PUBLICATION INFORMATION

Running head: Reduced net primary production in tropical peatlands

Article type: SI: Tropical Peatlands Under Siege

Title: Land cover changes reduce net primary production in tropical coastal peatlands of West Kalimantan, Indonesia

Acknowledgments

We wish to thank Randi Ade Chandra, Samsudin, and the community of Sungai Pelang village for their assistance in the field, as well as Yudi Almanggari, M. Agus Salim, Rahayu Subekti, Beni Okarda, Sigit D. Sasmito, Meli F. Saragih and Erwin Tumengkol for their advice on spatial and statistical data. We also wish to thank Flora Fauna Indonesia, the United State Agency International Development - Indonesia Forest and Climate Support (USAID - IFAC), Yayasan Palung and International Animal Rescue for their collaboration during the field research. We are grateful for the work of Dr. Iswandi Anas and Mrs. Asih Karyati of Bogor Agricultural University's Biotechnology Laboratory, who conducted the carbon analysis. This paper is based on a PhD dissertation submitted to the Department of Fisheries and Wildlife, Oregon State University. This study was made possible through funding provided by the United States Agency for International Development (USAID), and USAID's Kalimantan Wetland and Climate Change Studies.

Abstract

Tropical peat swamp forests are carbon-rich ecosystems that have been threatened by high rates of land use change (LUC). Despite the ecosystem's shifts from sequestering carbon (C) to emitting carbon, few studies have quantified the changes in ecosystem productivity associated with LUC in tropical peatlands. This study quantified net primary production (NPP) in intact peat swamp forests (PSF), logged forests (LPSF), early seral sites (ES) and smallholder oil palm plantations (OP) in a peat dome of West Kalimantan, Indonesia. All sites were dominated by peat forest prior to deforestation. The NPP of intact forests was 13.2 Mg C ha^{-1} yr^{-1} making it among the world's most productive terrestrial ecosystems, exceeding that of many tropical rainforests and similar to the most productive mangrove ecosystems (12.9 Mg C ha^{-1} yr^{-1}). Land cover change resulted in large shifts in NPP. Logged forest and early seral sites were <11.1 Mg C ha^{-1} yr^{-1}. The NPP of oil palm plantations was 3.7 Mg C ha^{-1} yr^{-1}. Aboveground NPP was recorded at 10.5 Mg C $ha^{-1}yr^{-1}$ in forests, exceeding the NPP of LPSF, ES and OP (8.9, 5.1, and 3.5 Mg C ha^{-1} yr^{-1}, respectively). Early seral sites (5.7 Mg C ha^{-1} yr^{-1}) were estimated to have the highest belowground NPP ($p = 0.05$). Root productivity in PSF, LPSF and OP was 2.7 Mg C ha^{-1} yr^{-1}, 2.1 Mg C ha^{-1} yr^{-1}, and 0.2 Mg C ha^{-1} yr^{-1}, respectively. Land use change and forest degradation have reduced the productivity of tropical peatlands.

Keywords: Land use changes, forest degradation, tropical peat swamp forests, oil palm plantation, NPP

1. Introduction

Global deforestation and land use change in forests have contributed significantly to the global greenhouse gas (GHG) emissions from terrestrial ecosystems. In Indonesia, recent estimates suggest that deforestation rates are 1,000 – 5,000 km^2 $year^{-1}$ (Hansen et al. 2013; Margono et al. 2014; BP-REDD+ 2015); the highest deforestation rates in the world. Forests, including peat swamp forests (PSF), have mostly been converted for oil palm (OP; *Elaeis guineensis*), food crops and timber plantations (Murdiyarso et al. 2010; Hergoualc'h and Verchot 2011).

Conversion of peat swamp forests involves cutting trees, burning and/or developing drainage canals (Anshari et al. 2010; Verwer and Meer 2010). The area used for oil palm, which in 2010 covered about 880,000 ha of Indonesian and Malaysian peatlands (Koh et al. 2011), has since increased to 2,046,000 ha (about 30% of Indonesia's remaining peat swamp forest area), reaching approximately 3 million ha across the region of Southeast Asia (Miettinen et al. 2016). This conversion of forests to oil palm was estimated by Koh et al. (2011) to result in losses of about 140 terra gram (Tg C = 10^{12} g C) of carbon. The current landscape in deforested areas is that of a fragmented mosaic of degraded forests, seral ecosystems and agricultural lands. Yet, only a few field studies to date have examined the impact of peat forest conversion on the ecosystem's carbon emissions in Southeast Asia (Novita 2016; Basuki 2017; Miettinen et al. 2017).

Carbon stock change from PSF degradation and land use change can be estimated using an approach which provides rates of carbon gains and losses (IPCC 2003). This approach has been used in many forested ecosystems (Golley et al. 1962; Cao and Woodward 1998; Komiyama et al. 2008). Case studies from neo-tropical forests demonstrated that carbon emissions from forest conversion are not balanced out by regrowth after land use change (Kauffman et al. 2009). Changes in net primary production in tropical peat swamp forest landscapes following LUC need to be verified through direct field measurements, to inform decision making regarding peat forests, and to increase accuracies of emission estimates.

Net primary production (NPP) is defined as the difference between gross primary production (GPP) and autotrophic respiration (Woodwell and Whittaker 1968). GPP is defined as the gross vegetation uptake of CO_2 from photosynthesis (Chapin et al. 2006). However GPP cannot be directly measured in the field (Clark and Brown 2001). As such, direct measurements of NPP have been developed in studies of carbon dynamics and the role of forests and global climate change.

Global NPP has been estimated at various values, e.g. 57.0 Pg C yr^{-1} (Cao and Woodward 1998), 0.19 Pg C yr^{-1} (Nemani et al. 2003) and – 0.06 Pg C yr^{-1} (Zhao and Running 2010). The NPP of global old growth, Malaysian lowland (dipterocarp and heath forests) and Peruvian montane tropical forests has been reported to range between 1.7 Mg C ha^{-1} yr^{-1} and 21.7 Mg C ha^{-1} yr^{-1} (Clark and Brown 2001; Girardin et al. 2010; Proctor 2013). The NPP of tropical mangrove forests has been estimated to range between 2 Mg C ha^{-1} yr^{-1} and 12 Mg C ha^{-1} yr^{-1} (Komiyama et al. 2008). Chimner and Ewel (2005) estimated that the NPP of tropical peat forest on the island of Kosrae in the Federated States of Micronesia was 11.2 Mg C ha^{-1} $year^{-1}$, of which 94.3% was aboveground NPP. The aboveground NPP (stem growth and litterfall) of degraded peat swamp forests in Central Kalimantan was estimated by Miyamoto (2016) and Saragi-Sasmito et al. (2018) as 7.9 Mg C ha^{-1} $year^{-1}$ and 7.3 Mg C ha^{-1} $year^{-1}$, respectively. The NPP of tropical peat swamp forests and other peatland ecosystems in Southeast Asia remains understudied.

1.1 Objectives and research questions

Productivity of peatlands in Indonesia and Southeast Asia has never been estimated using field measurements to record changes in NPP. To understand the role of peat swamp forest ecosystems as sources and sinks of GHG, it is crucial to determine the shifts in NPP that result from degradation of PSF into logged PSF (LPSF) and their conversion into early seral (ES) sites (i.e. sites that have previously been logged and exposed to fires eliminating the overstory tree canopy, which are now dominated by ferns and grasses) and oil palm (OP) plantations.

The objective of this study was to quantify the changes in NPP resulting from PSF disturbance through logging (LPSF), logging and fire (ES), and land conversion (OP). Our specific research questions included: How much is the NPP of intact, undisturbed peat swamp forests? How does this differ due to logging? How much is the NPP of early seral sites and oil palm plantations on sites which were previously PSF? How much are the changes in NPP caused by logging, logging and fire, and land conversion? And finally, how do these compare to the estimated NPP in other ecosystems?

Our main hypothesis was that logging and land use changes significantly alter the NPP of tropical peat swamp forests, due to the fact that such human-induced disturbances significantly reduce the ecosystem carbon stocks of forests.

2. Methods

2.1 Study site

The study area was located in Pematang Gadung, Ketapang, West Kalimantan, Indonesia (Figure 1). The Pematang Gadung is a coastal peat dome (34,651 ha) between the Pawan and Pesaguhan rivers that flow on the northern and southern ends of the peat dome, respectively. These two rivers run to the Karimata strait. Climate model of global dataset (https://id.climate-data.org/location/592593/) shows that the local rainfall averages at 2928 mm per year in the last 30 years (1982-2012), with the highest rate on December and lowest on August. The mean annual temperature is 27.3°C in the last 30 years (1982-2012). Information derived from Google Earth's Digital Elevation Model (DEM) (Rusli et al. 2016) shows that elevation in the study area ranges from 10 to 24 m above sea level.

We sampled three relatively intact peat swamp forests (PSF), and three logged peat swamp forests (LPSF) that had been selectively logged by local people. Common PSF species in the forest stands sampled included *Aglaia rubiginosa (Hirn.) Pannel*, *Dactylocladus stenostachys Oliv.*, *Dyera costulata Hook.f.*, *Palaquium spp.*, *Pandanus spp.*, and *Nepenthes spp*. They had a closed canopy height of approximately 15 m and more open canopy height approximately above 30 m, and grew near or towards the center of the peat dome and well away (>1 km) from roads. Basal area and tree density in PSF were 30.8 m^2 ha^{-1} and 1743 tree ha^{-1}, respectively. LPSF was dominated by similar tree species as PSF, but with lower maximum canopy (about 15 m), less basal area (18.7 m^2 ha^{-1}) and tree density (1282 tree ha^{-1}) than the PSF. Considering the tree canopy height and distance to the river (about 5-7 km), then both the PSF and LPSF area may belong to low pole forest zone (Page et al. 1999).

In addition to forests, we sampled three early seral (ES) sites and three smallholder oil palm (OP) plantations. ES ecosystems have no or very infrequent trees, and are dominated by ferns (e.g. *Stenochlaena palustris and Blechnum indicum*) and grasses (e.g. *Themeda triandra* and *Andropogon gerardi)* (Hoscilo 2009; Bond and Keane 2017). The OP (*Elaeis guineensis*) plantations were surrounded by ES sites and LPSF. The ES sites had been logged in the past and exposed to several fires that eliminated the overstory canopy. They were currently dominated by ferns and grasses. Based upon observation of satellite images and interviews with local people, the forests were logged approximately 25 years before sampling (in 1988). The early seral sites became as such when the logged forests first burned, approximately 19 years before sampling. The three oil palm plantations were three, four and five years old, respectively. They had been established on early seral sites, following construction of small drainage canals around their perimeters.

Insert Figure 1.

2.2 Field sampling

We quantified the ecosystem NPP of 12 different peatland sites, including three PSF sites, three LPSF sites, three ES sites, and three OP sites. We selected research sites based on field observations, discussions with local experts and analyses of Landsat images. Considerations included access to intact forests that were in relatively close proximity to other land covers, to ensure the sequential changes of land cover types (from forest to ES and OP).

2.3 Net primary production in intact and logged peat swamp forest

2.3.1 Aboveground net primary production

In this study, NPP was reported as the annual sum of tree growth and litterfall. Within each sampled site, six plots, each of a 10 m radius (circle area about 314 m^2), were established 30 m apart along a 150 m transect (adapted from Murdiyarso et al. 2009; Kauffman et al. 2016). The tree diameter at breast height (DBH) was measured for all trees in each plot, to extrapolate references for our tree diameter growth model (Figure 2).

Insert Figure 2.

In addition, a total of 120 trees (20 in each PSF and LPSF site) were randomly selected in 35 x 10 m^2 plots, located 10 m from the 150 m transect, to determine diameter growth. At each site, to quantify the NPP, tree growth was measured through the installation of tree (dendrometer) bands, 1.3 m aboveground - diameter at breast height (DBH) (Moser et al. (2014).

Diameter growth on each tree was measured for a one-year time interval, using a digital caliper with 0.01 mm precision. Based upon this data, we developed an allometric equation using linear regression, to estimate annual tree growth, based upon the tree DBH at Year 1. The model was used to predict tree DBH data at Year 2. We then applied this model using the DBH of all trees within all six plots at each site. Tree growth was then calculated, by subtracting the tree biomass from Year 1 by the predicted biomass at Year 2. The calculated tree growth was used to determine aboveground tree biomass, using allometric equations of peat swamp forests (Manuri et al. 2014). The allometric equation (Table 1) was developed in Sumatra and Borneo islands for peat swamp forest trees of 2–167 cm DBH. We used this general allometric equation as it is able to provide accurate estimates on above ground biomass of tropical peat swamp forests ($r^2 = 0.97$).

To determine litterfall, six litterfall traps were established, every 7 m apart, along the 35 m transect. With a radius of 0.27 m (an area of about 0.23 m^2), each trap was positioned a meter above ground and tied to surrounding trees. Litterfall samples were collected, two times during wet season (November and December 2015) and four times during dry seasons (September and October of 2014 and 2015). Samples were transported to the laboratory, dried at 60°C to constant mass, and then weighed. Laboratory analysis was conducted at the analytical laboratory at Bogor Agricultural University, Bogor, Indonesia, where C content was determined using the dry combustion method (induction furnace) with a LECO Analyzer. Branch fall production was estimated as 9.89% of the litterfall annual production (Chimner and Ewel 2005).

Insert Table 1.

2.3.2 Belowground net primary production

Coarse root production of all the forests trees was estimated using an allometric equation derived from analyses of root : shoot ratio in terrestrial biomass (Table 1; Mokany et al. 2006). Fine root production was estimated as 12% of the sum of tree, coarse root and litterfall annual production (Chimner and Ewel 2005).

Annual NPP of forest trees (in PSF and LPSF) was calculated by summing the aboveground and belowground NPP. This calculation captured the annual production associated with tree growth, coarse and fine root growth, and litter and branch fall production.

2.3.3 Oil palm plantations

Six 10 m radius plots of 150 m transect were established, in a similar manner to those in the intact and logged forests. The height of the apical meristem (the base of their young leaves; Figure 3) of all oil palm trees was measured at all OP sites. The height was re-measured two years later. The annual height growth of oil palm trees was calculated by subtracting the initial tree height from the tree height at Year 2, then dividing by two. Annual biomass growth for OP trees was estimated by applying the annual height growth into an allometric equation (Table 1; Dewi et al. 2010). The equation was developed in Sumatera and Kalimantan islands and used for oil palm trees < 1 – to 8 m in height on peatlands (Dewi et al. 2010).

Insert Figure 3.

Pruned frond biomass was estimated as 75.3% of frond production, that is 68.8% of the tree biomass growth (Henson and Dolmat 2003). Dead root biomass was estimated as 71.7% of root production, that is 14.2% of the tree biomass growth (Henson and Dolmat 2003).

Annual NPP of OP sites was quantified by summing tree production with the dead root and pruned frond (litter) production. As we began the study, the oil palm plantations were two and three years old, with no or very limited fruit production. As such, we did not quantify the contribution of fruit to the total NPP.

2.3.4 Early seral sites

The transect and plot design for fern and grass dominated ES sites differed from those designed for forests and oil palm plantations. In each of the three ES sites, six 1 m^2 plots of 35 m transect were established, at 7 m intervals (Figure 4). All aboveground standing herbaceous biomass and litterfall was harvested in 1 m^2 plots at the six locations on each site. These ES plots were burned in September 2014, unnaturally, which enabled us to estimate annual aboveground NPP of ES in September 2015. Standing mass and litterfall were sampled using destructive sampling. Samples were collected and weighed in the field, sub-sampled, transported to the laboratory, dried at 60°C to constant mass, and then weighed. Laboratory analyses were conducted at the analytical laboratory, where the concentration of C was determined with a LECO Analyzer.

Insert Figure 4.

Root annual production was estimated as 110% of total leaf and litterfall production/aboveground NPP (Scurlock and Olson 2012). This value was derived from a long global monitoring study (1939-1996); the value had been selected to cover only tropical grassland ecosystems. Although it may not be the best reference ecosystem for our ES sites, we believe it to be the closest available ecosystem that we can use to estimate the root production rate of grass- and fern-dominated ES ecosystems.

Biomass was converted to C using a conversion factor of 0.47 (Murdiyarso et al. 2009). Potential C emissions from a reduction in NPP, due to the impact of LUC, were reported as potential CO_2 emissions (C-CO_2) - calculated by multiplying C values by 3.67, the molecular ratio of CO_2 to C.

2.4 Statistical analyses

The normality of primary production data among the different land cover types was verified using Saphiro-Wilks and Kolmogorov-Smirnov tests. For normally distributed data, differences in mean site NPP within the same land cover were verified using a t-test; whereas a Mann-Whitney U test was performed when data were not normally distributed. Differences in NPP among land cover types were tested with analysis of variance (ANOVA), when the data were normally distributed. If the ANOVA was significant, a least significant difference (LSD) test was performed, to determine which means were significantly different. Kruskal-Wallis' H test was used for abnormally distributed data. Linear regression analysis was used to model the growth of forest trees, using diameter at breast height (DBH) data (Manuri et al. 2014). Statistical analysis was conducted using IBM SPSS software version 20 (IBM Corp. Release 2011).

3. Results

3.1 Net primary production in intact and logged peat swamp forests

We obtained data from 118 of the 120 dendrometer bands that were installed in the forests. We lost two tree bands due to logging. The initial mean diameter of measured trees in the 10 x 35 m^2 plots was 10.8 cm in PSF and 10.5 cm in LPSF. This values were similar to the initial mean diameter of measured trees in the 314 m^2 area of circle forest plots (10 m in radius; Figure 2) was 12.0 cm in PSF and 10.9 cm in LPSF.

The linear regression model using DBH at Year 1 to predict annual growth (r^2=0.98), was used to estimate the incremental growth of all trees in the 10 m radius plot (314 m^2 area) of forest plots (Figure 5).

Insert Figure 5.

Tree diameter growth was similar between PSF and LPSF, both averaging at 0.21 cm yr^{-1} (Table 2). On bigger trees (DBH > 5 cm), aboveground (wood and leaves) biomass production in LPSF (3.2 Mg C ha^{-1} yr^{-1}) was significantly lower than in PSF (4.6 Mg C $ha^{-1}yr^{-1}$; Mann-Whitney U test, $p < 0.05$). Due to higher basal area, tree density and bigger tree size in PSF than those in LPSF, though the annual tree growth was similar between the two, the resulted AGB production in PSF was higher. Belowground (coarse root) biomass production in LPSF (0.7 Mg C $ha^{-1}yr^{-1}$) was significantly lower than in PSF (1 Mg C $ha^{-1}yr^{-1}$; $p < 0.05$). Both in PSF and LPSF, aboveground biomass production (4.6 Mg C $ha^{-1}yr^{-1}$ and 3.2 Mg C $ha^{-1}yr^{-1}$, respectively) was significantly higher than the belowground biomass (1 Mg C $ha^{-1}yr^{-1}$ and 0.7 Mg C $ha^{-1}yr^{-1}$, respectively; Mann-Whitney U test, $p < 0.05$).

Insert Table 2.

Similar to the larger sized trees, small trees (DBH < 5 cm) in LPSF produced significantly less aboveground and belowground biomass than those in PSF (Mann-Whitney U test, $p < 0.05$). In logged forest, productivity of both aboveground and belowground biomass in LPSF was lower, by 0.3 Mg C $ha^{-1}yr^{-1}$ and 0.1 Mg C ha^{-1}yr^{-1}, respectively (Table 3). Aboveground biomass production was higher than belowground production in both PSF and LPSF by 0.4 Mg C ha^{-1}yr^{-1} and 0.2 Mg C ha^{-1}yr^{-1}, respectively (Mann-Whitney U test, $p = 0.043$).

Insert Table 3.

Annual production of litterfall did not differ between LPSF and PSF (5.2 Mg C ha^{-1}yr^{-1}; t-test, $p = 0.9$; Table 4). Litterfall production in PSF and LPSF during dry months (August – October; 2.5 and 2.6 Mg C ha^{-1}yr^{-1}, respectively) and wet months (November – July; 2.7 and 2.7 Mg C ha^{-1}yr^{-1}) was also similar in both forest ecosystems (t-test, $p = 0.7$). Despite both tree density and basal area between PSF (1743 and 31) and LPSF (1282 and 19) being different, the similarity in litterfall production conformed with the previous report (Averti and Dominique 2011).

Insert Table 4

Fine root production in PSF was 0.2 Mg C ha^{-1}yr^{-1} higher than in LPSF (t-test, $p = 0.15$; Table 5). As fine root production was estimated as 12% of the sum of tree, coarse root and litterfall annual production, thus significantly higher production of aboveground and belowground biomass in PSF than in LPSF has resulted in this higher fine root production of PSF.

Insert Table 5.

Overall, total plant productivity in LPSF was 7.9 Mg C-CO_2 ha^{-1}yr^{-1} lower than in PSF. In PSF, aboveground biomass accounted for 40% and litterfall accounted for 39% of total production. In contrast, aboveground biomass in LPSF accounted for 33% and litterfall accounted for 47% of total production.

3.2 Net primary production in early seral sites

In the early seral ecosystem, the average carbon content in root, leaves and litterfall was similar at 45.6%, 44.4% and 46.3% respectively. Total biomass production was 10.8 ± 1.3 Mg C $ha^{-1}yr^{-1}$ (Table 6). Of this, belowground biomass (root), litter and aboveground biomass (leaves) accounted for 53%, 17% and 30%, respectively. Belowground biomass was higher than litter mass and aboveground biomass (LSD test, $p < 0.05$, respectively). Belowground biomass sources dominated the NPP in the ES ecosystem.

Insert Table 6.

3.3 Net primary production in oil palm plantations

Total annual NPP in oil palm plantations was 3.7 Mg C $ha^{-1}yr^{-1}$ (Table 7). Belowground biomass (root), litter/necromass (pruned fronds) and aboveground biomass (tree) contributed 6%, 32% and 62% of the NPP, respectively. Roots were significantly lower in production than the fronds (Mann-Whitney U test, p-value = 0.02) and aboveground growth (Mann-Whitney U test, p-value = 0.03). Aboveground biomass production sources dominated NPP in the OP ecosystem.

Insert Table 7.

3.4 Net primary production among peatland ecosystems

PSF has the greatest aboveground biomass production (Mann-Whitney U test, $p = 0.05$). Aboveground biomass production was measured at 5.3 Mg C $ha^{-1}yr^{-1}$ in the intact forests. Aboveground NPP for LPSF, ES and OP was 3.7 Mg C $ha^{-1}yr^{-1}$, 3.3 Mg C $ha^{-1}yr^{-1}$, and 2.3 Mg C $ha^{-1}yr^{-1}$, respectively (Figure 6).

Among all land cover types, ES (5.7 Mg C $ha^{-1}yr^{-1}$) was estimated to have the greatest belowground biomass production (Mann-Whitney U test, $p = 0.05$). In contrast, OP showed the lowest (0.2 Mg C ha^{-1} yr^{-1}). Moderate belowground NPP was shown in forest sites, i.e. PSF (2.7 Mg C ha^{-1} yr^{-1}) and LPSF (2.1 Mg C ha^{-1} yr^{-1}).

Litterfall production rates in PSF and LPSF were similar (5.2 Mg C $ha^{-1}yr^{-1}$). This production was higher than in ES (1.8 Mg C $ha^{-1}yr^{-1}$) and OP (1.2 Mg C $ha^{-1}yr^{-1}$; Mann-Whitney U test, $p = 0.05$).

The total NPP of intact peat forests was significantly greater than any other cover type (Mann-Whitney U test, p-value = 0.05; 13.2 Mg C $ha^{-1}yr^{-1}$). The ecosystem NPP of LPSF was 11.1 Mg C $ha^{-1}yr^{-1}$, compared to 10.8 Mg C $ha^{-1}yr^{-1}$ for ES, and 3.7 Mg C $ha^{-1}yr^{-1}$ for OP.

Insert Figure 6.

4. Discussion

4.1 How land use change alters net primary production in tropical peatland ecosystems

Loss of trees from logging and land clearing has resulted in significant decreases of primary production in degraded peat landscapes. The NPP of intact forests exceeded that of other peatland ecosystems by more than 2.2 Mg C $ha^{-1}yr^{-1}$. Logged peat forests, early seral sites and oil palm plantations were significantly lower in NPP than intact peat forests (Table 5 - 7). The NPP of PSF was higher than LPSF because the PSF has higher tree density, basal area and bigger trees that leads to higher annual production of wood, leaves and roots than those in LPSF.

In the early seral sites dominated by grasses and ferns, productivity (10.8 Mg C $ha^{-1}yr^{-1}$) was similar to that of the logged peat forest. Belowground NPP in these early seral sites accounted for 53% of the total (5.7 Mg C $ha^{-1}yr^{-1}$; Table 6), which was the highest of all sampled sites. As we assumed that our early seral sites are comparable to a global dataset selected to cover only the tropical grassland ecosystem, they may typically have high turnover rates of aboveground and belowground biomass (Long et al. 1989). Because we did not directly measure belowground NPP, the high value in ES sites could also be due to methodology differences.

The estimated NPP of early seral sites in this study was higher than grassland ecosystems studies in Thailand (Kamnalrut 2015) and the Ivory Coast (Menaut et al. 1979). As our sites had burned just a year before sampling, the NPP may become higher in coming years (without further fire occurrence), because burning provides ash as additional nutrients for the regrowth. A study show that NPP of forest will linearly increase for 15 years after a fire occurrence, only reaching a steady state after at least 20 years (Amiro et al. 2000).

Oil palm plantations had the lowest NPP. Productivity of aboveground and belowground biomass, as well as litterfall was lowest in plantations (Table 6 and 7). This demonstrates that peatland is not the best choice of site to grow oil palm (Basuki and Sheil 2005; Lamade and Bouillet 2005; Wijedasa et al. 2016) and limits the ability of smallholder farmers to increase their oil palm production. In more established, intensive-managed oil palm plantations, NPP may be significantly higher; it has been suggested that a five-year-old oil palm plantation, with intensive management, can produce about 5.4 Mg C ha^{-1} yr^{-1} (Melling et al. 2008).

Tropical climates with adequate sunlight, temperatures and moisture availability throughout the year facilitate high productivity rates in lowland tropical forest (Chapin et al. 2011); NPP of this study was recorded as twice that of temperate forests in the Pacific Northwest, USA (13.2 vs. 6.5 Mg C $ha^{-1}yr^{-1}$; Waring et al. 2013). The NPP of the intact peat forest measured in this study (13.2 Mg C $ha^{-1}yr^{-1}$) was also higher than that reported in tropical forests in Brazil and Malaysia, (10.1 and 5.5 Mg C $ha^{-1}yr^{-1}$; Malhi 2012; Proctor 2013) and tropical mangrove forests (9.8 Mg C $ha^{-1}yr^{-1}$; Menaut et al. 1979). However, it was similar to that reported in Indonesian mangrove ecosystems (12.9 Mg C $ha^{-1}yr^{-1}$; Arifanti 2017) and lower than that reported in Amazonian tropical forests (16.9 Mg C $ha^{-1}yr^{-1}$; Girardin et al. 2010; Malhi 2012).

It is important to identify the factors that result in higher rates of NPP in tropical peat forests, especially since our result was derived during dry years due to the El Niño Southern Oscillation (ENSO). Long droughts have been reported to reduce litterfall productivity by up to 23% (Brando et al. 2008). The high carbon use efficiency (CUE; ratio between NPP and GPP) of peat forests likely contribute to their higher productivity compared with other tropical ecosystems, as also found in a freshwater marsh of California (Rocha and Goulden, 2009). Comparing our PSF's NPP (13.2 Mg C $ha^{-1}yr^{-1}$) to the GPP value (33 Mg C $ha^{-1}yr^{-1}$) of other PSF in central Kalimantan (Hirano et al. 2007) resulted in CUE value of 0.40, which is on the top range of few tropical forest sites in Asia and Amazonia that have reported CUE values (Malhi 2012). Our study suggests that tropical peat forests are among the most productive ecosystems, in term of primary productivity (Figure 7).

The NPP in the oil palm plantations studied (3.7 Mg C $ha^{-1}yr^{-1}$) was about a fifth of that observed in a review of oil palm production on mineral soils by Lamade and Bouillet (2005), and a third of that reported by Melling et al. (2008). This difference may be due to differences in sites and methods used in these studies. It may also be due to the low intensity of management and the young oil palms (1-5 years) studied in our smallholder plantation sites, the limited nutrient availability, saturated condition, and very porous material in peatland soils (Page et al. 2011). The fact that the smallholder OP plantations were located on drained peat, without proper water management, may also have resulted in the low NPP observed in our sites.

Insert Figure 7.

4.2 Implications for tropical peatland management

Tropical peat swamp forests show high annual productivity rates. Degradation and conversion (land use changes) of peat swamp forests significantly reduced their productivity. There are four times more degraded peat forests in Indonesia and Malaysia than there are intact forests (Miettinen et al. 2016). Likewise, intact peat swamp forest accounts for less than 7% of all peatland area in Indonesia's main islands, Sumatera and Kalimantan (Miettinen et al. 2016).

In 2015, there were more than three million hectares of oil palm plantations, and almost one million hectares of degraded grasslands/early seral (ES) sites formed from previous peat forests in Southeast Asia (Miettinen et al. 2016). Oil palm's NPP (13.6 Mg C-CO_2 $ha^{-1}yr^{-1}$; Table 7) is much lower than that of intact forest (48.5 Mg C-CO_2 $ha^{-1}yr^{-1}$; Table 5). As such, the 3 million ha of oil palm equates to a potential loss of CO_2 uptake from the atmosphere, as much as 105 Tg C-CO_2 yr^{-1}, at least for the first 5 years after planting. On the other hand, our results on early seral site NPP (39.6 Mg C-CO_2 $ha^{-1}yr^{-1}$) suggest that allowing grasses and ferns to regrow (secondary succession) begins to reverse the decline in NPP apparent due to land use change.

A million hectares of early seral sites on peatlands in Southeast Asia could absorb atmospheric carbon, especially if allowed to regrow and recover into forest. However, this ecosystem is currently largely unmanaged, and may be the most fire prone cover type of the region (Page et al. 2009; Blackham et al. 2014). Recurrent fires on this cover type may limit early seral sites' potential to absorb carbon. This is clear if we look at the loss of carbon stocks from conversion of peat forest into early seral ecosystems, which totaled 125 Mg CO_2 ha^{-1} yr^{-1} (Basuki 2017).

5. Conclusion

Intact tropical peat swamp forests are among the most productive of all terrestrial ecosystems, with an NPP exceeding that of many tropical rainforests, and similar to that of the most productive mangrove ecosystems. However, land use changes have significantly decreased the productivity of tropical peatland ecosystems. Peatland conservation, including protection from land conversion, and restoration, is urgently needed to prevent further loss of carbon stocks.

References

Amiro BD, Chen JM, Liu J (2000) Net primary productivity following forest fire for Canadian ecoregions. Can J For Researh 30:939–947. doi: 10.1139/cjfr-30-6-939

Anshari GZ, Afifudin M, Nuriman M, et al (2010) Drainage and land use impacts on changes in selected peat properties and peat degradation in West Kalimantan Province, Indonesia. Biogeosciences 7:3403–3419. doi: 10.5194/bg-7-3403-2010

Arifanti VB (2017) Influences of land use on carbon cycles in mangrove ecosystems of the Mahakam delta, East Kalimantan, Indonesia. Dissertation, Oregon State University

Averti I, Dominique N (2011) Litterfall , Accumulation and Decomposition in Forest Groves Established on Savannah in the Plateau Teke , Central Africa. J Environ Sci Technol. doi: 10.3923/jest.2011.601.610

Basuki I (2017) Carbon dynamics in response to land cover change in tropical peatlands, Kalimantan, Indonesia. Oregon State University

Basuki I, Sheil D (2005) Local Perspectives of Forest Landscapes: A Preliminary Evaluation of Land and Soils, and their Importance in Malinau. CIFOR, Bogor

Blackham G V, Webb EL, Corlett RT (2014) Natural regeneration in a degraded tropical peatland, Central Kalimantan, Indonesia: Implications for forest restoration. For Ecol Manage 324:8–15. doi: 10.1016/j.foreco.2014.03.041

Bond WJ, Keane RE (2017) Fires , Ecological Effects of. Ref Modul Life Sci 1–11. doi: 10.1016/B978-0-12-809633-8.02098-7

BP-REDD+ (2015) National Forest Reference Emission Level for Deforestation and Forest Degradation in the Context of the Activities Referred to in Decision 1 / CP . 16 , Paragraph 70 (REDD +) Under the UNFCCC : A Reference for Decision Makers

Brando PM, Nepstad DC, Davidson EA, et al (2008) Drought effects on litterfall , wood production and belowground carbon cycling in an Amazon forest : results of a throughfall reduction experiment. 1839–1848. doi: 10.1098/rstb.2007.0031

Cao M, Woodward F (1998) Net primary and ecosystem production and carbon stocks of terrestrial ecosystems and their responses to climate change. Glob Chang Biol 4:185–198

Chapin FS, Woodwell GM, Randerson JT, et al (2006) Reconciling carbon-cycle concepts, terminology, and methods. Ecosystems 9:1041–1050. doi: 10.1007/s10021-005-0105-7

Chapin FSI, Matson PA, Vitousek PM (2011) Principles of Terrestrial Ecosystem Ecology, 2nd edn. Springer, New York

Chimner RA, Ewel KC (2005) A tropical freshwater wetland: II. Production, decomposition, and peat formation. Wetl Ecol Manag 13:671–684. doi: 10.1007/s11273-005-0965-9

Clark DA, Brown S (2001) Net primary production in tropical forests: an evaluation and synthesis of existing field data. Ecol Appl 11:371–384

Dewi S, Khasanah N, Rahayu S, et al (2010) Carbon Footprint of Indonesian Palm Oil Production : I . a Pilot Study. http://www.worldagroforestry.org/sea/Publications/files/poster/PO0236-10.PDF

Girardin CAJ, Malhi Y, Aragão LEOC, et al (2010) Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. Glob Chang Biol 16:3176–3192. doi: 10.1111/j.1365-2486.2010.02235.x

Golley F, Odum HT., Wilson RF. (1962) The Structure and Metabolism of a Puerto Rican Red Mangrove Forest in May. Ecology 43:9–19

Hansen MC, Potapov P V, Moore R, et al (2013) High-resolution global maps of 21st-century forest cover change. Science 134:2011–2014

Henson IE, Dolmat MT (2003) Physiological analysis of an oil palm density trial on a peat soil. J Oil Palm Res 15:1–27

Hergoualc'h K, Verchot L V (2011) Stocks and fluxes of carbon associated with land use change in Southeast Asian tropical peatlands: A review. Global Biogeochem Cycles 25:1–13. doi: Gb2001 10.1029/2009gb003718

Hirano T, Segah H, Harada T, et al (2007) Carbon dioxide balance of a tropical peat swamp forest in Kalimantan, Indonesia. Glob Chang Biol 13:412–425. doi: 10.1111/j.1365-2486.2006.01301.x

Hoscilo A (2009) FIRE REGIME, VEGETATION DYNAMICS AND LAND COVER CHANGE IN TROPICAL PEATLAND, INDONESIA. University of Leicester

IBM Corp. Release (2011) IBM SPSS Statistics for Windows, Version 20.0. Armonk, NY: IBM Corp. IBM Corp., Armonk, NY

IPCC (2003) Good Practice Guidance for Land Use, Land-Use Change and Forestry. Institute for Global

Environmental Strategies (IGES) for the IPCC, Hayama, Kanagawa

Kamnalrut A (2015) NPP Grassland : Klong Hoi Khong , Thailand , 1984-1990 , R1. Data set. http://dx.doi.org/10.3334/ORNLDAAC/147

Kauffman JB, Arifanti VB, Basuki I, et al (2016) Protocols for the measurement, monitoring, and reporting of structure, biomass, carbon stocks and greenhouse gas emissions in tropical peat swamp forests. CIFOR, Bogor

Kauffman JB, Donato DC (2012) Protocols for the measurement, monitoring and reporting of structure, biomass and carbon stocks in mangrove forests. CIFOR, Bogor

Kauffman JB, Hughes RF, Heider C (2009) Carbon pool and biomass dynamics associated with deforestation, land use, and agricultural abandonment in the neotropics. Ecol Appl 19:1211–1222. doi: 10.1890/08-1696.1

Koh LP, Miettinen J, Liew SC, Ghazoul J (2011) Remotely sensed evidence of tropical peatland conversion to oil palm. Proc Natl Acad Sci U S A 108:5127–32. doi: 10.1073/pnas.1018776108

Komiyama A, Ong JE, Poungparn S (2008) Allometry, biomass, and productivity of mangrove forests: A review. Aquat Bot 89:128–137. doi: 10.1016/j.aquabot.2007.12.006

Lamade E, Bouillet J (2005) Carbon storage and global change: the role of oil palm. Oléagineux, corps gras, lipides 7:154–160

Long SP, Garcia Moya E, Imbamba SK, et al (1989) Primary productivity of natural grass ecosystems of the tropics: A reappraisal. Plant Soil 115:155–166. doi: 10.1007/BF02202584

Malhi Y (2012a) The productivity, metabolism and carbon cycle of tropical forest vegetation. J Ecol 100:65–75. doi: 10.1111/j.1365-2745.2011.01916.x

Malhi Y (2012b) The productivity, metabolism and carbon cycle of tropical forest vegetation. J Ecol 100:65–75. doi: 10.1111/j.1365-2745.2011.01916.x

Manuri S, Brack C, Nugroho NP, et al (2014) Tree biomass equations for tropical peat swamp forest ecosystems in Indonesia. For Ecol Manage 334:241–253. doi: 10.1016/j.foreco.2014.08.031

Margono BA, Potapov P V, Turubanova S, et al (2014) Primary forest cover loss in Indonesia over 2000–2012. Nat Clim Chang 4:1–6. doi: 10.1038/NCLIMATE2277

Melling, L., Kah Joo Goh, Beauvais, C., Hatano R (2008) Carbon Flow and Budget in a Young Mature Oil Palm Agroecosystem on Deep Tropical Peat. Plant 84:21–25

Menaut JC, Cesar J, Suiperieure EN (1979) Structure and Primary Productivity of Lamto Savannas, Ivory Coast.

Ecology 60:1197–1210

Miettinen J, Shi C, Liew SC (2016) Land cover distribution in the peatlands of Peninsular Malaysia, Sumatra and Borneo in 2015 with changes since 1990. Glob Ecol Conserv 6:67–78. doi: 10.1016/j.gecco.2016.02.004

Miettinen J, Hooijer A, Vernimmen R., Liew SC, Page SE (2017) From carbon sink to carbon source: extensive peat oxidation in insular Southeast Asia since 1990. Environmental Research Letters, 12(2), 024014. doi: 10.1088/1748-9326/aa5b6f

Miyamoto K, Kohyama TS, Rahajoe JS et al (2016) Forest structure and productivity of tropical heath and peatland forests. In: Miyamoto K, Noboyuki T (eds) Tropical Peatland Ecosystems, Springer, pp. 151-166

Mokany K, Raison R, Prokushkin A (2006) Critical analysis of root: shoot ratios in terrestrial biomes. Glob Chang Biol 12:84–96

Moser G, Schuldt B, Hertel D, et al (2014) Replicated throughfall exclusion experiment in an Indonesian perhumid rainforest: Wood production, litter fall and fine root growth under simulated drought. Glob Chang Biol 20:1481–1497. doi: 10.1111/gcb.12424

Murdiyarso D, Donato D, Kauffman JB, et al (2009) Carbon storage in mangrove and peatland ecosystems. A preliminary account from plots in Indonesia. CIFOR, Bogor

Murdiyarso D, Hergoualc'h K, Verchot L V (2010) Opportunities for reducing greenhouse gas emissions in tropical peatlands. Proc Natl Acad Sci U S A 107:19655–60. doi: 10.1073/pnas.0911966107

Novita N (2016) Carbon Stocks and Soil Greenhouse Gas Emissions Associated with Forest Conversion to Oil Palm Plantations in Tanjung Puting Tropical Peatlands, Indonesia. Oregon State University

Page S, Hoscilo A, Wösten H, et al (2009) Restoration ecology of lowland tropical peatlands in Southeast Asia: Current knowledge and future research directions. Ecosystems 12:888–905. doi: 10.1007/s10021-008-9216-2

Page SE, Morrison R, Malins C, et al (2011) Review of Peat Surface Greenhouse Gas Emissions From Oil Palm Plantations in Southeast Asia. International Council on Clean Transportation, Washington DC

Page SE, Rieley JO, Shotyk W, Weiss D (1999) Interdependence of peat and vegetation in a tropical peat swamp forest. Philos Trans R Soc Lond B Biol Sci 354:1885–1897. doi: 10.1098/rstb.1999.0529

Proctor J (2013) NPP Tropical Forest: Gunung Mulu, Malaysia, 1977-1978, R1. Data set. Oak Ridge Natl Lab Distrib Act Arch Center, Oak Ridge, Tennessee, USA. doi: 10.3334/ORNLDAAC/474

Ritung S, Wahyunto, Nugroho K, Sukarman, Hikmatullah, Suparto, Tafakresnanto C (2011) Peta Lahan Gambut

Indonesia. Balai Besar Penelitian dan Pengembangan Sumberdaya Lahan Pertanian (Ministry of Agriculture), Indonesia

Rocha A V, Goulden ML (2009) Why is marsh productivity so high? New insights from eddy covariance and biomass measurements in a Typha marsh. Agric For Meteorol 149:159–168. doi: 10.1016/j.agrformet.2008.07.010

Rusli N, Majid MR, Din AHM (2016) A comparative accuracy of Google Earth height with MyGeoid, EGM96 and MSL. In: IOP Conference Series: Earth and Environmental Science. IOP Conference Series, pp 1–6

Saragi-Sasmito M F, Murdiyarso D, June T, Sasmito SD (2018). Carbon stocks, emissions, and aboveground productivity in restored secondary tropical peat swamp forests. *Mitigation and Adaptation Strategies for Global Change*, 1-13.

Scurlock J, Olson R (2012) NPP Multi-Biome: Grassland, Boreal Forest, and Tropical Forest Sites, 1939-1996, R[evision] 1. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A. doi:10.333

Verwer C, Meer P Van Der (2010) Carbon pools in tropical peat forest - Towards a reference value for forest biomass carbon in relatively undisturbed peat swamp forests in Southeast Asia. Alterra Wageningen, UR, Wageningen

Waring RH, Law B, Bond B (2013) NPP Temperate Forest : OTTER Project Sites , Oregon , USA , 1989-1991 , R1. Data set. http://daac.ornl.gov

Wijedasa LS, Jauhiainen J, Könönen M, et al (2016) Denial of long-term issues with agriculture on tropical peatlands will have devastating consequences. Glob Chang Biol. doi: 10.1111/gcb.13516

Zhao M, Running S (2010) Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. Science (80-) 329:940

Figure legends

Figure 1 Site locations within the study area, Pematang Gadung peat dome, Ketapang, West Kalimantan, Indonesia. Peat dome area (dark green) was delineated by Ritung et al. (2011), represents deeper (>3 m peat depth) peatlands in between Pawan and Pesaguhan rivers. White symbols represent the sample sites. Black line represents road. White areas represent the sea (Karimata Straits), light green areas represent the shallower peatland areas or outside the Pematang Gadung peat dome. Grey areas represent the non-peat areas. PSF represents intact peat forests, LPSF means logged forests, OP means oil palm plantation and ES means early seral sites.

Figure 2 (a) 150 m transect and plot design to measure all tree diameter (DBH), and (b) 35 x 10 m plot design to collect litterfall and measure diameter growth of 20 trees in intact (PSF) and logged peat forests (LPSF).

Figure 3 150 m transect and plot design to measure tree height in oil palm (OP) plantation.

Figure 4 35 m transect and plot design to collect standing biomass and litterfall in early seral (ES) sites. Standing herbaceous biomass and litterfall were collected in 1 m^2 area (all plots).

Figure 5 Linear regression model between tree diameter measured in Year 1 and Year 2. A total of 118 trees were used in the analyses.

Figure 6 Productivity of belowground and aboveground biomass, litterfall and NPP in intact and logged peat forest, early seral sites (ES) and oil palm plantations (OP). Production of biomass and litterfall, and NPP reported as mean value. Error bars show ± standard error (SE) of the production. Lower case letters represent statistical significance in productivity. PSF represents intact peat forests and LPSF means logged forests.

Figure 7 NPP among terrestrial ecosystems. Data for temperate forests are from Waring et al. (2013). Tropical and temperate forest data comes from Clark and Brown (2001); Girardin et al. (2010); and Proctor (2013). Mangrove data comes from Golley et al. (1962), Komiyama et al. (2008) and Arifanti (2017). Grassland data comes from Menaut et al. (1979) and Kamnalrut (2015). Tropical peat forest data comes from Chimner and Ewel (2005) and this study (outlined with bold black).

Table legends

Table 1 Equations used to determine biomass and carbon gain in peat forests, early seral sites and oil palm plantations.

Table 2 Annual growth of tree DBH and production of aboveground biomass (AGB) and belowground biomass (BGB) in intact and logged peat swamp forest (tree DBH > 5 cm). PSF represents intact peat swamp forests and LPSF means logged peat swamp forests.

Table 3 Annual growth of tree DBH and production of aboveground biomass (AGB) and belowground biomass (BGB) in intact and logged peat swamp forest (tree DBH < 5 cm). PSF represents intact peat swamp forests and LPSF means logged peat swamp forests.

Table 4 Litterfall (Mg C $ha^{-1}yr^{-1}$) in intact and logged peat forest. Biomass production of litterfall during dry and wet months (August to October, and November to July, respectively), and annually reported as mean ± SE. PSF represents intact peat forests and LPSF means logged forests.

Table 5 Productivity of aboveground biomass (AGB), litterfall, belowground biomass (BGB; fine and coarse root) and net primary production (NPP) in intact peat swamp forests (PSF) and logged peat swamp forests (LPSF). Potential sequestered carbon through biomass production reported as mean ± SE, or otherwise as mean only. Annual sequestered C-CO_2 presented in the NPP[1] column.

Table 6 Productivity of aboveground biomass (AGB), litterfall, belowground biomass (BGB) and net primary production (NPP) in early seral (ES) ecosystems. Annual sequestered C-CO_2 presented in the NPP[1] column.

Table 7 Productivity of aboveground biomass (AGB), litterfall, belowground biomass (BGB) and NPP of oil palm (OP) plantations. Annual sequestered C-CO_2 presented in the NPP[1] column.

Authors:

Imam Basuki[1,2,3*], J. B. Kauffman[1], James Peterson[1], Gusti Anshari[4] and Daniel Murdiyarso[2,5]

Affiliations:

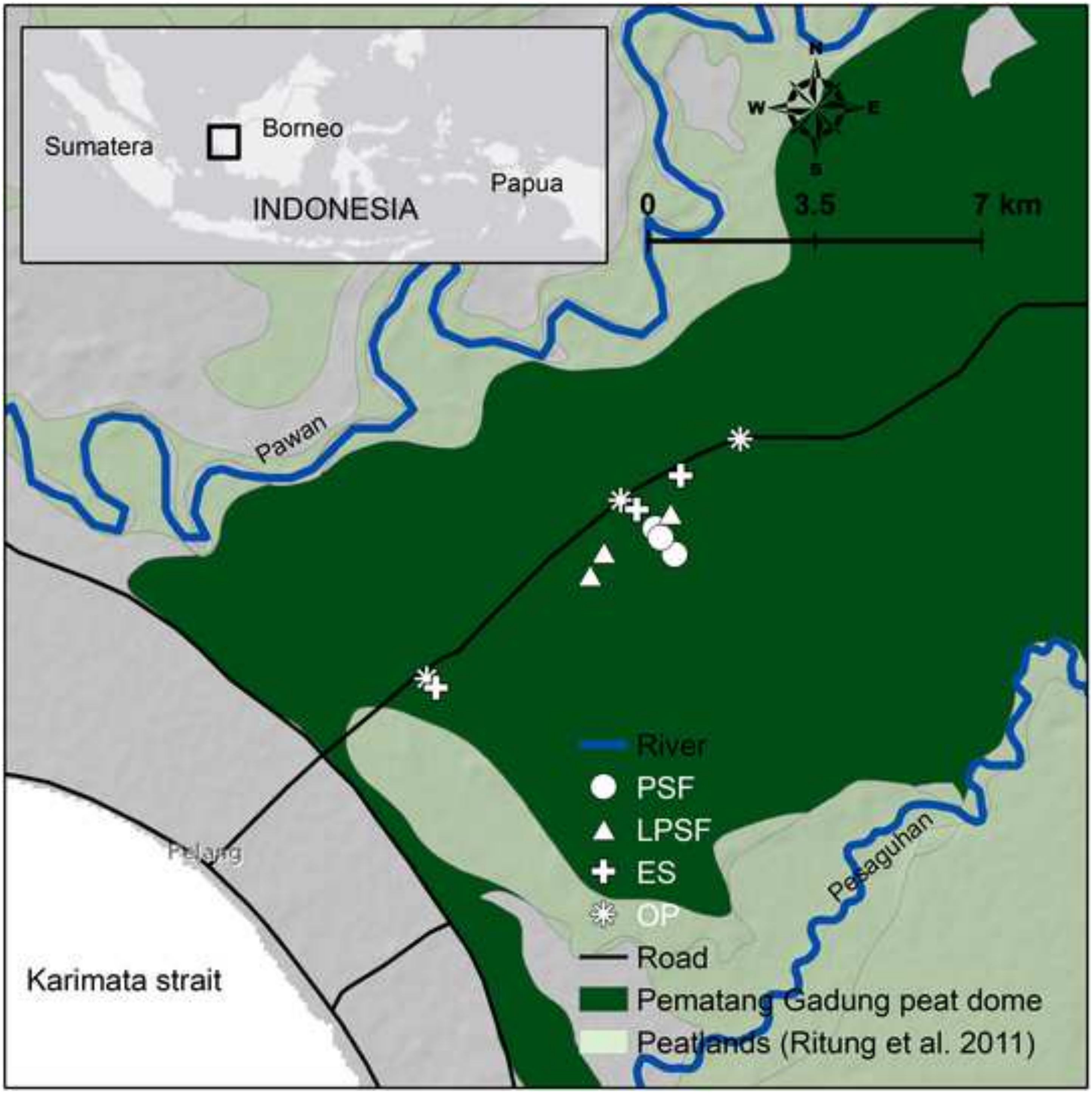
[1]Dept. of Fisheries and Wildlife, Oregon State University, Oregon, USA
[2]Center for International Forestry Research, Bogor, Indonesia
[3]Winrock International, Jakarta, Indonesia
[4]Dept. of Soil Science, and Magister of Environment, Tanjungpura University, Pontianak, Indonesia
[5]Bogor Agricultural University, Bogor, Indonesia

[*]Corresponding author:

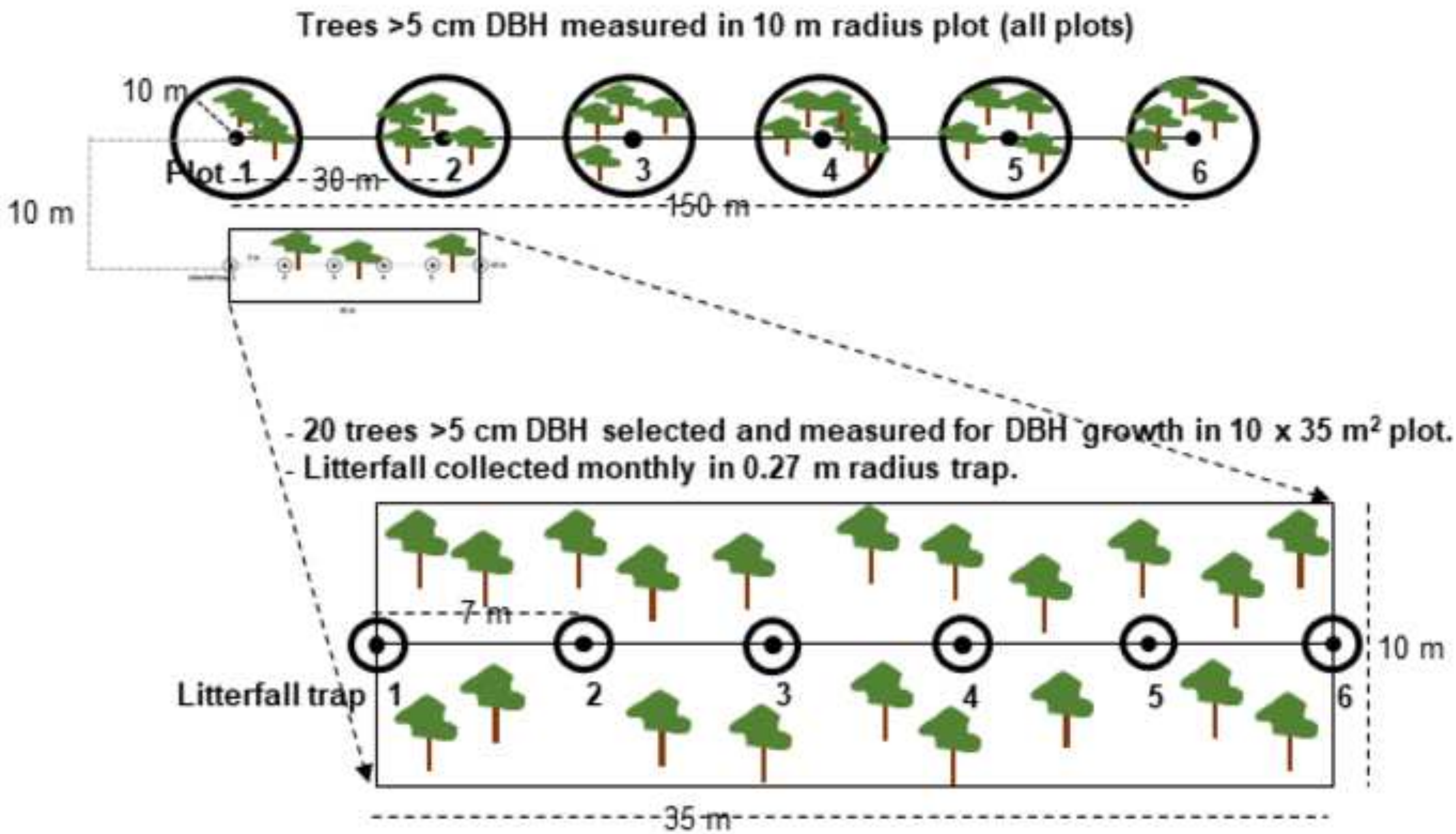
Imam Basuki (imambasuki1974@gmail.com)

Address: Bukit Asri, D12 No. 23, Pagelaran, Ciomas, Bogor Barat, Bogor, Jawa Barat, Indonesia, 16610.

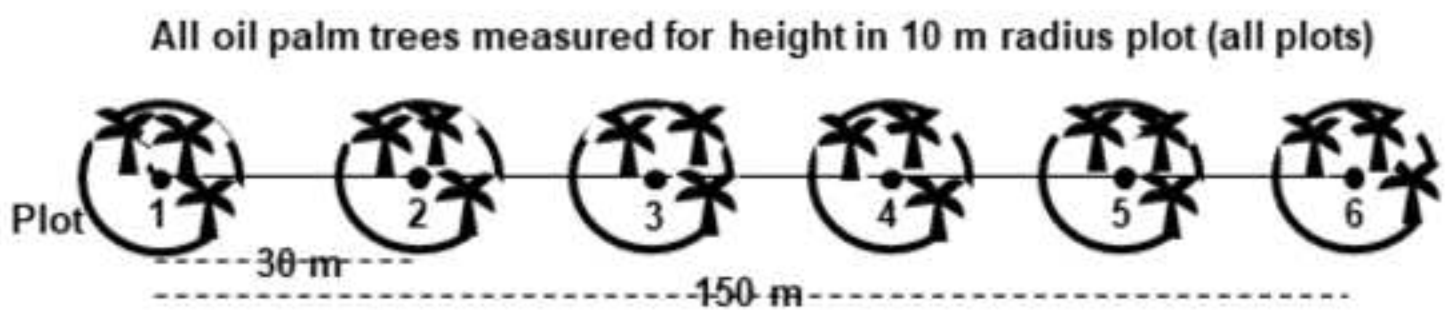
colour figure



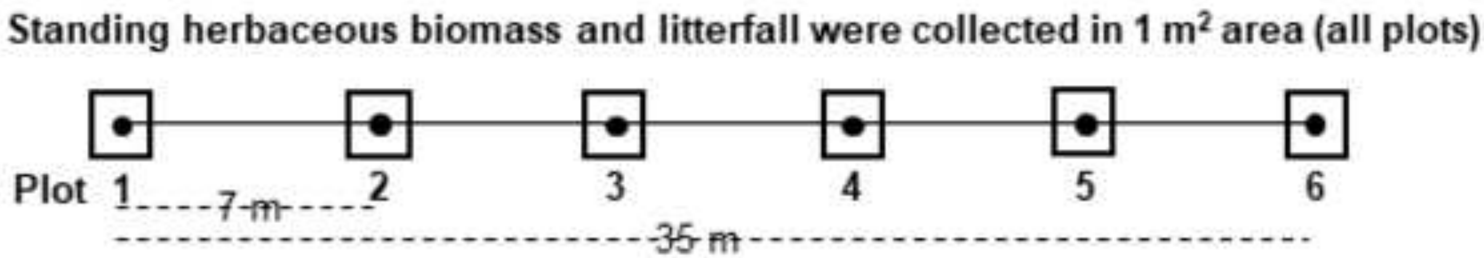
colour figure



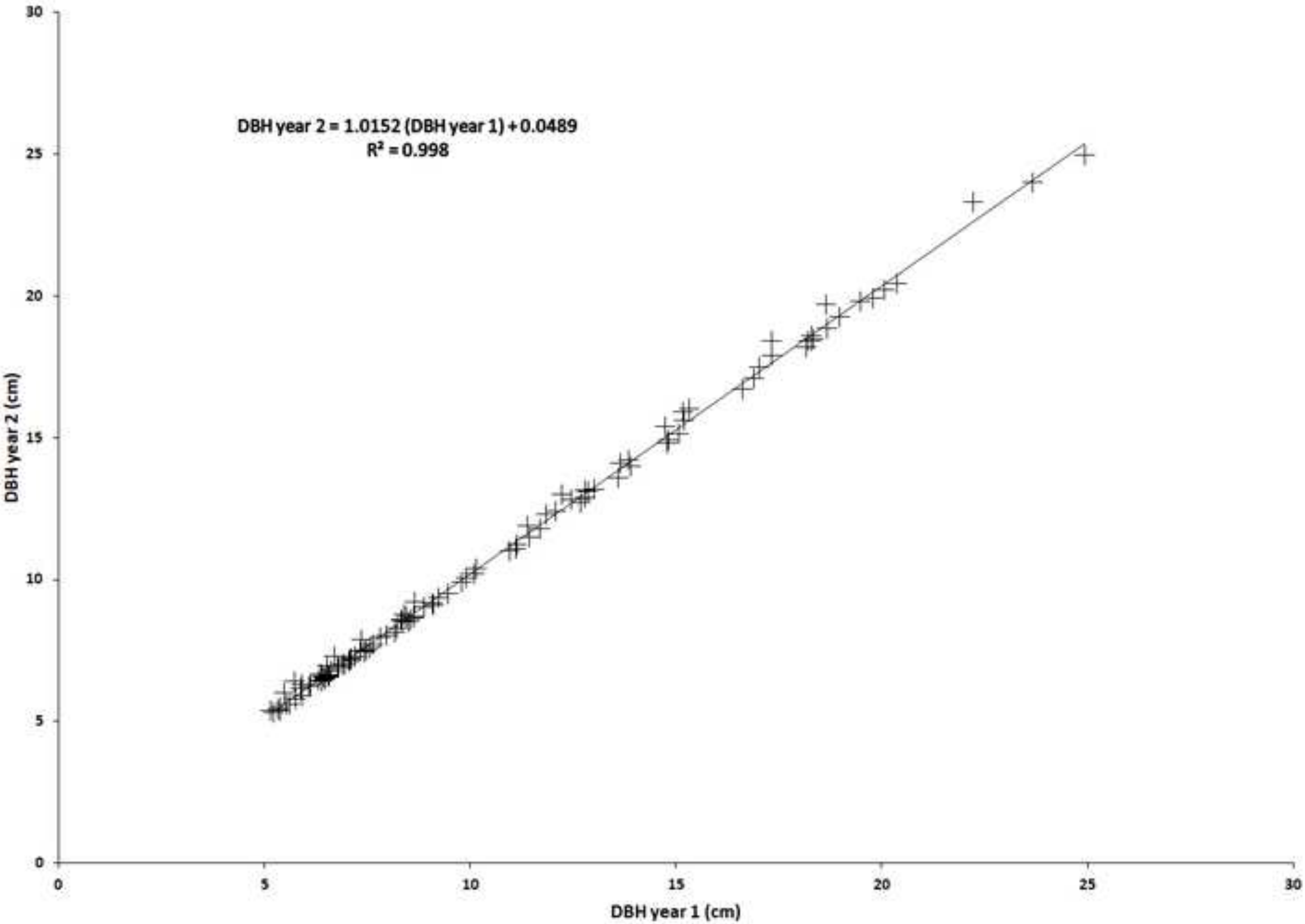
colour figure



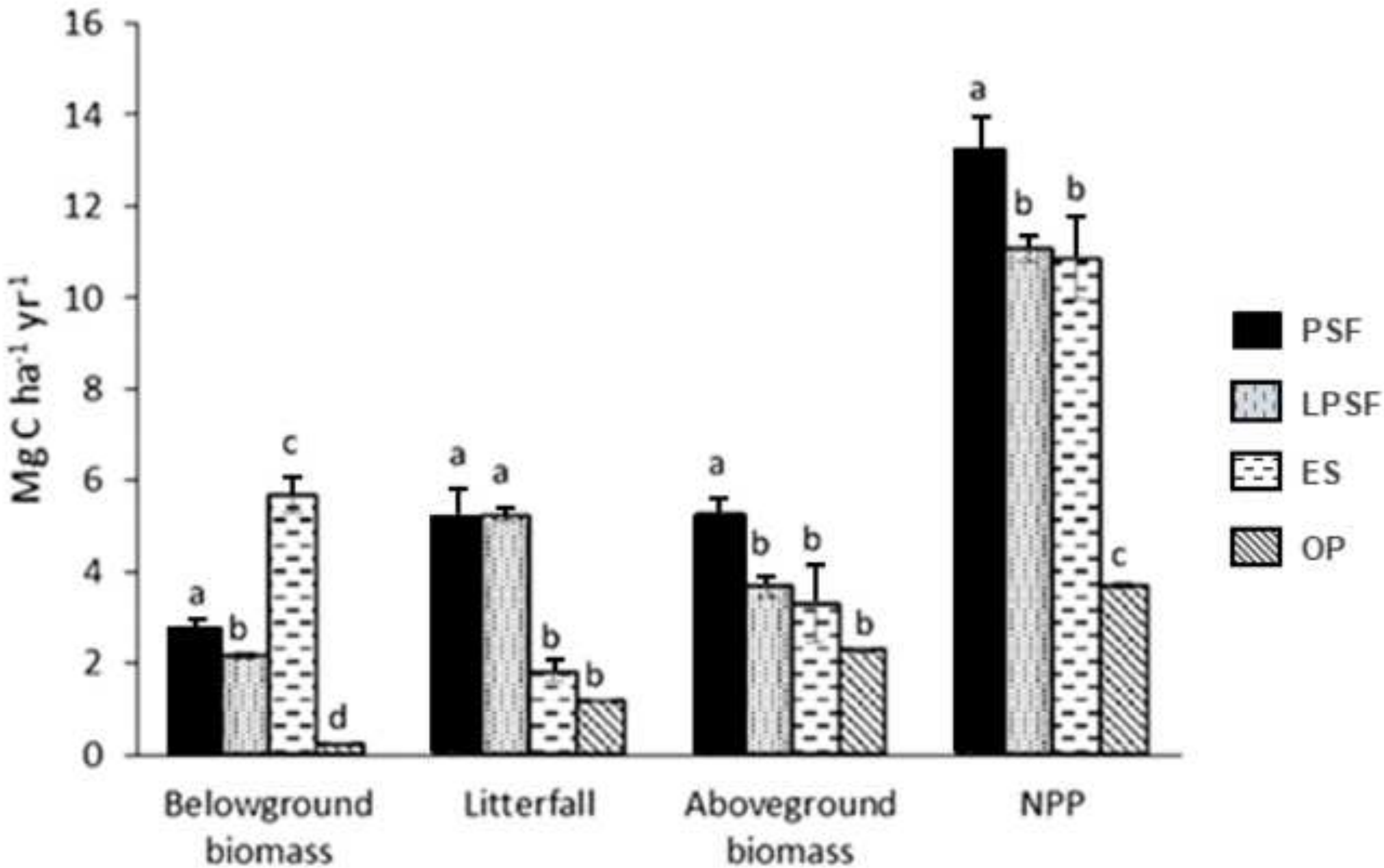
colour figure



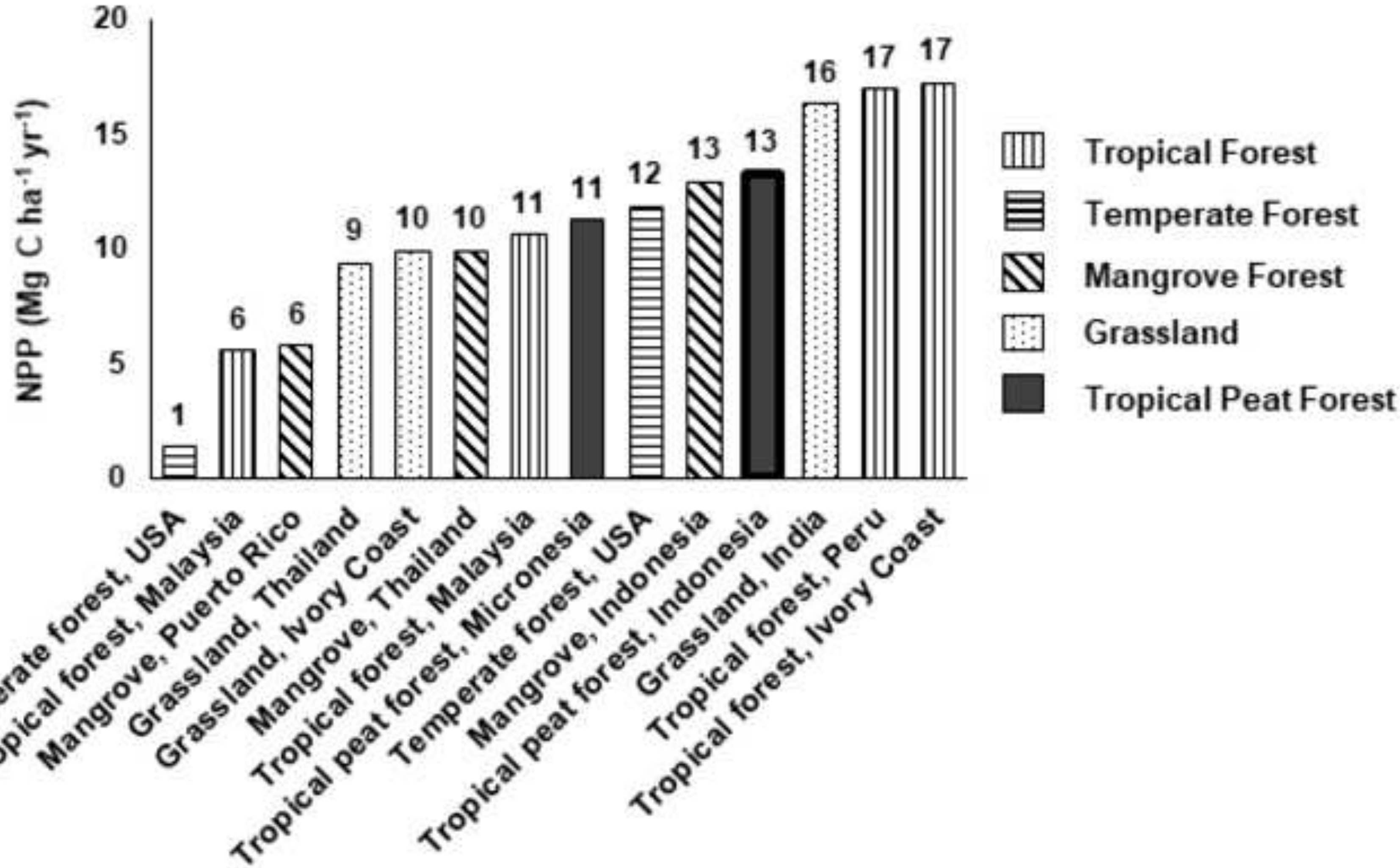
line figure


DBH year 2 = 1.0152 (DBH year 1) + 0.0489
R² = 0.998
DBH year 2 (cm)
DBH year 1 (cm)
0
5
10
15
20
25
30

colour figure



colour figure



Tables

Table 1 Equations used to determine biomass and carbon gain in peat forests, early seral sites and oil palm plantations.

Data	Equation	Results	Reference
Forest tree diameter at breast height, dbh (cm)	0.136*Forest tree dbh^2.513	Tree biomass (kg)	Manuri et al. 2014
Forest tree biomass (kg)	0.489*Forest tree biomass^0.89	Tree coarse root biomass (kg)	Mokany et al. 2006
Forest litterfall (g)	9.89%*Forest litterfall	Branch fall production (kg)	Chimner and Ewel, 2005
Forest tree and root biomass, litterfall and branchfall (kg)	12%*sum of forest tree, root, litterfall and branchfall	Fine root production (kg)	Chimner and Ewel, 2005
Oil palm height (cm)	0.0976*(Oil palm height) + 0.0706	Oil palm biomass (kg)	Dewi et al. 2010
Oil palm biomass (kg)	14.2%*Oil palm biomass	Oil palm root production (kg)	Henson and Dolmat, 2003
Oil palm biomass (kg)	68.8%*Oil palm biomass	Oil palm frond production (kg)	Henson and Dolmat, 2003
Early seral leaf and litterfall (g)	110%*ES leaf and litterfall	Eearly seral root production (kg)	Scurlock and Olson, 2013

Table 2 Annual growth of tree DBH and production of aboveground biomass (AGB) and belowground biomass (BGB) in intact and logged peat swamp forest (tree DBH > 5 cm). PSF represents intact peat swamp forests and LPSF means logged peat swamp forests.

Site	DBH Year 1	DBH growth	AGB Year 1	AGB growth	BGB Year 1	BGB growth	Total growth
	----------cm----------		Mg C ha^{-1}	Mg C ha^{-1}yr^{-1}	Mg C ha^{-1}	Mg C ha^{-1}yr^{-1}	
PSF1	11.7±0.3	0.2±0.0	90.4 ± 10.2	4.2 ± 0.4	24.8 ± 2.5	1.0 ± 0.1	5.2 ± 0.5
PSF2	12.1±0.4	0.2±0.0	102.0 ± 17.9	4.5 ± 0.7	25.7 ± 3.7	1.0 ± 0.1	5.6 ± 0.9
PSF3	12.1±0.3	0.2±0.0	114.8 ± 12.8	5.1 ± 0.5	28.4 ± 2.4	1.1 ± 0.1	6.2 ± 0.6
PSF mean	**12.0±0.1**	**0.2±0.0**	**102.4 ± 7**	**4.6 ± 0.3**	**26.3 ± 1.1**	**1.0 ± 0**	**5.7 ± 0.3**
LPSF1	10.4±0.8	0.2±0.0	61.2 ± 18.2	2.7 ± 0.7	15.1 ± 3.5	0.6 ± 0.1	3.3 ± 0.9
LPSF2	10.7±0.3	0.2±0.0	78.0 ± 9.3	3.5 ± 0.4	20.2 ± 2.5	0.8 ± 0.1	4.3 ± 0.5
LPSF3	11.7±0.6	0.2±0.0	78.0 ± 15.1	3.5 ± 0.6	20.2 ± 3.3	0.8 ± 0.1	4.3 ± 0.8
LPSF mean	**10.9±0.4**	**0.2±0.0**	**72.4 ± 5.6**	**3.2 ± 0.3**	**18.5 ± 1.7**	**0.7 ± 0.1**	**4 ± 0.3**

Table 3 Annual growth of tree DBH and production of aboveground biomass (AGB) and belowground biomass (BGB) in intact and logged peat swamp forest (tree DBH < 5 cm). PSF represents intact peat swamp forests and LPSF means logged peat swamp forests.

Site	DBH Year 1	DBH growth	AGB Year 1	AGB growth	BGB Year 1	BGB growth	Total growth
	----------cm----------		Mg C ha^{-1}	Mg C ha^{-1}yr^{-1}	Mg C ha^{-1}	Mg C ha^{-1}yr^{-1}	
PSF1	1.5±0.1	0.1±0	7 ± 1.1	0.6 ± 0.1	3.2 ± 0.5	0.3 ± 0	0.9 ± 0.1
PSF2	1.8±0.1	0.1±0	5.8 ± 0.8	0.5 ± 0.1	2.7 ± 0.3	0.2 ± 0	0.7 ± 0.1
PSF3	1.7±0.2	0.1±0	9.8 ± 2.4	0.9 ± 0.2	4.5 ± 1	0.4 ± 0.1	1.2 ± 0.2
PSF mean	**1.7±0.1**	**0.1±0**	**7.5 ± 1.2**	**0.7 ± 0.1**	**3.5 ± 0.5**	**0.3 ± 0.1**	**0.9 ± 0.1**
LPSF1	1.5±0.1	0.1±0	4.4 ± 0.5	0.4 ± 0	2.1 ± 0.2	0.2 ± 0	0.6 ± 0.1
LPSF2	2.2±0.4	0.1±0	4.7 ± 1.8	0.4 ± 0.1	2.2 ± 0.8	0.2 ± 0.1	0.6 ± 0.2
LPSF3	1.8±0.2	0.1±0	4.7 ± 0.6	0.4 ± 0	2.2 ± 0.3	0.2 ± 0	0.6 ± 0.1
LPSF mean	**1.8±0.2**	**0.1±0**	**4.6 ± 0.1**	**0.4 ± 0**	**2.2 ± 0**	**0.2 ± 0**	**0.6 ± 0**

Table 4 Litterfall (Mg C ha^{-1}yr^{-1}) in intact and logged peat forest. Biomass production of litterfall during dry and wet months (August to October, and November to July, respectively), and annually reported as mean ± SE. PSF represents intact peat forests and LPSF means logged forests.

Site	Dry months litterfall	Wet months litterfall	Total litterfall
	---------------------Mg C ha^{-1}yr^{-1}---------------------		
PSF1	3.3 ± 0.2	2.9 ± 1.4	6.2 ± 1.5
PSF2	2.1 ± 0.4	1.9 ± 0.3	4 ± 0.5
PSF3	2.1 ± 0.3	3.3 ± 0.9	5.4 ± 1
PSF mean	**2.5 ± 0.4**	**2.7 ± 0.4**	**5.2 ± 0.6**
LPSF1	2.8 ± 0.2	2.7 ± 0.5	5.4 ± 0.6
LPSF2	2.6 ± 0.4	2.4 ± 0.2	5 ± 0.5
LPSF3	2.4 ± 0.3	2.9 ± 0.7	5.3 ± 0.9
LPSF mean	**2.6 ± 0.1**	**2.7 ± 0.1**	**5.2 ± 0.1**

Table 5 Productivity of aboveground biomass (AGB), litterfall, belowground biomass (BGB; fine and coarse root) and net primary production (NPP) in intact peat swamp forests (PSF) and logged peat swamp forests (LPSF). Potential sequestered carbon through biomass production reported as mean ± SE, or otherwise as mean only. Annual sequestered C-CO_2 presented in the NPP[1] column.

Site	AGB	Litterfall	BGB (Fine root)	BGB (Coarse root)	NPP	NPP[1]
	---------------------------- Mg C $ha^{-1}yr^{-1}$----------------------------					Mg C-CO_2 $ha^{-1}yr^{-1}$
PSF1	4.8 ± 0.4	6.2 ± 1.5	1.5	1.3 ± 0.1	13.7	50.4
PSF2	5 ± 0.7	4 ± 0.5	1.2	1.3 ± 0.1	11.6	42.4
PSF3	5.9 ± 0.5	5.4 ± 1	1.6	1.5 ± 0.1	14.4	52.8
PSF mean	**5.3 ± 0.4**	**5.2 ± 0.6**	**1.4 ± 0.1**	**1.3 ± 0.1**	**13.2 ± 0.8**	**48.5 ± 2.8**
LPSF1	3.2 ± 0.8	5.5 ± 0.6	1.2	0.8 ± 0.1	10.6	38.8
LPSF2	3.9 ± 0.5	5 ± 0.5	1.2	1 ± 0.1	11.1	40.7
LPSF3	3.9 ± 0.7	5.3 ± 0.9	1.3	1 ± 0.1	11.5	42.2
LPSF mean	**3.7 ± 0.2**	**5.2 ± 0.1**	**1.2 ± 0**	**0.9 ± 0.1**	**11.1 ± 0.3**	**40.6 ± 1.0**

Table 6 Productivity of aboveground biomass (AGB), litterfall, belowground biomass (BGB) and net primary production (NPP) in early seral (ES) ecosystems. Annual sequestered C-CO_2 presented in the NPP[1] column.

Site	AGB	Litterfall	BGB	NPP	NPP[1]
	---------------------------Mg C $ha^{-1}yr^{-1}$---------------------------				Mg C-CO_2 $ha^{-1}yr^{-1}$
ES1	1.9 ± 0.2	2.1 ± 0.3	4.5 ± 0.5	8.5 ± 0.9	31.3 ± 3.3
ES2	4.8 ± 1.5	1.4 ± 0.4	6.9 ± 1.9	13.1 ± 3.5	48.1 ± 13
ES3	3.2 ± 0.5	2.0 ± 0.3	5.7 ± 0.8	10.9 ± 1.5	39.9 ± 5.5
ES mean	**3.3 ± 0.8**	**1.8 ± 0.2**	**5.7 ± 0.7**	**10.8 ± 1.3**	**39.8 ± 4.9**

Table 7 Productivity of aboveground biomass (AGB), litterfall, belowground biomass (BGB) and NPP of oil palm (OP) plantations. Annual sequestered C-CO_2 presented in the NPP[1] column.

Site	AGB	Litterfall	BGB	NPP	NPP[1]
	---------------- (Mg C ha^{-1} yr^{-1}) ---------------				(Mg CO_2 ha^{-1} yr^{-1})
OP1	2.4 ± 0.2	1.2 ± 0.1	0.2 ± 0.0	3.8 ± 0.4	14.1 ± 1.4
OP2	2.3 ± 0.6	1.2 ± 0.3	0.2 ± 0.1	3.7 ± 1.0	13.4 ± 3.5
OP3	2.3 ± 0.2	1.2 ± 0.1	0.2 ± 0.0	3.7 ± 0.3	13.4 ± 1.0
OP mean	**2.3 ± 0.0**	**1.2 ± 0.0**	**0.2 ± 0.0**	**3.7 ± 0.1**	**13.6 ± 0.2**