grassland may be due to the rather high carbohydrate content of the SOM, which is considered easily decomposable. Further research is needed especially to explore the relation between carbon stocks and chemical composition of SOM. Such insight may help to better understand and predict soil carbon changes in relation to climate and vegetation change.

Keywords: Carbon isotopes, Imperata grasslands, succession, soil organic matter

PERUBAHAN BAHAN ORGANIK TANAH PADA PROSES SUKSESI SEKUNDER PADA LAHAN ALANG-ALANG DI KALIMANTAN TIMUR, INDONESIA. Perubahan bahan organik tanah pada proses suksesi di lahan alang-alang telah dipelajari dengan analisis isotop karbon. Data sampel tanah dan serasah dari dua puluh petak contoh dari empat tahapan proses suksesi yang berbeda dibandingkan. Tahapan dari proses suksesi tersebut diwakili oleh petak contoh yang terdiri dari: (1) 3 tahun setelah terbakar (kondisi alang-alang), (2) 9 tahun setelah terbakar, (3) hutan sekunder (≥ 15 tahun) dan (4) hutan primer. Hasil menunjukkan bahwa isotop karbon dari semua horizon tanah pada setiap tahapan regenerasi, secara statistik berbeda dengan isotop karbon dari hutan primer. Di Horizon-A pada petak contoh 3 tahun setelah terbakar masih berisi karbon C3 23%, dan fraksi ini meningkat menjadi 51% di horizon-B. Di petak contoh 9 tahun setelah terbakar dan di hutan sekunder, karbon C3 di horizon-A meningkat masing-masing menjadi 51% dan 96%. Di lapisan atas tanah (topsoil), hilangnya karbon C4 antara petak contoh 3 dan 9 tahun terjadi secara signifikan, akan tetapi tidak di horizon-AB. Pembusukan yang terjadi sangat cepat di lapisan tanah pada lahan alang-alang, kemungkinan disebabkan kandungan karbohidrat yang cukup tinggi dari bahan organik, yang dianggap mudah terurai. Penelitian lebih lanjut diperlukan terutama untuk menggali hubungan antara stok karbon dan komposisi kimia bahan organik tanah. Pengetahuan tersebut diharapkan dapat lebih membantu untuk memahami dan memprediksi perubahan karbon tanah dalam kaitannya dengan perubahan iklim dan vegetasi.

Kata kunci: Isotop karbon, lahan alang-alang, suksesi, bahan organik tanah

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I. INTRODUCTION

Imperata grassland is a common vegetation type in Kalimantan, Indonesia and in neighbouring parts of Southeast Asia. It indicates a high degree of degradation of the vegetation, and mostly occurs after slashing and burning of the primary forests. Through secondary succession, Imperata grassland is converted into new secondary forest and most of the original biodiversity is restored. During this succession, plant species composition and soil properties change, as discussed in previous publications (Van der Kamp, Yassir & Buurman, 2009; Yassir, Van der Kamp & Buurman, 2010). It was shown that soil carbon stocks were lower under primary forests than under Imperata grasslands in East Kalimantan and this is contrary to the situation in the other forest systems.

In order to better understand the process of succession in Imperata grassland, more should be learnt about its SOM dynamics. A common way to explore SOM dynamics in soils that have been under consecutive vegetation (succession) with a different photosynthetic pathway is by using the relative abundance of the stable isotopes ^{13}C and ^{12}C, expressed as $\delta^{13}C$ (Balesdent & Mariotti, 1996; Roscoe, Buurman, Velthorst & Pereira, 2000).

Plants with difference in photosynthetic pathway have different ^{13}C discrimination; for instance C3 are more efficient in discriminating ^{13}C than C4 plants. Therefore, C4 plants have significantly more ^{13}C in their tissue and residues than C3 plants. Plants take up carbon from the atmosphere, but ^{13}C contents in the atmosphere have changed over time, and atmospheric ^{13}C is therefore not a good reference. ^{13}C discrimination is therefore expressed with respect to a geological standard, the PeeDee belemnite, or its gas equivalent (Vienna-PeeDee). The discrimination is expressed as $\delta^{13}C$ and calculated as $\delta^{13}C$ (per mil) $= 1000 *(^{13}R_{sample} - {}^{13}R_{standard}) / {}^{13}R_{standard}$, in which ^{13}R is the $^{13}C/^{12}C$ ratio. Plants with a C3 photosynthetic pathway have $\delta^{13}C$ values ranging from -32 to -22 $^0/_{00}$ (mean of -27$^0/_{00}$), and C4 plants have $\delta^{13}C$ values of -16 to -9$^0/_{00}$

(mean of -13$^0/_{00}$), while the present $\delta^{13}C$ value in the atmosphere is -8$^0/_{00}$ (Boutton, 1996; Balesdent & Mariotti, 1996; Roscoe et al., 2000). Plant litter and the SOM derived from it, inherits the ^{13}C signature of the living plant. Hence, the isotopic signature of SOM can be used to explore its dynamics, when C4 plants are replaced by C3 plants or vice-versa. As Imperata is a C4 grass, the contribution of Imperata-derived SOM and its disappearance upon secondary succession, as well as the new input of C3 SOM from trees and shrubs, can be studied this way.

$\delta^{13}C$ values have been used and analysed in many studies on SOM dynamics in a variety of vegetation and land use types, including tropical ones (Boutton, Archer, Midwood, Zitzer & Bol, 1989; Vitorello, Cerri, Andreux, Feller & Victoria, 1989; Martin, Mariotti, Balesdent, Lavelle & Vuattoux, 1990; Veldkamp, 1994; Roscoe et al., 2000; Magnusson et al., 2002; Qiming, Shijie, Hechun & Ziyuan, 2003; Wilcke & Lilienfein, 2004; Marin-Spiotta, Silver, Swanston & Ostertag, 2009; Katsuno, Miyairi, Tamura, Matsuzaki & Fukuda, 2010). Nevertheless, such studies have not been carried out on the effect of a conversion of forests into Imperata grasslands or the succession from Imperata grassland to secondary forest. So far in Indonesia, most of the studies on *Imperata* grasslands focussed on soil carbon stocks changes in relation to changing land use (Van Noordwijk, Cerri, Woomer, Nugroho & Bernoux, 1997; Lal & Kimble, 2000; Woomer et al., 2000; Ohta, Morisada, Tanaka, Kiyono & Effendi, 2000; Van der Kamp et al., 2009; Yonekura et al., 2010).

The present study describes SOM dynamics upon secondary succession in Imperata grassland using stable carbon isotopes. The data of litter and soil samples of twenty plots in four different stages of succession were compared. We compared the effect of succession on proportions and absolute amounts of C3- and C4-derived SOM in order to determine differences in accumulation and decay. Such information may indicate why carbon stocks
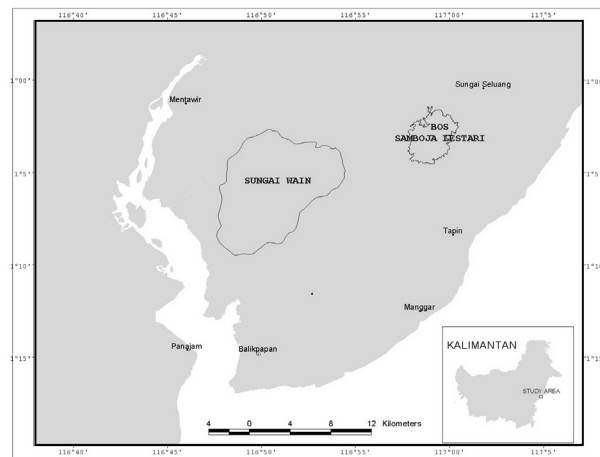
Figure 1. Location of Sungai Wain protection forest and BOS Samboja Lestari

under primary forest are lower than under Imperata grassland.

II. MATERIAL AND METHOD

A. Study Area

The study areas Sungai Wain and BOS Samboja Lestari are situated in East Kalimantan, Indonesia (Figure 1). Sungai Wain is a unique protected forest of about 10,000 hectares that contains one of the last primary forests of the Balikpapan – Samarinda area (Whitehouse & Mulyana, 2004). Samboja Lestari is a 1,850 hectares reforestation project owned by the Borneo Orang-utan Survival Foundation (BOS). Plots selected for the analysis of the regeneration impacts were situated at Samboja Lestari, whereas the primary forest plots were chosen in the area of Sungai Wain and functioned as controls. The Köppen system classifies the climate of the research area as Af (Tropical Rainforest). Average annual precipitation is 2,250 mm. The daily maximum temperature varies from 23°C to 31°C and the relative humidity is high. The soil in both areas, Samboja Lestari and Sungai Wain, is formed on marine sediments and it is classified as Acrisol according to the FAO classification system (FAO, 2001). This soil has a low level of nutrients, especially that of available phosphorus. Its pH value varies between 4.09 and 4.55 (Yassir & Omon, 2006).

B. Data Collection and Analysis

All field data and soil samples were collected in the areas of Samboja Lestari and Sungai Wain. The classification of the plots in Samboja Lestari was based on the fire history and previous studies (Van der Kamp et al., 2009). The general descriptions of the soil properties and vegetation dominances in each of the sample plots are summarized in Table 1.

In total, twenty plots of 2 m x 2 m were analysed, representing four different stages of successions. Five plots were sampled in each stage. The defined stages were found in using plot areas that were burnt 3 years and 9 years before sampling, a secondary forest of at least 15 years growth, and a primary forest. Logging in the area started around 1970 and was followed by continued slashing and burning. In 1982 to 1983 after droughts and forest fires, induced by the El Nino Southern Oscillation (ENSO) event, the area was fully covered by Imperata grassland, which was burnt again virtually every year afterwards, except in the protected area of Samboja Lestari. When the 3-years plots were sampled in 2007, there were about 25 years of decay of the C3 SOM in these plots. Soil samples were taken from the A-, AB- and B-horizons, except under the primary forest where AB-horizons were lacking. After drying and mixing, the soil was sieved over a 2 mm sieve and packed in smaller labelled bags for transport to

Table 1. Soil properties and dominant species in sampled plots

Regeneration Stage	Bd[a] (g cm^{-3})	pH	Means C (g kg^{-1})	N (g kg-1)	C/N	P (mg kg^{-1})	K (cmol$^+$ kg^{-1})	Dominant species
3 years (n=47)								
A-horizon	1.18	5.29	14.52	1.43	10.53	4.04	0.16	*Imperata cylindrica*
AB-horizon	1.32		8.99					*Eupatorium inulaefolium*
B-horizon	1.38		3.75			3.16	0.11	
9 years (n=126)								
A-horizon	1.10	5.09	15.96	1.54	10.36	4.47	0.16	*Melastoma malabathricum*
AB-horizon	1.34		9.10					*Eupatorium inulaefolium*
B-horizon	1.39		3.99			3.72	0.11	*Vernonia arborea* etc.
Secondary forest (> 15 years) (n=43)								
A-horizon	1.10	5.11	16.71	1.58	10.58	4.08	0.18	*Syzigium lineatum*
AB-horizon	1.32		8.93					*Fordia splendidissima*
B-horizon	1.41		4.04			3.60	0.10	*Pternandra azurea*
								Macaranga sp.
								Vernonia arborea
								Vitex pinnata etc.
Primary forest (n=28)								
A-horizon	1.2	4.82	14.33	1.19	12.04	5.31	0.11	*Shorea* sp.
AB-horizon								*Madhuca* sp.
B-horizon	1.43		3.43			7.27	0.13	*Macaranga* sp.
								Syzigium sp.
								Gironniera sp. etc.

Note: [*] Bda) = bulk density

the laboratory in Bogor Agricultural University (Java) for some soil chemical properties and to the laboratory in the University of California at Davis for stable carbon isotope analysis.

As the $\delta^{13}C$ value of any soil sample is a linear mixture of the contributions of the vegetation dominated by C_3 and C_4 plants, the relative contribution of each can be calculated from $\delta^{13}C_{sample} = x * \delta^{13}C_{C3} + (1-x) * \delta 13C_{C4}$), in which x is the fraction of C_3-derived, and (1-x) the fraction of C_4-derived soil organic carbon, while the $\delta^{13}C$ values denote the typical means of the relevant C_3 and C_4 litter. Data were analysed

using SPSS. Least Significant Difference (LSD) tests were performed to determine statistically significant differences between $\delta^{13}C$ values of the various stages of succession.

III. RESULT AND DISCUSSION

A. Soil Properties and Vegetation in Different Phases of Regeneration

In our case study, carbon and nitrogen content in the A-horizon showed a small increase with regeneration stage, but C and N contents decreased in the primary forest (Table

Table 2. Means of δ^{13C} parameters in litter and soil samples following the different phases of successions

Descriptions	3 years (n=5)		9 years (n=5)		Secondary forest (n=5)		Primary forest (n=5)	
	Mean	sd[1]	Mean[2]	sd	Mean	sd	Mean	sd
Litters $\delta^{13}C$ ($^0/_{00}$)	-19.83[a]	3.75	-27.72[b]	0.83	-29.91[bc]	0.67	-31.07[c]	0.32
A-horizon (0-10 cm) $\delta^{13}C$ ($^0/_{00}$)	-22.14[a]	1.00	-25.09[b]	1.11	-28.19[c]	0.84	-29.86[d]	0.33
AB-horizon (10-18 cm) $\delta^{13}C$ ($^0/_{00}$)	-23.00[a]	0.75	-25.12[b]	1.16	-27.63[c]	0.55		
B-horizon (18-45 cm) $\delta^{13}C$ ($^0/_{00}$)	-24.54[a]	0.43	-26.09[b]	0.68	-27.30[c]	0.52	-29.14[d]	0.24

Note: [1]*Standard deviation,* [2]*Means followed by different letters within one soil parameter differ significantly (P<0.05) as established by the LSD- test*

1). The plots of the primary forest showed low N content, which was also reflected in a higher C/N ratio than in the other plots. The pH of the A-horizon was highest in the Imperata grassland and lowest in the primary forest samples. When the vegetation was reduced to ashes through burning, as happened in the grassland plots, the pH increased due to the formation of carbonates. With time, the carbonates were leached and exchangeable cations (especially calcium) were lost, resulting in a decline of the pH (Binkley, Valentine, Wells & Valentine, 1989; Cruz & del Castillo, 2005; Farley, Pineiro, Palmer, Jobbagy & Jackson, 2008; Yamashita, Ohta & Hardjono, 2008). The P of the A-horizon was also lowest in the Imperata grassland and highest in the primary forest samples. The increase in P content in the soil is not surprising, because this nutrient is mostly induced by plant inputs under vegetation succession from Imperata grassland to primary forest (Vitousek, 1984; Yassir et al., 2010). The P increase with regeneration may be also attributable to Arbuscular mycorrhiza fungi.

For instance, some pioneers such as *Melastoma malabathricum*, *Vitex pinnata*, *Vernonia arborea*, *Ficus* sp. plants are dependent and associated with Arbuscular mycorrhiza fungi (Yassir & Omon, 2006). Table 1 also indicates vegetation structure and floral composition change under vegetation succession from Imperata grassland to primary forest. Grasslands dominated by *Imperata cylindrica* were replaced by shrubs and young growth of trees. In the plots that were burnt 3 years and 9 years before sampling, *Melastoma malabathricum*, *Eupatorium inulaefolium*, *Ficus* sp. and *Vitex pinnata* became the dominant species, but these species were rarely found in the secondary forest. More detailed information related to Table 1 is described by Van der Kamp et al. (2009) and Yassir et al. (2010).

B. $\delta^{13}C$ Signature

Table 2 indicates that the ^{13}C signatures of the four litters are significantly different. This difference is reflected in the signatures of the soil horizons, which reflect the differences of the litters. The largest difference is between the

Table 3. Means and standard deviations of the C3 carbon fraction in soils under various succession stages

Depth	C-fraction from C3 [1]					
	3 years (n=5)		9 years (n=5)		Secondary forest (n=5)	
	Mean	Sd [2]	Mean [3]	Sd	Mean	Sd
A-horizon (0-10 cm)	0.23[a]	0.10	0.51[b]	0.19	0.96[c]	0.09
AB-horizon (10-18 cm)	0.31[a]	0.07	0.43[a]	0.23	0.93[b]	0.10
B-horizon (18-45 cm)	0.51[a]	0.04	0.47[a]	0.20	0.82[b]	0.15

Note: [1] *Imperata grassland fraction; 2) Standard deviation; 3) Means followed by different letters within one soil parameter differ significantly (P<0.05) between regeneration stages as established by the LSD- test*

3-years plots and the other stages. In general the mean $\delta^{13}C$ value of the litter samples from the Imperata grassland plots ($-19.83^0/_{00}$) was lower than that of C_4 plants ($-13^0/_{00}$). These low values reflect that the grasslands, in addition to *Imperata*, also contain the C_3 plants *Eupatorium inulaefolium* and *Melastoma malabathricum*. The common occurrence of these C_3 species and their variations in abundance explains the exceptionally high variability (standard deviation = 3.75) of the $\delta^{13}C$ value in the 3-years litter samples compared to the other plots (Table 2).

In all the plots, the $\delta^{13}C$ value increased gradually with soil depth (Table 2). It also increased from litter to topsoil (A-horizon) except in the 3-years plot. The causes for an increase with depth of $\delta^{13}C$ values that have not undergone a C3-C4 change have been discussed in detail by other authors (Nadelhoffer & Fry 1988; Martin, Mariotti, Balesdent, Lavelle & Vuattoux, 1990; Ehleringer, Buchmann & Flanagan, 2000; Balesdent, Girardin & Mariotti, 1993; Balesdent & Mariotti, 1996; Roscoe et al., 2000; Garten, Hanson, Todd, Lu & Brice, 2007; Chen et al., 2008). As selective decay, which has been suggested as a cause, would result in relative accumulation of 13C-depleted compounds such as aromatic and aliphatic (Boutton, 1996), this cannot be an explanation. We consider the decay of primary plant material and the admixture of microbial SOM as the most likely cause, as microbial matter has higher $\delta^{13}C$ values than the corresponding SOM (Dijkstra et al., 2006).

C. C4-C3 Replacement During the Succession

The vegetation sequence started with primary forest, which was followed – through logging and slashing and burning – by Imperata grassland. The latter was in turn replaced by shrubs and trees. To calculate the remaining forest C in the 3-years plot, we used the mean values of the $\delta^{13}C$ soil samples under primary forest for the initial stage, and the $\delta^{13}C$ of the 3-years litter to calculate the relative contribution of the Imperata and the forest SOM. This implies that the '*Imperata* contribution' includes that of the C3 plants in that vegetation. No correction was applied for a possible increase in $\delta^{13}C$ signature from Imperata litter to SOM.

Table 3 shows that the fractions of C3 carbon (thus of C4 carbon) in the A-horizon were significantly different in the three regeneration stages. In the deeper horizons, there is no significant difference between the 3-years and the 9-years stage. The 3-years stage retained 23% of forest C in the topsoil, which increased to 51% in the B-horizon. The 9-years stage showed a significant increase in the C3

Table 4. The means and standard deviations of absolute amounts of C3 and C4 carbon in the various succession stages

Depth	C4)[1] (g kg⁻¹)						C3)[2] (g kg⁻¹)					
	3 years (n=5)		9 years (n=5)		Secondary forest (n=5)		3 years (n=5)		9 years (n=5)		Secondary forest (n=5)	
	Mean	Sd)[3]	Mean)[4]	Sd	Mean	Sd	Mean	Sd	Mean	Sd	Mean	Sd
A-horizon (0-10 cm)	12.10ᵃ	2.83	7.18ᵇ	2.77	0.77ᶜ	1.02	3.56ᶜ	1.45	8.32ᵇ	4.18	17.64ᵃ	7.79
AB-horizon (10-18 cm)	6.52ᵃ	1.45	5.96ᵃ	2.62	1.03ᵇ	0.82	2.92ᵇ	0.72	4.50ᵇ	2.34	8.98ᵃ	3.04
B-horizon (18-45 cm)	2.06ᵃ	0.66	2.44ᵃ	1.16	1.03ᵃ	0.73	2.14ᵃ	0.92	2.02ᵃ	0.73	3.28ᵃ	0.99

Note: *[1] Absolute amounts of C from Imperata grassland; 2) absolute amounts of C from primary forest; 3) Standard deviation; 4) Means followed by different letters within one soil parameter differ significantly (P<0.05) between regeneration stages as established by the LSD- test*

Table 5. Factors determining carbon stocks in East Kalimantan

Imperata grassland	**Secondary forest**	**Primary forest**
Seasonally high temperature	Temperature maxima decreasing with time	Moderate temperature
Seasonally low moisture	Moisture deficit decreasing with time	Permanent moisture
High root litter production	High litter production	Moderate litter deposition
Less efficient SOM decay	Increasingly efficient SOM decay	Efficient SOM decay
Higher carbon stocks	Carbon stock first increases further and then decreases when primary forest equilibrium is regained	Low carbon stocks

fraction in the A-horizon, but not in the deeper horizons. The secondary forest had the highest C3-C fractions (82-96%) in all horizons. In the 9-years plot, the increase in C3-C is due to (1) input of the C3-plants (*Melastoma malabathricum*, *Eupatorium inulaefolium* and *Vernonia arborea*), and (2) loss of the C4 fraction through decomposition. The further increase in C3-C fraction from the 9-years plot to the secondary forest is due to the different set of C3 species (*Syzigium lineatum*, *Fordia splendidissima*, *Pternandra azurea*, *Macaranga* sp., *Vernonia arborea*, *Vitex pinnata*), and to further decay of the C4-C fraction. To distinguish between the effects of accumulation and decay, we will consider the absolute amounts of C3- and C4-derived carbon. Table 4 shows that the absolute amounts

of C4 and C3-carbon in the A-horizons differ significantly between all plots. The amount of C4-C decreased from 12.1 to 7.18 g kg⁻¹ between the 3-and 9-years plots, while the secondary forest had only 0.77 g kg⁻¹. For the AB-horizon, there was a significant difference between the secondary forest and the other two stages, while no significant differences in quantities were found in the B-horizons. Figure 2 depicts the absolute amounts of C3 and C4 carbon in the three succession stages, while in Figure 2A also the contents of the primary forest are included.

Figure 2 shows that under secondary forest, the absolute amount of C4 carbon was very low throughout. Considering that there was no significant decrease in C4-C in the AB-horizon from the 3-years to the 9-years plot, it
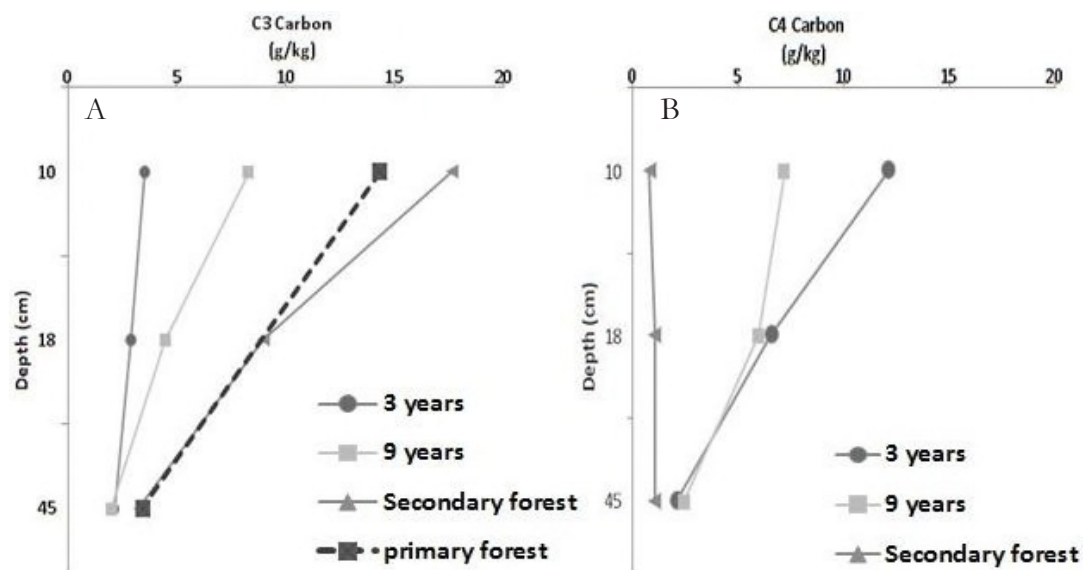
Figure 2. Location of Sungai Wain protection forest and BOS Samboja Lestari

is unlikely that decay could explain the very low contents of C4-C in the secondary forest plot. It is therefore likely, that the secondary forest plot represented a regeneration of the primary forest after logging and burning, but without a significant Imperata phase. This implies that the secondary forest plot cannot be used to estimate decay of C4-C. In that case, the calculated (low) C4-C contributions in the soil under secondary forest are due to the choice of parameters (δ^{13}C of Imperata grassland and secondary forest litter) rather than to actual Imperata input.

Figure 2b and Table 4 indicate that the loss of C4-C in the topsoil between the 3- years and the 9-years plot is considerable, while it appears negligible in the AB-horizon. The decay of C4-C in the topsoil amounted to approximately 4.92 g kg-1 in approximately 6 years or a decay rate of C4-C of 0.82 g C kg^{-1} per year. In the primary forest, the A-horizon contained 14.33 g kg-1 C3-C, of which only 3.56 g kg-1 remained in the 3-years plot. This is a loss of 10.74 g kg^{-1} in approximately 25 years, or a decay rate of 0.43 g C kg^{-1} per year. The differences between decay rate of C4-C and C3-C in A-horizon should be associated with litter quality and substrate quality. The strong decay of C4-C in topsoil under vegetation succession indicates

that C4-C (*Imperata cylindrica*) – derived SOM is more easily removed by decomposition than C3-SOM. The strong decay of C4-C in the topsoil may be due to rather high carbohydrate contents in both of the litter and soil organic matter.

However, external factors also change in response to vegetation change. Upon clearing of the forest and invasion of the Imperata vegetation, fluctuations in soil temperature will increase especially maximum temperature will be considerably higher. As a result, soil moisture will be strongly reduced during the dry season. This combined effect leads to a reduction in SOM decay because both higher temperature and lower moisture availability reduce microbial activity (Cortez, 1998; Liang, Das & McClendon, 2003; Risch, Jurgensen & Frank, 2007). During the secondary succession, the process is reversed and soil temperature and moisture gradually revert to those of the primary forest. Higher microbial activity increases the amount of soil-nitrogen and thus also stimulates decomposition. The combined effects of production and decay on soil-C stocks are summarized in Table 5.

Figure 2 also indicates that from the 3-years to the 9-years stage the increase in C3-C

approximately equals the loss of C4-C. It further suggests that the differences in stock between primary forest and the three succession stages is largely due to the insertion of an AB-horizon (not present under primary forest) which, as observed in the field, has a large volume of Imperata roots. The dense root system under Imperata grassland might cause higher potential carbon storage in the soil than surface litter. The largest difference between profiles under primary forest and under Imperata grassland is the insertion of an AB-horizon under the latter. This horizon contains a large amount of roots, and Figure 2 clearly suggests that this horizon causes the increase in carbon stock. Whether the differences in carbon stocks are also related to different chemical composition of the litter input and the resulting SOM will be investigated later. Such insight may help to better understand and predict soil carbon changes in relation to climate and vegetation change.

IV. CONCLUSION

Isotopic signatures of all soil horizons of the regeneration stages were statistically different from those of the primary forest. The A-horizon under the 3-years Imperata plot still contained 23% forest (C3) carbon, and this fraction increased to 51% in the B-horizon. In the 9-years plot and in the secondary forest, the C3 carbon in the A-horizon increased to 51% and 96%, respectively. Our data show that the decay rate in the topsoil of C4-C is 0.82 g kg^{-1} C ha^{-1} per year whereas that of the primary forest is 0.43 g kg^{-1} C ha^{-1} per year. Under equal external circumstances, the differences between decay rate of C4-C and C3-C in the A-horizon should be associated with litter quality and substrate quality. Although too little information is available for further evaluation of the decomposition speed and stock changes, it is possible that the final C-stock equilibrium will not revert to that of the primary forest. Because both the removal of the forest and the maintenance of the Imperata grassland involved burning, the soils of the secondary

successions should have some charcoal. As this is a very stable fraction, it is likely that soil-C equilibrium stocks under secondary forest will be somewhat higher than those under primary forest.

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