

**CARBON AND NITROGEN STOCKS OF DIFFERENT DEAD WOOD
DECAY STAGES IN NATURAL AND CONVERTED TROPICAL
LOWLAND FORESTS (JAMBI, INDONESIA)**

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Bogor, March 2016

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RINGKASAN

SELIS MERIEM. Stok Karbon dan Nitrogen pada Tingkat Pelapukan Kayu Mati yang Berbeda di Hutan Alam dan Hutan Konversi Dataran Rendah Tropis (Jambi, Indonesia). Dibimbing oleh TRIADIATI dan SOEKISMAN TJITROSOEDIRJO.

Kayu mati berperan signifikan sebagai bagian yang terintegrasi dari suatu hutan, menyediakan sumber nutrisi dalam jumlah besar dan habitat bagi dekomposer dan biota hutan lainnya. Transformasi hutan alam menjadi berbagai sistem pemanfaatan lahan di dataran rendah, Sumatra, Indonesia, menurunkan total biomassa permukaan atas tanah dan berdampak negatif terhadap siklus nutrisi. Sebagian besar hutan hujan tropis di provinsi Jambi telah dikonversi menjadi sistem agroforestri karet atau hutan karet. Transformasi ini dapat mengubah komponen dan fungsi hutan alam. Dampak perubahan konversi ini terhadap stok C dan N kayu mati masih kurang dipahami.

Penelitian ini bertujuan untuk menguji perbedaan massa, stok C, N dan lignin kayu mati antara sistem hutan alam dan hutan karet, dan menguji perbedaan konsentrasi kandungan kimia dan kelimpahan stok nutrisi tersebut pada tiga tahap pelapukan kayu mati. Penelitian ini bertujuan menganalisis kontribusi kayu mati pada berbagai tingkat pelapukan terhadap total stok C dan N di hutan hujan tropis Indonesia.

Penelitian dilakukan di hutan alam dan hutan karet dataran rendah tropis Propinsi Jambi, Sumatra. Pengambilan sampel kayu mati dilakukan dengan metode *non-destructive* dalam plot permanen berukuran 2500 m² (50 m x 50 m) dengan total plot sebanyak enam belas (delapan replikasi setiap penggunaan lahan: empat plot di lokasi daerah Harapan, kabupaten Muara Bulian, dan empat plot di lokasi Taman Nasional Bukit Duabelas (TNBD), kabupaten Sarolangun). Tegakan kayu mati yang dijadikan sampel memiliki diameter pohon setinggi dada (dbh) ≥ 10 cm dan tinggi ≥ 1.5 m, sedangkan untuk kayu mati tumbang memiliki diameter tengah ≥ 10 cm dan panjang ≥ 1 m.

Pelapukan kayu mati secara visual diidentifikasi berdasarkan indikator fisik yang merefleksikan kerusakan kayu dan diklasifikasikan ke dalam tiga tingkat pelapukan. Massa kayu mati diestimasi menggunakan persamaan alometrik. Untuk setiap tingkat pelapukan, sebanyak 48 sampel diseleksi secara acak untuk analisis kandungan kimianya. Konsentrasi C organik, N total dan lignin berturut-turut diukur menggunakan metode Walkley and Black, Kjeldahl dan Van Soest. Pengaruh sistem pemanfaatan lahan terhadap variabel yang diuji (massa, volume dan stok C, N dan lignin dalam kayu mati), juga pengaruh sistem di setiap tingkat pelapukan dibandingkan menggunakan Independent Sample t-test. Analisis varians (ANOVA), One-Way dengan post-hoc Tukey HSD test digunakan untuk menguji pengaruh tingkat pelapukan terhadap variabel stok dan konsentrasi nutrisi. Analisis komponen utama (PCA) terhadap variabel yang diuji pada tiga tingkat pelapukan di lokasi penelitian dilakukan menggunakan paket CANOCO, versi 4.5.

Konversi hutan alam menjadi hutan karet mereduksi stok C dan N kayu mati. Total stok C dan N kayu mati di hutan alam berturut-turut 4.5 t C ha⁻¹ dan 0.05 t N ha⁻¹ tiga kali lebih tinggi dibandingkan di hutan karet (1.5 t C ha⁻¹, 0.02 t N ha⁻¹). Stok C dan N pada tingkat pelapukan awal dan pelapukan lanjut di hutan alam

juga lebih tinggi dibandingkan di hutan karet. Nilai biomassa di atas permukaan tanah (AGB_{living}) dan produktivitas primer bersih (NPP_{wood}) yang tinggi di hutan alam dapat menjadi alasan penyebab tingginya massa kayu mati, hal ini berkaitan dengan kapasitas kayu mati untuk menyimpan C dan N. Nutrien dalam jumlah besar yang tersimpan dalam kayu mati di lantai hutan alam menyediakan pengembalian sumber nutrien besar ke tanah.

Konsentrasi rasio C/N menurun dan konsentrasi N meningkat seiring dengan peningkatan pelapukan kayu, sedangkan konsentrasi C dan lignin bervariasi antar tahap pelapukan. Kelimpahan massa kayu mati, stok C dan lignin lebih banyak ditemukan pada tingkat pelapukan awal dibandingkan pelapukan lanjut. Hal ini mengindikasikan bahwa pelapukan kayu mati berlangsung lambat. Stok lignin yang tinggi di hutan alam menyediakan sumber stok C diharapkan memberikan kontribusi sebagai penyimpan nutrien jangka panjang bagi regenerasi pepohonan. Input kayu mati yang tinggi di hutan alam mengindikasikan pentingnya fungsi pelapukan kayu mati di hutan alam dibandingkan di hutan karet.

Faktor penting yang membedakan tingkat pelapukan kayu mati di hutan karet adalah konsentrasi C dan N dalam kayu mati, rasio C/N dan berat jenis kayu. Sedangkan stok C, N dan lignin dalam kayu mati di hutan alam merupakan faktor penting yang mempengaruhi tingkat pelapukan kayu mati.

Penelitian ini menunjukkan bahwa mengganti hutan alam dengan hutan karet mereduksi total stok C dan N yang memberikan dampak negatif terhadap pengembalian dan siklus nutrien dalam ekosistem. Massa kayu mati yang rendah di hutan karet mengakibatkan perubahan keberlanjutan simpanan C dan N jangka panjang.

Kata kunci: kayu mati, perubahan konsentrasi nutrien, stok C dan N, tingkat pelapukan

SUMMARY

SELIS MERIEM. Carbon and Nitrogen Stocks of Different Dead Wood Decay Stages in Natural and Converted Tropical Lowland Forests (Jambi, Indonesia). Supervised by TRIADIATI and SOEKISMAN TJITROSOEDIRJO.

Dead wood plays a significant role as an integrity of forests, serves large nutrient source and habitat for decomposers and other forest biota. Rapid transformation of natural forests into other land-use systems in the lowlands of Sumatra, Indonesia, strongly reduces total aboveground biomass and negatively affects nutrient cycling. Most natural rainforests in Jambi province have often been converted into rubber agroforestry systems called 'jungle rubber'. This transformation is likely to change natural forest structure and its function. The consequences of this conversion for C and N stocks of dead wood contribution remains poorly understood.

This study aimed to examine differences in mass, stocks of C, N and lignin stored in dead wood between systems, and concentrations of these chemical contents and stocks of three decay stages of dead wood. This research aimed to analyze the contribution of dead wood in each decay stages to total C and N stocks in Indonesia tropical rainforests.

The research was conducted in natural forest and jungle rubber in the tropical lowlands of Jambi province, Sumatra. Dead wood inventory was carried out in a non-destructive way within permanent plots of 2500 m² (50 m x 50 m) in a total sixteen plots (eight replicates per land-use system: four were located within Harapan region, Muara Bulian regency, and four were located in the Bukit Duabelas National Park (TNBD), Sarolangun regency). Standing dead wood which recorded had diameter at breast height (dbh) ≥ 10 cm and height ≥ 1.5 m, while fallen dead wood which had diameters ≥ 10 cm at the midpoint.

Decay wood was visually identified based on physical indicators reflecting wood breakage and classified into three decay stages. Mass of dead wood was estimated using allometric equation. For each decay stage, 48 representative samples were selected randomly to analyse their chemical properties. Organic C, total N and lignin were measured using methods of Walkley and Black, Kjeldahl and Van Soest, respectively. The effect of land-use system on tested variables (mass, volume and stocks of C, N and lignin in dead wood), as well as in each decay stage, were compared using Independent Sample t-test. Analyses of variance (ANOVA), One-Way with post-hoc Tukey HSD test were used to determine the influence of decay stages on tested variables. A principal component analyses (PCA) of tested variables of the three different decay stages in study sites was conducted with the package CANOCO, version 4.5.

Converting natural forests to jungle rubber reduced C and N stocks of dead wood. Total C and N stocks in dead wood in the natural forest (4.5 t C ha⁻¹, 0.05 t N ha⁻¹, respectively) were three times higher than those in the jungle rubber (1.5 t C ha⁻¹, 0.02 t N ha⁻¹, respectively). The stocks of C and N at early and advanced wood decay stages in the natural forest were also higher than those in the jungle rubber. High aboveground tree biomass (AGB_{living}) and aboveground net primary productivity (NPP_{wood}) in natural forests could have a reason for higher dead

wood mass, bearing its capacity to store C and N. Large nutrient stored in dead wood on the forest floor provide large nutrient turnover to the soil.

Concentrations of C/N ratio were found to decrease and N concentrations to increase with advancing wood decay, while concentrations of C and lignin varied among decay stages of wood. The abundance of dead wood mass and stocks of C and lignin were found to be higher in the early decay than those in the advanced decay stage. This indicated that dead wood was slowly decayed. High lignin stocks in natural forests served as C stock source expected to contribute as a long-term nutrient storage for regenerating trees. Higher input of dead wood in natural forest indicated a higher importance of dead wood decay in natural forests than in jungle rubber systems.

The crucial factors separating the three dead wood decay stages in jungle rubber plots were concentrations of C, N, and C/N ratio as well as live wood density. Whereas stocks of C, N and lignin in natural forest were important factors affecting decay stages of dead wood.

The current study implies that replacing natural forest with jungle rubber strongly reduces total C and N stocks which have a marked negative effect on the ecosystems' nutrient turnover and cycle. Reduced dead wood mass in jungle rubber impacts changes of long-term C and N sustainability.

Key words: C and N stocks, dead wood, decay stages, changes of nutrient concentration

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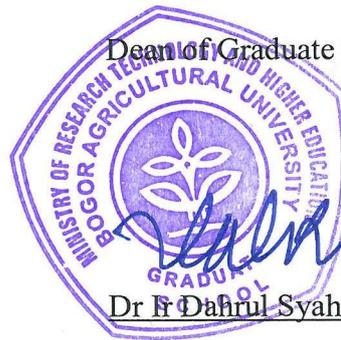
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FOREWORD

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TABLE OF CONTENTS

LIST OF TABLES	iv
LIST OF FIGURES	iv
LIST OF APPENDIX	iv
1 INTRODUCTION	1
Background	1
Research Goals	2
2 LITERATURES	2
Dead Wood	2
Decay of Dead Wood	4
Carbon, Nitrogen and Lignin in Dead Wood	4
Forest Land-use Change into Jungle Rubber	6
Effects of Forest Conversion to Dead Wood Contribution	6
3 METHODS	7
Study Sites	7
Dead Wood Inventory	9
Estimation of Dead Wood Mass	10
Analyses of Organic Carbon, Total Nitrogen and Lignin	11
Statistical Analyses	11
4 RESULTS AND DISCUSSION	12
Results	12
Discussions	17
5 CONCLUSIONS AND SUGGESTIONS	20
Conclusions	20
Suggestions	20
REFERENCES	20
APPENDIXES	25
BIOGRAPHY	30

LIST OF TABLES

1	Allometric equations of aboveground biomass	3
2	The main difference between organic and anorganic compounds	5
3	Sampling location and geographic sites of study sites	8
4	Classification of dead wood decay stages	10
5	Distribution of diameter of dead wood pieces in each wood decay stage in natural forest and jungle rubber	12
6	Distribution of height/length of dead wood pieces in each wood decay stage in natural forest and jungle rubber	13
7	Comparison of mass, volume, stocks of C, N and lignin of dead wood for each decay stage between natural forest and jungle rubber	14
8	Results from Principal component analysis (PCA) of C, N and lignin concentration as well as the C, N, and lignin stocks, and the ratio of C stock in dead wood to total of the three decay stages in the two land-use systems	17

LIST OF FIGURES

1	Profiles of natural forests and jungle rubber in lowland regions of Jambi Province	7
2	Map of study sites in Harapan Forest of two ecosystems from jungle rubber and natural forests	8
3	Map of study sites in Bukit Dua Belas National Park of two ecosystems from forests and jungle rubber	9
4	Permanent plot of experimental area	10
5	Effect of land-use systems on total total mass, volume, carbon stock, nitrogen stock, and lignin stock of dead wood	13
6	Effect of wood decay stages on concentrations of nitrogen and C/N ratio in dead wood for each decay stage	14
7	Effect of wood decay stages on concentrations of carbon and lignin in dead wood for each decay stage	15
8	Effect of wood decay stages on mass, volume, carbon stock, nitrogen stock, and lignin stock of dead wood	15
9	PCA of C, N, and lignin concentration as well as the C, N, and lignin stocks, and the ratio of C stock in dead wood to total of the three decay stages in the two land-use systems	16

LIST OF APPENDIXES

1	Data of total mass, volume, stocks of C, N and lignin, and chemical concentrations of C, N, C:N and lignin	26
2	Data of mass, volume, stocks of C, N and lignin, and chemical concentrations of C, N, C:N and lignin for every wood decay stages	27

1 INTRODUCTION

Background

Dead wood has been recognized to have an important ecological function as a resource for the ecosystem and structural components of forests (Harmon *et al.* 1986). A high abundance of dead wood on the forest floor maintains a high biodiversity of species such as saproxylic beetles (Floren *et al.* 2014) and fungi community which composition depends on the stage of decay of the dead wood (Kebli *et al.* 2012; Blaser *et al.* 2013). Enhancing dead wood amounts was expected to increase the habitat for forest biota. Dead wood also contributes a significant proportion to the total C stocks of aboveground wood mass (Pfeifer *et al.* 2015). This input serves as an important source to the nutrient flux to soil and consequentially affects the forest nutrient cycle. Carbon sequestered in dead wood biomass effluxes through decomposition processes, thus dead wood plays a crucial role in global C cycling as well (Chambers *et al.* 2000). Dead wood not only stores C retention as a fraction of total above-ground carbon pool, but also contributes to soil C sequestration (Pan *et al.* 2011).

Vegetation in forests without fertilizer inputs depend on available nutrients released from decomposition of dead organic matter including litter and woody debris. Dead wood not only composes active soil organic matter serving nutrient reservoirs for plant, but C and N stored in dead wood are also rapidly utilized by soil decomposer as main energy source for growth (Boddy & Watkinson 1995; Lambers *et al.* 2008). Dead wood sequesters a large amount not only of C but also of nutrients, but decomposes at a lower rate than fine litter (Harmon & Hua 1991) and has been reported to slowly release N to soil (Hafner & Groffman 2005). Despite the low rate of decomposition, dead wood can be assumed to persist as C and N long-term storage form which makes it an important contribution to C and N cycles (Laiho & Prescott 1999). The C stock source in dead wood is predominantly derived from lignin compounds (Austin & Ballaré 2010). The lignin in dead wood consists of recalcitrant complex polymers considered as the inhibition factor for microorganism to decompose; thus causing the low decay rate and remaining long-term on the forest floor (Vanholme *et al.* 2010). Based on the crucial role of lignin in controlling C release, further studies on lignin stock in dead wood are highly required.

Given the importance of dead wood in nutrient cycling of forests, the storage and nutrient turnover are determined by substrate quality, decay stage, size, environmental factors such as moisture and temperature, and disturbance history (Harmon *et al.* 1986; Liu *et al.* 2013). Nutrient concentrations likely vary with decay stages as a result of decomposer activity, thus the amount of nutrients stored in dead wood may be altered during the decomposition process. Examining these concentrations in each decay stage will indirectly reflect on the dead wood nutrients which are transferred to the soil. Further, measuring C stocks of dead wood by utilizing C concentrations in each decay stages can avoid a biased estimation compared to using the C expansion factor (CEF). Since a high abundance of dead wood on the forest floor is expected to store large amounts of

nutrients, neglecting to measure dead wood mass makes the estimate of nutrients returned to the soil remain inadequate.

The ecological functions of dead wood have been studied extensively in temperate as well as in tropical forests (Aakala 2010; Palviainen *et al.* 2010; Yang *et al.* 2010). The mean stocks of dead wood C across tropical forests accounted for 17.5 t C ha⁻¹ (Pregitzer & Euskirchen 2004). Dead wood contributes 16.6 t ha⁻¹ and 11% carbon stock of the world's forests (FAO 2010). In contrast with large C storages, there was a decrease of the C stocks of dead wood since 1990-2010 as reported by FAO (2010) which was mainly driven by a reduced forest area. Deforestation of tropical forests in Indonesia occurs at a higher rate than natural forest cover loss in other tropical areas (Margono *et al.* 2014). Particularly lowland tropical rainforests in Jambi, Sumatra, have lost 78 % of forest cover by land-use changes since 1985–2008 which turns them into critically endangered ecosystems (WWF 2010). Many native tree species in the natural forests of Jambi (Indonesia) have been logged and replaced with rubber trees, since rubber latex is of high economic value for the communities (Gouyon *et al.* 1993). Natural forest transformed into other land-use forms is likely to change forest structure and its function. These changes probably alter dead wood contribution in the ecosystem. While recently most rubber land-use systems represent intensively managed monocultures, in earlier times natural rainforests have often been converted into rubber agroforestry systems containing a tree cover of natural tree species called 'jungle rubber'. Nevertheless, the effects of transformation of natural forest to jungle rubber on C and N stocks of dead wood are not investigated yet.

Research Goals

Based on the crucial role of dead wood contribution to nutrient cycle, this study aims (1) to compare the total mass, stocks of C and N in dead wood between natural forest and jungle rubber, (2) to assess the nutrient concentrations in each decay stage of wood, and (3) to investigate the effect of decay stages on mass, volume, and nutrient stocks in dead wood mass. Our overarching goal is to obtain a basic and new idea of dead wood contribution to total C and N stocks in Indonesia tropical lowland rainforests.

2 LITERATURES

Dead Wood

Dead wood is all non-living woody materials without leaves (Sutaryo 2009) excluding dead parts attached on living trees (Merganičová *et al.* 2012). Yan *et al.* (2006) determines non-living woody materials which has diameter ≥ 10 cm at largest trunk and can be further classified as its position on the ground: fallen, standing, stump or large branches. Fallen dead wood is distinguished from standing dead wood based on gradient towards the forest floor (fallen $> 45^\circ$, standing $< 45^\circ$). FAO (2010) defines dead wood as non-living wood buried in the

soil i.e., dead roots with large diameter ≥ 10 cm. Based on these definitions, dead wood can be classified as structural components of above- and below ground.

Input source of dead wood in terrestrial land is driven by natural mortality and human disturbance. Naturally, input of dead wood is caused by extrinsic factors (wind, fire, insects, disease and competition) and intrinsic factors (Harmon *et al.* 1986). Wind can knock down single or small clusters of trees to be fragmented parts. Extreme fires burn stems, crowns and even root systems. Basal wounds of trees allow penetration of microorganisms to weaken the wood structure. Although there are some survivals, but weaken structure of wood causes those trees to be more susceptible to windthrow. Insect is another factor contributing input of standing dead trees by attacking nutrient flows which rich in phloem. Logging residues left on the forest floor is an input source of dead wood (Köhl *et al.* 2008). Further, forest management determines its abundance.

Dead wood contribute to total aboveground biomass estimations since it composes a structural component in ecosystem. Mass estimation of dead wood is crucial especially to observe the impact of changes in forest functions. Generally, mass of dead wood can be estimated using destructive or non-destructive methods (Vashum & Jayakumar 2012). The destructive method, harvesting, were rarely used because this consume inventory time and expensive, need rehabilitation process and is not recommended for degraded forest with rare or protected species and small area. The non-destructive method is more adapted and applicable because it just takes a little part as a sample to calculate its dry mass. The non-destructive method uses allometric equations to estimate biomass.

The importance parameter predictors to estimate biomass are diameter, wood density, length or height and forest type. Chave *et al.* (2005) provided reliable prediction of aboveground biomass allometric equation (AGB_{est}) based on climate zone (dry, moist and wet) for lowland tropical forests (Table 1). Mass of dead wood was estimated by using live tree allometric equations (Kauffman & Donato 2012). The difference is subtracting with 2.5% of leave estimation for early decay and 10-20% of both leave and branches estimation for intermediate decay. As decay proceed results in high breakage, it is difficult to subtract from live tree biomass. Thus, advanced decay of wood was estimated by approaching cylinder volume multiplied with wood density (Hairiah *et al.* 2011).

Table 1 Allometric equations of aboveground biomass (AGB) (Chave *et al.* 2005)

Climate zone	Allometric equation
Dry forest stands ($< 1500 \text{ mm y}^{-1}$)	1. $(AGB)_{est} = 0.112 \times (\pi d^2 h)^{0.916}$ 2. $(AGB)_{est} = \pi \times \exp(-0.667 + 1.784 \ln(d) + 0.207(\ln(d))^2 - 0.0281(\ln(d))^3)$
Moist forest stands ($1500 - 4000 \text{ mm y}^{-1}$)	1. $(AGB)_{est} = 0.0509 \times \pi d^2 h$ 2. $(AGB)_{est} = \pi \times \exp(-1.499 + 2.148 \ln(d) + 0.207(\ln(d))^2 - 0.0281(\ln(d))^3)$
Wet forest stands ($> 4000 \text{ mm y}^{-1}$)	1. $(AGB)_{est} = 0.0776 \times (\pi d^2 h)^{0.940}$ 2. $(AGB)_{est} = \pi \times \exp(-1.239 + 1.980 \ln(d) + 0.207(\ln(d))^2 - 0.0281(\ln(d))^3)$

Decay of Dead Wood

Decay is a process of polymer materials of wood by which broken down into simple compound. The first steps in decomposition are degradation by invertebrate fauna that reduce the size of wood particles. This process allow microbes to access the tissues after damaged cuticle and ruptured membrane causing leaching of mobile phenols. Carbon is used for microbe respiration emitted to the atmosphere while particulate N in wood is dissolved and used as energy demand. In limited-N organic, absorbed dissolved N is mineralized or microbe immobilizes N from environment to meet their N demand (Lambers *et al.* 2008). Decay status of wood depends on (1) biotic factors such as wood quality (structure and chemical properties), tree species, wood dimensions (diameter, length or height), wood density and decomposer activities (driver of transformation process), and (2) abiotic factors or environmental factors such as air temperature and moisture. Other factors of leaching, fragmentation, content of dead wood with the ground also influence on decay process (Harmon *et al.* 1986).

Wood structure is distinguished into hard wood layer located near to pith and soft wood layer near to bark. In live tree starch deposit in soft wood may be reconverted to glucose for plant growth, but when the tree is dead wood-storage starch is retained as permanent deposit in wood cells (Bamber 1987). Not only starch, other soluble materials of sugars, amino acids, and proteins in sapwood are highly invaded by most fungi and bacteria attacks that are able to degrade. Hard wood provides component of structural support containing polymers-cellulose, hemicelluloses and lignin. These compounds can be degraded only by decomposers that able to decompose these structurally complicated high-polymeric materials. Other secondary metabolite products also deposited in hard wood such as polyphenol, terpenes, alkaloids that toxic for decomposers (Kirk & Cowling 1984).

Low decay of dead wood would take over a long term studies. Thus, physical characteristics of dead wood is the most common approach to assess decay status. Visual assessment indicators to determine decay stage are (1) bark, (2) branches and twigs, (3) bole shape, (4) structural integrity, (5) color of wood, (6) portion of log on ground, (7) root invasion and (8) vegetation growing (mosses, shrubs, seedlings) (Yan *et al.* 2006). Tobin *et al.* (2007) used five stage to determine decay status but there were no significant difference in mean densities between stages 2 and 3 and between stages 4 and 5, thus combining two similar value was possible to decrease numbers of decay stages. According to those, in this study three decay stage classification (no decay, moderate decay and advanced decay) is convenient to adapt.

Carbon, Nitrogen and Lignin in Dead Wood

Plants uptake C from CO₂ in the atmosphere and store it as organic C in dead wood compartments. Organic compound is composed of C as the main constituent atoms forming C backbone or contain C bonded to H and other atoms of O, N, P, S and the halogens, excluding bicarbonate, carbonic acid, and hydrogen cyanide. These organic matter is mineralized as inorganic compound by decomposers.

Inorganic compounds is defined as compounds without C–H bound. The difference between organic and anorganic compounds are showed in Table 2 (Neuman 1999).

Table 2 The main difference between organic and anorganic compounds

Variables	Organic compound	Anorganic compound
Binding within molecules	usually covalent	often ionic
Flammability	flammable	nonflammable
Solubility in water	undissolved	dissolved
Boiling point	low	high
Solubility in organic solvent	dissolved	undissolved
Conductivity of aqueous solutions	nonconductor	conductor

Dead wood acts as storage of C and N since it able to store them in wood compartments. Carbon accounts 45% in dry matter and is stored as component of most compounds due to its binding with dissolved water compounds such as cellulose, hemicellulose and with undissolved compounds such as lignin and other secondary metabolites. Woody plants contain 0.03–0.10% of N and stored in wood compartments as (1) protein in the cell cytoplasm, (2) Peptide, amino acid, lypoprotein that most accumulate near pith or sapwood, (3) compounds containing N: secondary metabolite accumulate in the heartwood, and (4) structural N as components of primary cell wall: hydroxyprolin-rich protein, proline-rich protein and glycine-rich protein, arabinogalactan protein, (5) structural N as components of secondary cell wall: structural N bounded to lignin (Taiz & Zeiger 2010).

Lignin is a secondary growth of dicotyledonae plants and composed of cell secondary xilem that form wood (Campbell & Sederoff 1996). Lignin is phenol polymer consisted of one or more than monolignols such as coniferyl, coumaryl and sinapyl alkohol (Taiz & Zeiger 2010). Those lignol monomers bind each other to constitute phenylpropanoid. Lignin compositions between Angiosperms (dominant of syringyl) and Gymnosperms (dominant of guaiacyl) are differ due to biosynthesis pathway Binds of branching C-C and C-O-C on structure of phenylpropanoid cause the complex lignin compounds are resistant to degradations (Campbell & Sederoff 1996).

Dead wood acts as a function of organic fertilizer in nutrient cycle and contribute to soil organic matter. Soluble compound of dead wood is mineralized into anorganic ions. This compound is dissolved matter in water such as cellulose, starch and protein, and susceptible to decomposer attacks. Whereas complex compound of dead wood composes the humus components by humification process. This compound is undissolved matter in water and resistant to microbial attack such as lignin, resin, oil and fatty acid (Coleman *et al.* 2004).

Decomposers degrade soluble organic matters in the early stage of decay. Nitrogen in organic mass is broke down become dissolved organic N and directly taken by immobilization for decomposer growth demand (Coleman *et al.* 2004). The accumulation of N may be due to product of non-structural compound in the form of pectin and lignin, aromatic compounds produced by fungi degradation (Strukelj *et al.* 2013). Organic C is absorbed as component of decomposer cells and released as CO₂. The accumulation of N in the advanced decay and emission

of C thereby decrease C/N ratio. Toward decay process, organic storage in dead wood mass is lessen.

Forest Land-use Change into Jungle Rubber

Primary forests are defined as forest composed of native species with no indication of past or recent human activities (FAO 2010). Natural forests in this study are defined as primary forest, the remaining human activities. Land-use refers to change land cover due to human intervention. Converted or deforested forest is removing forest cover with direct human activities into other land use forms without regenerating purpose (IPCC 2000). Forest covers were reduced by other land-use forms in the world since 1990. Asia lost more than 2.2 million ha of forest cover per year. This change was high in the tropical forest. Indonesia accounted for 94 million ha forest in 2010 and increased in loss remaining 91 million ha forest in 2015 from the large forest area among ten countries i.e., Russian Federation, Brazil, Canada, United States of America, China, Democratic Republic of the Congo, Australia, Sudan, and India (FAO 2010, FAO 2015). However, Indonesia was the second large net loss of forest amounted to 684 thousand ha in the world after Brazil in the period of 2010-2015 (FAO 2015).

Asia largely had a decreased primary forest which 20% of total forest area replaced by planted forests. Rubber plantation is planted mainly in Southeast Asia of which Indonesia had more than 10 million ha of that. These land-use greatly increased in the period of 1990–2010 (FAO 2010). Rubber seeds had been introduced to Indonesia from Malaysia in the early 1910s. This plant is intentionally planted in the forest fallows “jungle rubber” since it promise of high incomes and can grow on the low soil fertility (Gouyon *et al.* 1993). In case, characteristics of forest according to FAO (2010) jungle rubber is categorized as a deforested with planted forest.

The effect of converting natural forest into planted forest i.e., jungle rubber will change structure and function of forest. Forest mainly acts a source and sink of C. Such changes induced unbalanced C cycle due to removal forest component affecting C stock. Even conversion of natural forests to planted forests with fast-growing species rapid C fixing, this changes do not decrease the accumulation of CO₂ in the atmosphere but reduce C storage (Harmon *et al.* 1990).

Effects of Forest Conversion to Dead Wood Contribution

Forest biomass is the largest source of primary productivity and largest terrestrial C storage (Malhi *et al.* 1999). The world's forests were estimated to account for 289 Gt C or 161.8 t C ha⁻¹ in 2010 including both above- and belowground biomass (FAO 2010). Carbon sequestered into living biomass through photosynthesis (GPP; gross primary production) then released by respiration is denoted as net primary production (NPP). When living tree dies and turns into dead wood, C stored in dead wood is a considered compartment in C budgets of ecosystem. Dead wood stores C as net ecosystem production (NEP) while releasing CO₂ to the atmosphere as it decomposes (IPCC 2000).

The importance of measuring dead wood is emphasized by other studies since it can store C. Carbon in dead wood is a significant C reservoir since it contributes to estimating C pool (IPCC 2000). FAO (2010) reported that dead wood in South and Southeast Asia contributed 20.3 t ha⁻¹ in biomass and 3.6 t C ha⁻¹. These were decreased in the period of 1990–2010 which mainly driven by decrease C stock as a result of decrease forest area. However, data of dead wood estimate were less reported from other countries (Köhl *et al.* 2015). Thus, C stock of dead wood is important to be measured. The logging residue remaining in forest floor is a source of dead wood. However, when dead woods are removed from the forest, it will reduce total C stock.

The conversion of natural forests into other land-use forms reducing C stock of dead wood, subsequently reduces nutrient reservoirs in ecosystem. Furthermore, it affects the sustainability and cycles of nutrient (Harmon & Hua 1991) and changes wood-associated species diversity (Jonsson *et al.* 2005).

3 METHODS

Study Sites

The research was conducted in natural forest (Figure 1a) and jungle rubber land-use systems (Figure 1b) in the tropical lowlands (51–95 m above sea level) of Jambi province, Sumatra (Table 3). We investigated eight 50 m x 50 m plots of which four were located within Harapan region, Muara Bulian reGENCY (Figure 2) and four were located in the Bukit Duabelas National Park (TNBD), Sarolangun reGENCY (Figure 3).

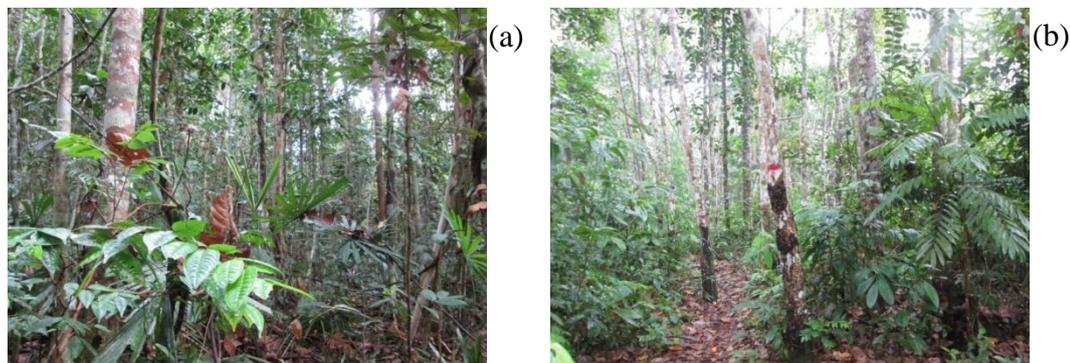


Figure 1 Profiles of natural forest (a) and jungle rubber (b) in lowland regions of Jambi Province

The climate is tropical humid (2374 mm yr⁻¹) with a mean annual air temperature of 26.9°C and mean relative humidity of 86% (climate data from Jambi climate station (Stasiun Klimatologi Jambi: N 1°62.1', E 103°53.1'). The natural forest was degraded primary forest with selective logging in the past. The jungle rubber system was a rubber agroforest with natural tree cover where forest trees were logged and rubber trees planted in the gaps between 1973 and 2006. Canopy cover and total basal area in the natural forest were 92.1 ± 0.5% and 30.1

$\pm 0.9 \text{ m}^2 \text{ ha}^{-1}$, respectively, whereas in the jungle rubber the numbers were $87.6 \pm 0.8\%$ and $18.3 \pm 1.1 \text{ m}^2 \text{ ha}^{-1}$, respectively (Kotowska *et al.* 2015).

Concentrations of C and N were analyzed in SEAMEO BIOTROP, and lignin concentration was analyzed in Feed Science and Technology laboratory, Nutrition and Feed Technology Department, IPB.

Tabel 3 Sampling location of study sites. In TNBD site, 'BF' refers to natural forest and 'BJ' refers to jungle rubber. In Harapan site, 'HF' refers to natural forest and 'HJ' refers to jungle rubber.

Study sites	Plots	Geographical location	Altitude (a.s.l)	
TNBD	Natural forest	BF1	01°59'42.5"S, 102°45'08.1"E	83
	Natural forest	BF2	01°58'55.1"S, 102°45'02.7"E	77
	Natural forest	BF3	01°56'33.9"S, 102°34'52.7"E	87
	Natural forest	BF4	01°56'31.0"S, 102°34'50.3"E	87
	Jungle rubber	BJ1	02°08'34.1"S, 102°51'05.1"E	74
	Jungle rubber	BJ2	02°01'49.7"S, 102°46'16.7"E	76
	Jungle rubber	BJ3	02°03'46.7"S, 102°48'03.5"E	89
	Jungle rubber	BJ4	02°00'57.3"S, 102°45'12.3"E	60
Harapan	Natural forest	HF1	02°09'09.9"S, 103°21'43.2"E	76
	Natural forest	HF2	02°09'29.4"S, 103°20'01.5"E	75
	Natural forest	HF3	02°10'30.1"S, 103°19'57.8"E	58
	Natural forest	HF4	02°11'15.2"S, 103°20'33.4"E	77
	Jungle rubber	HJ1	01°55'40.0"S, 103°15'33.8"E	51
	Jungle rubber	HJ2	01°49'31.9"S, 103°15'39.2"E	84
	Jungle rubber	HJ3	01°50'56.9"S, 103°17'59.9"E	95
	Jungle rubber	HJ4	01°47'07.3"S, 103°16'36.9"E	57

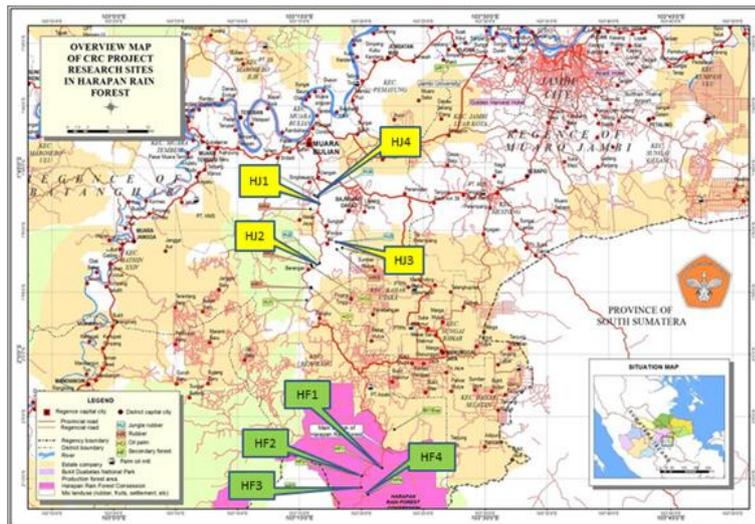


Figure 2 Map of study sites in Harapan Forest of two ecosystems from jungle rubber; HJ1, HJ2, HJ3, HJ4 (yellow, at top) and natural forests; HF1, HF2, HF3, HF4 (green, at base) (CRC990 EForTS 2014)

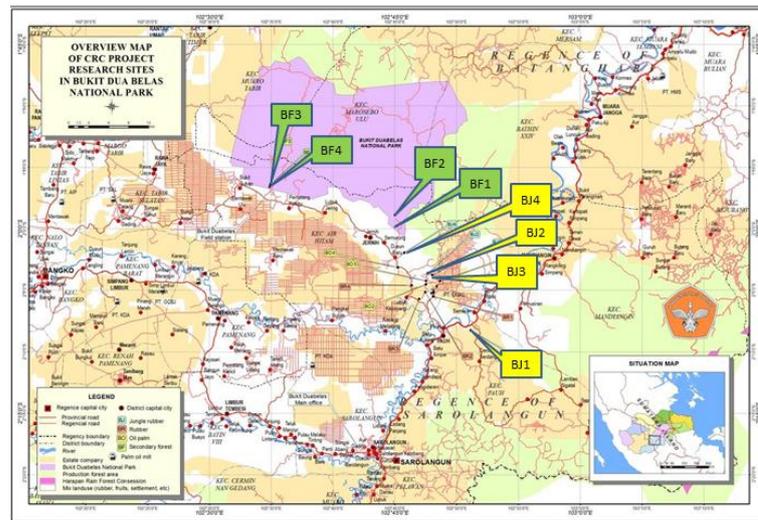


Figure 3 Map of study sites in Bukit Dua Belas National Park (TNBD) of two ecosystems from forests; BF1, BF2, BF3, BF4 (green, at top) and jungle rubber; BJ1, BJ2, BJ3, BJ4 (yellow, at base) (CRC990 EFForTS 2014)

Dead Wood Inventory

The sampling method was carried out in a non-destructive way. Dead wood i.e. standing and fallen dead wood pieces were monitored within permanent plots of 2500 m² (50 m x 50 m) (Figure 4) in a total of sixteen plots (eight replicates per land-use system). The size standing dead wood (dbh ≥ 10 cm, height ≥ 1.5 m) and fallen dead wood (diameters ≥ 10 cm at the midpoint, length ≥ 1 m) were measured. Dead wood diameter was measured using a dendrometer tape (UMS, Munchen, Germany), height of standing dead wood measured using a Vertex III height meter (Haglof, Langsele, Sweden), and length of fallen dead wood measured using a meter tape. Wood density (ρ) was measured using Pilodyn 6J wood tester (PROCEQ SA, Zürich, Switzerland). The penetration depth (h) of the pin was converted using a calibration equation derived by Kotowska *et al.* (2015) (Equation 1), based on 204 trees which wood core samples were analyzed.

$$\ln(p) = 0.8711 - 0.5763 \ln(h) \quad (1)$$

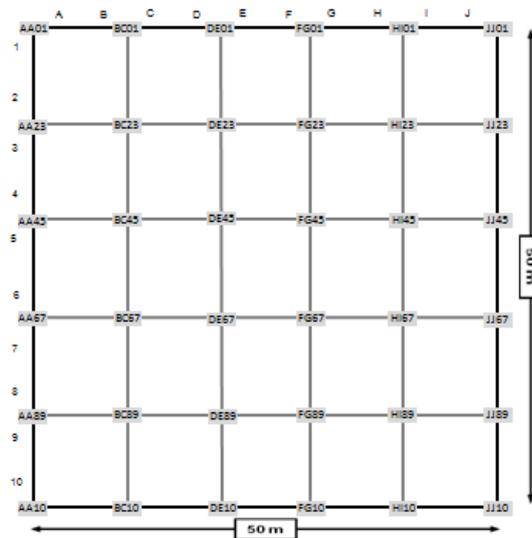


Figure 4 Permanent plot of experimental area (50 m x 50 m). Letters of the alphabet and Roman numerals indicate the boundary points between sub-plots (AA01-AA23-BC01-BC23) and the edge of the plot (AA01-JJ01, JJ01-JJ10, JJ10-AA10, AA10-AA01). This boundary markers facilitate the sampling direction and ensured that are not repeated of recorded samples in the same subplot.

Decay wood was qualitatively identified based on physical indicators according to Grove (2001) and classified into one of three stages: (I) early decay, (II) intermediate decay, and (III) advanced decay (Table 4). Sampling point on the fallen dead wood referred to Pyle and Brown (1999) method which had one of the dominant decay stage criteria i.e. more than 50% while sample of standing dead wood was taken at dbh 1.5 m.

Table 4 Classification of dead wood decay stages (Grove 2001)

Decay stages of wood	Indicators
I (early decay)	Intact bark, loss of leaves, retaining wood integrity
II (intermediate decay)	Less intact bark, slight rot wood structure but still supporting mechanically, partially invaded root
III (advanced decay)	Loose bark, no longer retains original shape, largely disintegrated, spreading invaded root

Estimation of Dead Wood Mass

Allometric equations were used to estimate the mass of dead wood. Mass of decay stage I and II were estimated using the equation for AGB (aboveground biomass) by Chave *et al.* (2005) (Equation 2). The proportion of missing components was subtracted from the outcome (Kauffman & Donato 2012). The mass of decay stage I was subtracted by 2.5% of leaf mass estimate (Equation 3). The mass of decay stage II was subtracted by 15% of lost branches and twigs (Equation 4). The mass measurement for decay stage III used the cylinder volume

and multiplied by wood density (Equation 5) (Hairiah *et al.* 2011). The value of the mass measurements (kg) were converted in tonnes per hectare. Volume of dead wood was measured by dividing wood mass with its density (Equation 6). The parameters which were used in the formula were wood density (ρ , g cm⁻³), diameter (d, cm) and height or length (h, m).

$$AGB = 0.0509 \times \rho \times d^2 \times h \quad (2)$$

$$Decay\ stage\ I = AGB - 2.5\% \quad (3)$$

$$Decay\ stage\ II = AGB - 15\% \quad (4)$$

$$Decay\ stage\ III = \frac{\rho \times \pi \times d^2 \times h}{40} \quad (5)$$

$$Volume = \frac{dead\ wood\ mass}{wood\ density} \quad (6)$$

Analyses of Organic Carbon, Total Nitrogen and Lignin

In total, 261 pieces of dead wood were extracted and cut into smaller pieces; cleaned from roots, soil, mosses, fungi, and insects; samples were then dried at 80°C to a constant weight then ground. For each decay stage, 48 representative samples were selected randomly to analyse their chemical properties.

Organic C was measured using Walkley and Black method following boiled of 0.1 g (dried weight) sampel at 90°C for 2 h in 10 ml of K₂Cr₂O₇ 2 N and 7.5 ml of H₂SO₄ p.a., diluted with aquadest up to 100 ml, pipetted 10 ml and added with 3 drops of ferriin, and titrated with 0.2 N FeSO₄.

Total N was measured using the Kjeldahl method following destruction of 0.1 g sample by heated at 340°C for 45 m in 5 ml H₂SO₄ and 0.2 selenium then diluted with 50 ml aquadest, destilation with NaOH 40% for 3½ m and fixation of vapour NH₃ in solution of 3 drops conway and 10 ml boric acid, and titration with 0.02 N HCl. The C/N ratio was determined by dividing total C by total N.

Lignin content was measured using Van Soet method after analyzed ADF (Acid Detergent Fiber) content which represented undissolved cell wall compartment in CTAB souldution (Cetyl Trimethyl Ammonium Bromide). One g sample was extracted for 1 h in 100 ml ADS solution (Acid Detergent Solution) which made by dissolved 20 g CTAB and 27.5 ml H₂SO₄ 1 N in 1 L aquadest, filtrated through sintered glass plate, rinsed residue with hot water and acetone, and dried at 105°C for ± 4 h. The residue was burned at ± 600°C for lignin content.

Stocks of C, N, and lignin were calculated by multiplying the mass (t ha⁻¹) of each compartment by its respective mean chemical concentration (%) for each decay stage.

Statistical Analyses

In this study, two plots (one jungle rubber and one forest plot) were excluded from further analysis due to their discrepancy of vegetation and structural characteristics; thus value of those plots have been transformed by approaching the mean value from the similar region in similar system. In the excluded jungle rubber plot, large dead wood amounts of slowly decomposing

hardwood remained after recent conversion from natural forest. The excluded forest plot showed a small number and biomass of dead wood which indicated distinct differences compared to all other forest sites. In case, data analyses were tested using square root transformation value of $(x + 1)^{1/2}$.

The effect of land-use system on parameters (mass, volume and stocks of C, N and lignin in dead wood), as well as in each decay stage, were compared using Independent Sample t-test. Analyses of variance (ANOVA), One-Way with post-hoc Tukey HSD test were used to determine the influence of decay stages on these parameters and on the nutrient concentrations of C, N, C/N ratio and lignin. All analyses were conducted using SPSS version 19 with statistical significance established at $\alpha = 5\%$ level. A principal component analyses (PCA) of chemical, anatomical dead wood properties and chemical stand stocks in of the three different decay stages in the two different land-use systems was conducted with the package CANOCO, version 4.5 (Biometris, Wageningen, The Netherlands).

4 RESULTS AND DISCUSSION

Results

Dead wood in natural forest had larger total diameter and length of wood than those in jungle rubber (Table 5 and Table 6). In natural forest there was dead wood piece with maximum diameter of 66.5 cm and length of 46 m. While there was no dead wood with diameter more than 57 cm and height more than 28 m in jungle rubber. The early decay of dead wood were found more abundant than other stages in natural forest and jungle rubber. In advanced wood decay stage, there were no large dead wood with diameter more than 40 cm in both systems.

Table 5 Distribution of diameter of dead wood pieces in each wood decay stage in natural forest and jungle rubber

Variable	Natural forest			Total	Jungle rubber			Total
	Decay stages				Decay stages			
	I	II	III		I	II	III	
Diameter (cm)								
10 - \leq 20	35	28	15	78	33	25	23	81
21 - \leq 30	14	7	15	36	9	8	8	25
31 - \leq 40	6	5	4	15	3	5	2	10
41 - \leq 50	2	1	-	3	2	2	-	4
51 - \leq 60	2	2	-	4	2	-	-	2
61 - \leq 70	2	1	-	3	-	-	-	-
	Range			10-66.5				10-56.6

Table 6 Distribution of height/length of dead wood pieces in each wood decay stage in natural forest and jungle rubber

Variable	Natural forest			Total	Jungle rubber			Total
	Decay stages				Decay stages			
	I	II	III		I	II	III	
Height/length (m)								
1 - ≤10	36	30	23	89	27	34	25	86
11 - ≤20	19	11	7	37	15	6	8	29
21 - ≤30	4	3	4	11	7	-	-	7
31 - ≤40	-	-	1	1	-	-	-	-
41 - ≤50	-	-	1	1	-	-	-	-
Range				1 - 46.0				1 - 27.9

Total dead wood mass and volume in natural forest were significantly higher than those in jungle rubber ($p < 0.05$) (Figure 5a and 5b). The higher mass of dead wood in the natural forest subsequently led to a highly significant differences in stocks of C, N and lignin compared to the jungle rubber ($p < 0.05$) (Figure 5c–e).

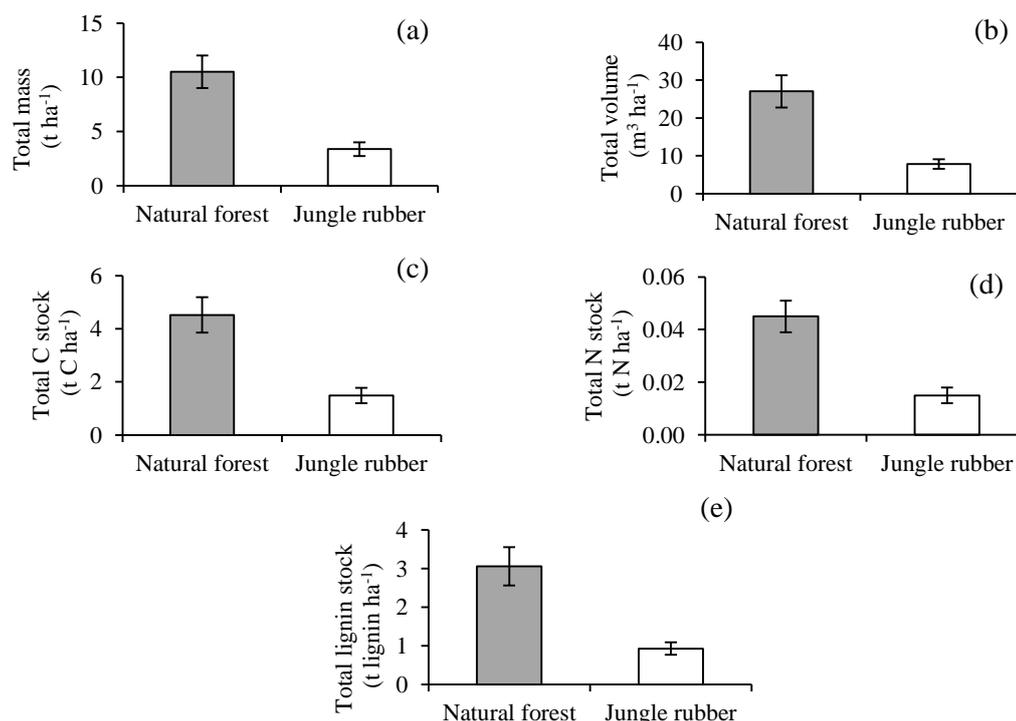


Figure 5 Effect of land-use systems on total total mass (a), volume (b), carbon stock (c), nitrogen stock (d), and lignin stock (e) of dead wood. Bars represent mean \pm SE. Significance was obtained with Independent Sample t-test at $p < 0.05$).

Each decay stage of dead wood had different mass, volume, and stocks of C, N, and lignin that differed as well as between natural forest and jungle rubber (Table 7). These variables were significantly higher for decay stage I in the natural forest compared to the jungle rubber ($p < 0.05$) as well as for decay stage III ($p < 0.05$), while there was no significant difference between the two systems for decay stage II ($p > 0.05$) (Table 7).

Table 7 Comparison of mass, volume, stocks of C, N and lignin of dead wood for each decay stage between natural forest and jungle rubber

Variables	Decay stages of wood	Natural forest	Jungle rubber
Mass (t ha ⁻¹)	I	4.87 (0.71)*	1.49 (0.41)*
	II	2.93 (0.95) ^{n.s}	1.27 (0.29) ^{n.s}
	III	2.71 (0.78)*	0.62 (0.15)*
Volume (m ³ ha ⁻¹)	I	10.15 (1.31)*	2.38 (0.66)*
	II	7.40 (2.79) ^{n.s}	3.25 (0.62) ^{n.s}
	III	9.48 (2.72)*	2.17 (0.54)*
Carbon stock (t C ha ⁻¹)	I	2.07 (0.32)*	0.67 (0.18)*
	II	1.31 (0.43) ^{n.s}	0.55 (0.13) ^{n.s}
	III	1.15 (0.33)*	0.26 (0.07)*
Nitrogen stock (t N ha ⁻¹)	I	0.019 (0.003)*	0.005 (0.001)*
	II	0.012 (0.004) ^{n.s}	0.005 (0.001) ^{n.s}
	III	0.015 (0.004)*	0.004 (0.001)*
Lignin stock (t lignin ha ⁻¹)	I	1.45 (0.23)*	0.45(0.11)*
	II	0.76 (0.25) ^{n.s}	0.32 (0.05) ^{n.s}
	III	0.85 (0.23)*	0.18 (0.05)*

* $p < 0.05$. ^{n.s} Not significant. Values show mean (SE). Significance was obtained with Independent Sample t-test at $p < 0.05$.

There were strong significant influences of the decay stages on N concentration and C/N ratio in dead wood ($p < 0.05$). Figure 6a shows that the N concentration in decay stage III was significantly the highest among the decay stages ($p < 0.05$), whereas the C/N ratio in the decay stage III was significantly the lowest among the decay stages ($p < 0.05$) (Figure 6b). However, there were no significant effects of dead wood decay stages on C and lignin concentrations ($p > 0.05$) (Figure 7a and 7b).

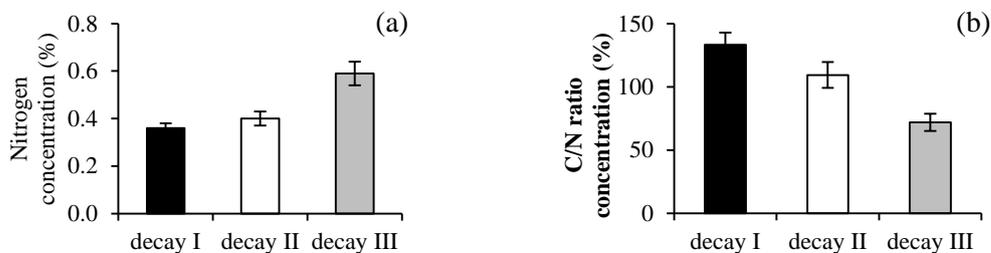


Figure 6 Effect of wood decay stages on concentrations of nitrogen (a) and C/N ratio in dead wood for each decay stage. Bars represent mean \pm SE.

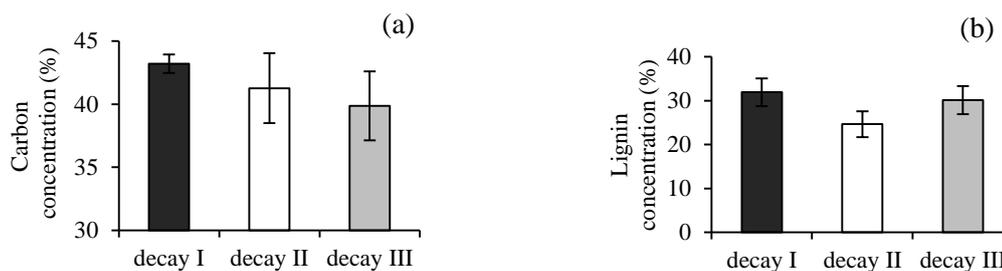


Figure 7 Effect of wood decay stages on concentrations of carbon (a) and lignin (b) in dead wood for each decay stage. Bars represent mean \pm SE.

Nutrient stocks of dead wood in each decay stage represented the value from both systems. Dead wood mass and stocks of C, and lignin were significantly influenced by the decay stage of wood ($p < 0.05$) (Figure 8), while no significant effects were found in volume of dead wood and N stock ($p > 0.05$) (Figure 8). The mass and stocks of C and lignin of dead wood were significantly higher in the decay stage I than the decay stage III (Figure 8). These variables decreased with advancing wood decay stages.

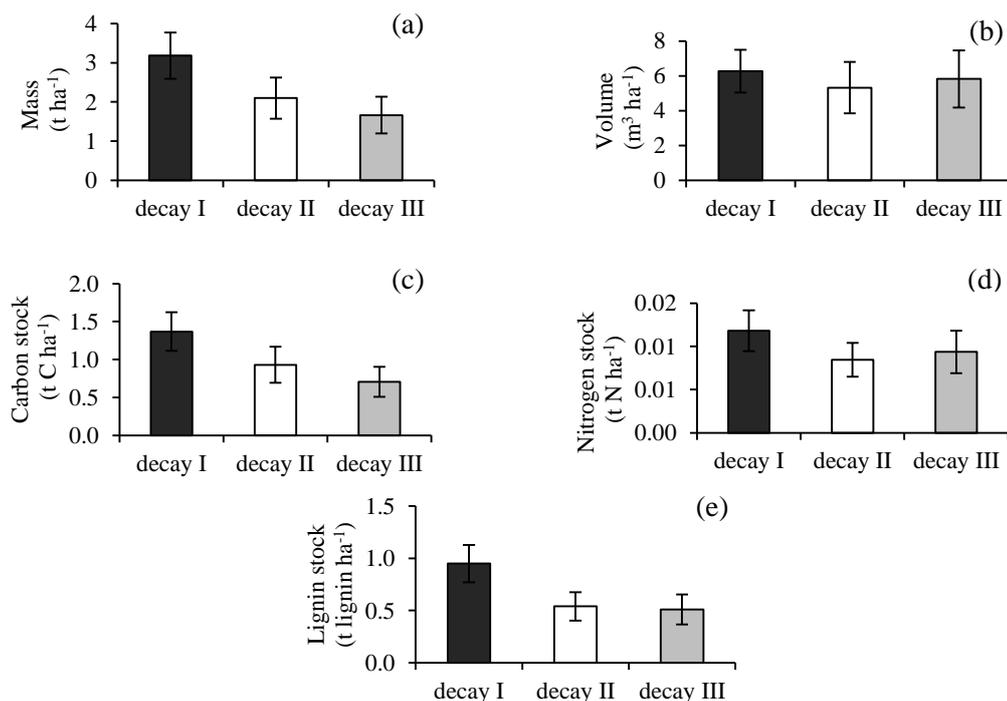


Figure 8 Effect of wood decay stages on mass (a), volume (b), carbon stock (c), nitrogen stock (d) and lignin stock (e) of dead wood. Bars represent mean \pm SE.

The results from the principal component analysis show that the natural forest and the jungle rubber plots are clearly separated from each other (Figure 10). Axis #1 with the highest explanatory value (EV 0.56) is closest associated with the proportional dead wood C in total aboveground C stock as well as with the

chemical dead wood properties (but not lignin content), and live stem wood density (Figure 9, Table 8). Therefore, dead wood C and N content, and C/N ratio as well as live wood density are the crucial factors separating the three dead wood decay stages in jungle rubber plots, but not in natural forest plots (Figure 10). C, N and lignin stocks are partly associated with axis #1 as well, but were even more strongly correlated with axis #2. Lignin content was closest associated with the axis #3 and was explanatory for the separation of the three decay stages in the natural forest plots.

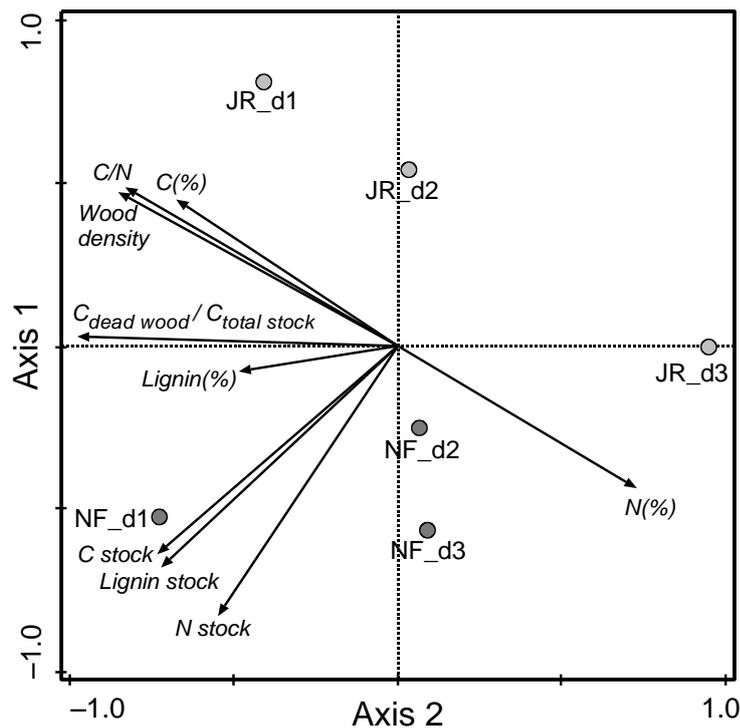


Figure 9 Principal component analysis (PCA) of C, N, and lignin concentration as well as the C, N, and lignin stocks, and the ratio of C stock in dead wood to total (live and dead above-ground C stock) of the three decay stages in the two land-use systems. 'NF' refers to the natural forest plots, 'JR' refers to the jungle rubber plots. 'd1' (decay I), 'd2' (decay II), 'd3' (decay III) specifies the three different dead wood decay stages.

Table 8 Results from PCA of C, N and lignin concentration as well as the C, N, and lignin stocks, and the ratio of C stock in dead wood to total (live and dead above-ground C stock) of the three decay stages in the two land-use systems. Given are the loadings of the selected variables along the four explanatory axes. Numbers below the axes indicate the eigenvalues of the axes. Numbers in brackets behind the loadings indicate the cumulative percentage of variance explained by the loadings. Numbers in bold mark the variables with closest correlation to the respective axis.

Variables	Axis 1 EV 0.557	Axis 2 EV 0.272	Axis 3 EV 0.150	Axis 4 EV 0.018
Chemical/anatomical properties				
C concentration	-0.678 (0.46)	0.453 (0.66)	-0.526 (0.94)	-0.244 (1.00)
N concentration	0.735 (0.54)	-0.442 (0.74)	-0.513 (0.99)	0.033 (1.00)
C/N	-0.855 (0.73)	0.476 (0.96)	0.166 (0.99)	-0.116 (1.00)
Lignin concentration	-0.492 (0.24)	-0.081 (0.25)	-0.861 (0.99)	0.105 (1.00)
Live wood density	-0.837 (0.70)	0.483 (0.93)	0.012 (0.93)	0.248 (1.00)
Chemical stand stocks				
C stock	-0.738 (0.55)	-0.646 (0.96)	0.179 (0.99)	-0.078 (1.00)
N stock	-0.550 (0.30)	-0.834 (1.00)	-0.011 (1.00)	-0.034 (1.00)
Lignin stock	-0.727 (0.53)	-0.684 (1.00)	0.058 (1.00)	0.018 (1.00)
C stock dead wood / total C stock wood	-0.983 (0.97)	0.030 (0.97)	0.084 (0.98)	0.094 (0.99)

Discussion

Conversion of natural forest to jungle rubber reduced the total biomass and volume (Figure 5a-b), as well as stocks of C, N and lignin of dead wood (Figure 5c-e). The natural forest stored three times more C and N stocks of dead wood than the jungle rubber. These differences may be associated with the living stand productivity from which dead wood originates. In the natural forest total aboveground tree biomass (AGB) was more than two times higher and aboveground net primary productivity (NPP_{wood}) was also higher than in the jungle rubber systems (Kotowska *et al.* 2015). The high AGB and NPP_{wood} in the natural forest could have one reason for the higher dead wood mass, bearing on its capacity to store stocks of C and N. The larger mean diameter and height of dead wood in this study (Table 5 and Table 6) as well as those of living trees in the aboveground structure of the natural forest provided evidence for a higher dead wood biomass (Kotowska *et al.* 2015). As a result, jungle rubber systems apparently lack large dead wood pieces which is more of a structural characteristic of natural forests.

The differences in dead wood mass and volume, as well as in C, N and lignin stocks in dead wood between natural forest and jungle rubber systems varied among decay stages of wood (Table 7). High stocks of C and N in the natural forest, i.e. in the early and advanced stages of wood decay, were also caused by high stand productivity and probably derived also from past logging residues remained in the forest. In general, the effect of disturbance history determines the amount of dead wood in an ecosystem (Gurdak *et al.* 2013; Pfeifer *et al.* 2015). As almost all primary forests were at least logged over in the Jambi province (Gouyon *et al.* 1993), it is difficult to disentangle the effects of natural

processes from human disturbance effects. In the intermediate decay stage, large residues of recent logging could be the possible cause of dead wood accumulation in the jungle rubber, therefore accounting for similar results in both systems. In the jungle rubber system human influence is much more pronounced, therefore tree mortality might increasingly occur due to the anthropogenic damage or tree logging. The abundance of fast-growing species such as *Macaranga* sp. in the jungle rubber system may also cause a high input source of dead wood (Rembolt *et al.* unpublished data). Despite this, the dead wood stocks of C and N were still higher in the natural forest.

Dead wood in the natural forest retained long-term C as well as N storage (Olajuyigbe *et al.* 2011), these stocks provide a large potential for chemical element transfer to the soil. We assumed that high lignin stocks in the natural forest served as the C stock source are expected to retain a long-term storage in this system supporting the longevity of dead wood on the forest floor. A dense canopy cover and high basal area in the natural forest are clear reasons for lower air temperature and higher air humidity than in the jungle rubber system (Kotowska *et al.* 2015). These microclimate properties in the natural forest plots represent favourable conditions for microorganism degrading dead wood (Zhou *et al.* 2007). Conversion of natural forest into jungle rubber systems may not only impact the microclimate conditions, but may likely alter also other environmental factors such as soil organic matter composition, which therefore alter the microbial and fungal community as well which in turn will influence the dead wood degradation. These findings are strongly supported by Guillaume *et al.* (2015) who reported loss of soil organic C and soil organic N in the top soil of jungle rubber at the same study sites. The reduced soil organic matters give evidence that decreased stocks of dead wood in the jungle rubber may be one of the factors leading to reduced C and N input to the soil. Therefore, high stocks of C and N from dead wood in the natural forest indirectly indicate a better soil fertility.

Dead wood mass in our study accounted for 2.7% and 2.3% of total AGB in natural forest and in jungle rubber, respectively. Comparing with similar studies from other tropical rainforests, this current finding was lower than in Peru in which dead wood accounted for 7.5–9.3% of total AGB (Baker *et al.* 2007). Pregitzer & Euskirchen (2004) reported that the mean C pool of woody debris across tropical forests amounted to 10% of the total carbon stocks. Dead wood contributed 2.3% of total aboveground C stocks in the natural forest and 1.9% of that in the jungle rubber (Kotowska *et al.* 2015). These values were five times lower compared to 33% of the C stock in Costa Rican natural forests (Clark *et al.* 2002).

Regarding the importance of dead wood in the nutrient cycle of forest ecosystems it is not only important to assess nutrient concentrations and stocks in dead wood, but to consider that nutrient release from degraded dead wood in each decay stage of dead wood is indirectly linked to microbial activities during the decay that allow the breakdown of organic compounds. In accordance with previous findings by Lombardi *et al.* (2013) and Strukelj *et al.* (2013), N concentration increased and C/N ratio decreased with the advancing stage of wood decay in our study (Figure 6a and 6b). Substrate quality and microbial activity probably enhanced N concentration in advanced decaying dead wood through (1)

N translocation from immobilized soil nutrient mediated by microorganisms i.e., fungi (Philpott *et al.* 2014), (2) increased activity of asymbiotic N-fixing bacteria (Brunner & Kimmins 2003) and (3) increased N structural binding with lignin, aromatic and phenolic compounds which were resistant to be degraded (Hishinuma *et al.* 2015). In our study, neither lignin nor C concentrations differed markedly among wood decay stages (Figure 7a and 7b), as also found by Harmon *et al.* (2013). Lignin has a complex structure of phenylpropanoid polymers that is rich in C-C bond and ether. Therefore, C is the largest constituent of lignin (63-72%) (Harmon *et al.* 2013). During decaying processes, soluble C in active organic C of dead wood is consumed for microorganism demand (Anderson & Dousch 1989), while passive C fraction is slowly decomposing because of its accumulation in persistent organic matter of lignin (Bonanomi *et al.* 2013). Similar to finding of Hishinuma *et al.* (2015), increased lignin-C content and decreased polysaccharide-C were found in advanced decay of wood in this study.

The abundance of dead wood mass and stocks of C, N and lignin were dominated by early decayed wood which might reflect a low decay process intensity of the woody debris in our plots. The influence of wood decay stages to these parameters might be affected by factors of wood mass and changes of its respective chemical concentrations. High mass in early decay stage led to high stocks of C and lignin, but not N stock (Figure 8). These were primarily related to the high dead wood mass toward high mean concentration of C and lignin. As well as in advanced decay stage, low mass of dead wood caused low stocks of C and lignin. The variability of N stocks among decay stages was mostly due to the high dead wood mass with low N concentration in the early decay of wood and in contrast to advanced stage, as also found by Guo *et al.* (2014). Diameter and length of dead wood were variable among decay stages, and thus influencing the volume value (Figure 8). Given that wood density determined the decay advances, mass estimated by measuring wood density more appropriately reflected the stage of wood decay than volume. Large amounts of nutrient retained on the forest floor in early decay stage are expected to contribute as a nutrient source for regenerating trees and decomposer biomass. Low dead wood abundance in advanced decay stage might be due to the losses of its mass and nutrients caused by degrading process by decomposers. Essentially, this indicates that nutrient stocks in dead wood are transferred to the environment.

Vegetation composition, stand productivity, substrate quality, canopy closure and microclimate were altered in jungle rubber from natural forests, as well as the two systems were separated in PCA results (Figure 9 and Table 8). Low mass of small dead wood diameter in jungle rubber cause soil decomposers rapidly colonize wood compartment (Harmon *et al.* 1986). When nutrient released faster by decomposers, the substrate quality of C, N and C/N ratio, and live wood density were primarily factors to distinguish wood decay stages. The C is effluxed by decomposer respiration as decay proceeds and N is immobilized into the biomass of decomposers and retained as structural resistance hence C/N ratio is decreased as well as wood density (Rajala *et al.* 2012). In natural forests, high stand productivity and lignin concentrations contributed to high dead wood stocks of C, N and lignin. Decomposers slowly degrade wood fractions spreading throughout large piece of dead wood (Mackensen & Bauhus 2003), while lignin concentrations is a resistant factor for decomposer activities. Thus, stored nutrient

in mass and lignin of dead wood were strongly main factors in separating wood decay in natural forests.

5 CONCLUSIONS AND SUGGESTIONS

Conclusions

The findings of this study showed that (1) total mass, C and N stocks of dead wood in natural forest were higher than those in jungle rubber, as well as found in the early and advanced wood decay stages. Transformation of natural forest into jungle rubber resulted in losses of C and N stocks, thus reduced dead wood contribution which is regarded as an important component of the ecosystem, (2) N concentrations were found to increase with advancing wood decay contrary to the C/N ratio, while C and lignin concentrations remained variable among decay stages of wood, and (3) the abundance of biomass, stocks of C and lignin of dead wood were higher in the early stage than the advanced stage of wood decay. Consequently, the current study implies that converting natural forest to jungle rubber systems not only reduces total mass of dead wood, but also decreases C and N stocks both in total and in the different stages of wood decay. As a consequence, this will affect long-term sustainability of soil nutrients. Nutrient stocks in jungle rubber will decrease in the future and this reduction will continue to increase if remaining forest vegetation is replaced with young rubber stands. We suggest allowing a proportion of dead wood amount to decay by natural process as an indirect approach to maintain soil fertility.

Suggestions

Given a basic research of dead wood in Indonesia forests, it is important to assess soil C and N concentration below fallen dead wood in different decay stages to determine the contribution of dead wood to nutrient soil. For further research, it is also crucial to determine the species identification for appropriate nutrient content affecting decay stages.

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APPENDIXES

Appendix 1 Data of total mass, volume, stocks of C, N and lignin, and chemical concentrations of C, N, C:N and lignin in dead wood

Ecosystem	N	Mass (t ha ⁻¹)	Volume (m ³ ha ⁻¹)	Stock C (t ha ⁻¹)	Stock N (t ha ⁻¹)	Stock lignin (t ha ⁻¹)	C (%)	N (%)	C:N ratio	Lignin (%)
Natural forest	HF1	11.858	34.328	5.228	0.040	1.159	43.657	0.360	130.545	9.946
	HF2	12.084	21.225	5.185	0.045	2.433	42.043	0.439	131.881	26.014
	HF3	9.832	29.311	4.265	0.048	3.847	43.593	0.468	108.307	38.640
	HF4	15.982	41.048	6.785	0.066	4.625	42.499	0.418	111.563	29.002
	BF1	5.329	13.745	2.124	0.022	2.271	41.350	0.415	99.748	42.578
	BF2	4.065	9.875	1.529	0.022	1.531	39.818	0.582	73.459	31.173
	BF3	15.165	42.678	6.656	0.062	4.911	43.405	0.435	110.000	36.477
	BF4	9.814	24.012	4.407	0.054	3.690	45.065	0.644	77.888	38.266
Jungle rubber	HJ1	3.051	5.228	1.368	0.012	1.055	44.097	0.392	112.754	32.765
	HJ2	1.702	4.425	0.752	0.007	0.774	43.938	0.439	114.415	44.510
	HJ3	4.333	8.972	1.927	0.016	0.914	43.912	0.385	126.313	20.432
	HJ4	5.890	13.887	2.718	0.029	1.839	45.957	0.521	112.329	32.304
	BJ1	1.417	4.327	0.627	0.007	0.336	44.304	0.468	130.551	23.767
	BJ2	1.823	5.483	0.746	0.010	0.559	42.237	0.504	91.361	31.374
	BJ3	5.750	11.379	2.466	0.019	1.219	43.243	0.427	126.197	19.911
	BJ4	3.058	8.706	1.298	0.014	0.780	42.620	0.584	90.648	30.391

N = number of replications

Appendix 2 Data of mass, volume, stocks of C, N and lignin, and chemical concentrations of C, N, C:N and lignin for every wood decay stages

Ecosystem	Decay stages of wood	N	Mass (t ha ⁻¹)	Volume (m ³ ha ⁻¹)	Stock C (t ha ⁻¹)	Stock N (t ha ⁻¹)	Stock lignin (t ha ⁻¹)	C (%)	N (%)	C:N ratio	Lignin (%)
Natural forest	Early decay	HF1	5.097	11.445	2.294	0.013	0.236	45.017	0.260	173.792	4.637
		HF2	8.771	16.630	3.760	0.033	1.528	42.873	0.377	120.409	17.427
		HF3	3.243	8.035	1.426	0.010	1.170	43.963	0.303	152.774	36.060
		HF4	6.358	10.361	2.746	0.019	1.852	43.180	0.307	142.748	29.120
		BF1	3.880	8.678	1.477	0.016	1.656	38.070	0.420	90.643	42.670
		BF2	2.855	5.855	1.019	0.014	1.266	35.690	0.497	72.024	44.357
		BF3	3.262	6.360	1.360	0.012	1.404	41.692	0.380	114.688	43.038
		BF4	5.523	13.818	2.426	0.030	2.488	43.933	0.540	84.035	45.053
	Intermediate decay	HF1	1.118	3.201	0.473	0.005	0.123	42.353	0.427	99.556	11.037
		HF2	2.600	2.093	1.145	0.008	0.650	44.043	0.303	201.970	25.007
		HF3	2.328	6.332	1.036	0.010	0.873	44.513	0.447	106.984	37.500
		HF4	4.350	12.243	1.916	0.016	1.316	44.043	0.367	120.434	30.263
		BF1	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
		BF2	0.711	2.271	0.308	0.004	0.064	43.270	0.610	70.934	9.070
		BF3	8.440	24.221	3.782	0.030	2.047	44.807	0.357	134.101	24.257
		BF4	3.905	8.840	1.807	0.020	1.035	46.272	0.520	97.872	26.500

Appendix 2 Data of mass, volume, stocks of C, N and lignin, and chemical concentrations of C, N, C:N and lignin for every wood decay stages (continued)

Ecosystem	Decay stages of wood	N	Mass (t ha ⁻¹)	Volume (m ³ ha ⁻¹)	Stock C (t ha ⁻¹)	Stock N (t ha ⁻¹)	Stock lignin (t ha ⁻¹)	C (%)	N (%)	C:N ratio	Lignin (%)
Jungle rubber	Advanced decay	HF1	5.643	19.682	2.460	0.022	0.799	43.600	0.393	118.286	14.163
		HF2	0.713	2.501	0.280	0.005	0.254	39.213	0.637	73.264	35.610
		HF3	4.261	14.944	1.803	0.028	1.805	42.303	0.653	65.162	42.360
		HF4	5.274	18.444	2.124	0.031	1.457	40.273	0.580	71.507	27.623
		BF1	1.449	5.067	0.647	0.006	0.616	44.630	0.410	108.854	42.485
		BF2	0.499	1.750	0.202	0.003	0.200	40.493	0.640	77.418	40.093
		BF3	3.463	12.097	1.514	0.020	1.459	43.715	0.568	81.212	42.138
		BF4	0.386	1.355	0.174	0.003	0.167	44.990	0.873	51.759	43.243
	Early decay	HJ1	2.033	2.377	0.941	0.008	0.776	46.303	0.383	120.782	38.180
		HJ2	0.671	1.115	0.313	0.002	0.367	46.573	0.300	156.271	54.720
		HJ3	2.355	2.79	1.064	0.007	0.498	45.18	0.317	147.812	21.147
		HJ4	3.073	5.097	1.433	0.012	0.876	46.637	0.390	134.388	28.500
		BJ1	0.186	0.396	0.082	0.000	0.041	43.900	0.200	219.88	21.860
		BJ2	0.477	1.081	0.213	0.002	0.121	44.547	0.373	119.492	25.310
		BJ3	2.631	5.178	1.119	0.007	0.724	42.525	0.258	179.38	27.530
		BJ4	0.505	0.979	0.209	0.002	0.158	41.34	0.427	101.294	31.327

Appendix 2 Data of mass, volume, stocks of C, N and lignin, and chemical concentrations of C, N, C:N and lignin for every wood decay stages (continued)

Ecosystem	Decay stages of wood	N	Mass (t ha ⁻¹)	Volume (m ³ ha ⁻¹)	Stock C (t ha ⁻¹)	Stock N (t ha ⁻¹)	Stock lignin (t ha ⁻¹)	C (%)	N (%)	C:N ratio	Lignin (%)
	Intermediate decay	HJ1	1.018	2.852	0.426	0.004	0.278	41.890	0.400	104.725	27.350
		HJ2	0.518	1.513	0.228	0.002	0.229	44.028	0.458	105.847	44.158
		HJ3	1.145	3.262	0.522	0.004	0.300	45.603	0.347	142.594	26.190
		HJ4	1.390	3.780	0.637	0.008	0.506	45.803	0.553	103.482	36.403
		BJ1	0.721	2.143	0.313	0.003	0.146	43.443	0.420	111.866	20.230
		BJ2	0.409	1.116	0.183	0.002	0.160	44.823	0.450	99.607	39.063
		BJ3	2.800	5.084	1.206	0.011	0.443	43.087	0.380	129.476	15.807
		BJ4	2.124	6.250	0.900	0.008	0.458	42.367	0.373	120.689	21.547
	Advanced decay	HJ1	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
		HJ2	0.512	1.797	0.211	0.003	0.178	41.213	0.560	81.126	34.653
		HJ3	0.833	2.920	0.341	0.004	0.116	40.953	0.493	88.533	13.960
		HJ4	1.428	5.010	0.649	0.009	0.457	45.433	0.620	99.116	32.010
		BJ1	0.510	1.789	0.232	0.004	0.149	45.570	0.785	59.907	29.210
		BJ2	0.937	3.286	0.350	0.006	0.279	37.340	0.690	54.984	29.750
		BJ3	0.319	1.117	0.141	0.002	0.052	44.117	0.643	69.733	16.397
		BJ4	0.429	1.477	0.189	0.004	0.164	44.153	0.953	49.960	38.300

N = number of replications

BIOGRAPHY

The author was born on Merauke 02th October 1990. The author is the 1st daughter of three siblings from Budirman and Sitti Khomariyah. The author was graduated from SMA Negeri 05 Unggulan Parepare, South Sulawesi, in 2008. In the same year, the author was accepted as undergraduated student of Biology Education Major, Faculty of Mathematics and Natural Sciences, Makassar State University then graduated in 2012. In 2013, the author was accepted as a graduate student of Plant Biology Major, Faculty of Mathematics and Natural Sciences, Bogor Agricultural University and grantee academic scholarsip from Directorate of Higher Education of Indonesia for 2013-2015.

As one of requirements to obtain the degree of Master of Science, the author conducted a research entitled Carbon and Nitrogen Stocks of Different Dead Wood Decay Stages in Natural and Converted Tropical Lowland Forests (Jambi, Indonesia). The research was supervised by Dr Dra Triadiati, MSi and Soekisman Tjitrosoedirdjo, PhD. This research article has been submitted in the journal of "*Annals of Forest Research*" on 9th February 2016.