

# Physical and chemical properties of tropical peat under stabilised land uses

M. Könönen<sup>1</sup>, J. Jauhiainen<sup>1</sup>, R. Laiho<sup>2</sup>, K. Kusin<sup>3</sup> and H. Vasander<sup>1</sup>

<sup>1</sup>Department of Forest Sciences, University of Helsinki, Finland

<sup>2</sup>Natural Resources Institute Finland, Parkano, Finland

<sup>3</sup>CIMTROP, University of Palangka Raya, Indonesia

---

## SUMMARY

Land-use change has transformed large areas of tropical peatland into globally significant carbon sources. Associated changes in the properties of peat are important for soil processes including decomposition and nutrient cycling. To characterise the changes induced by stabilised land uses, we studied the physical and chemical properties of peat from four land management conditions (undrained and drained forest, degraded land, and managed agricultural land). Peat was sampled from depths of 10–15 cm, 40–45 cm, 80–85 cm and 110–115 cm then partitioned into woody ( $\varnothing > 1.5$  mm), fibric ( $\varnothing 0.15$ – $1.5$  mm) and amorphous ( $\varnothing < 0.15$  mm) fractions. Bulk density and total concentrations of ash, C, N, P, K, Ca, Mg, Mn, Zn, Na, Al, Fe, S and Si were determined. There were clear differences between land uses in the characteristics of surface peat down to the 40–45 cm layer, the primary differences being between forested and open sites. Due to smaller particle sizes, the bulk density of peat was higher at the open sites, where Ca and Mg concentrations were also higher but N and P concentrations were lower. Changes in drainage and vegetation cover had resulted in differing outcomes from decomposition processes, and the properties of fire-impacted peats on the open sites had undergone extreme changes.

**KEY WORDS:** Central Kalimantan; deforestation; drainage; land use; tropical peat characteristics

---

## INTRODUCTION

Tropical peat swamp forests are ombrotrophic wetland ecosystems that sequester carbon (C) into vegetation and, especially, into peat below the forest floor. The woody peat formed in these ecosystems is rich in C (~56 % on a dry mass basis) and the peat deposits can be several metres thick over vast areas, making tropical peatlands globally important C stores (Page *et al.* 2011). Tropical peat extending over an area of 25 Mha in south-east Asia is estimated to contain 11–14 % (68.5 Gt) of the global peat C reservoir (Page *et al.* 2011). Land-use change in tropical peatlands has accelerated during the past few decades, and in 2007 approximately 60 % of the peat swamp forest in south-east Asia had been impacted by logging (Miettinen & Liew 2010). A major concern in relation to this rapidly advancing land-use change has been the transformation of large parts of the peatland ecosystems into C sources of global significance (Hooijer *et al.* 2010, Page *et al.* 2011, Comeau *et al.* 2013). Less attention has been paid to changes taking place in the peat matrix after land-use change, even though the physical and chemical properties of peat are important constraints for all soil processes including decomposition and nutrient cycling.

Peat is formed primarily from decaying organic substrates and the biomass of the decomposer communities consuming them. Vegetation facilitates peat accumulation by adding organic substrates (litter), both onto the peat surface and into the peat in the rooting zone. Therefore, peat processes and properties interact closely and dynamically with the vegetation (Radjagukguk *et al.* 1998, Page *et al.* 1999). Oxygen availability, in turn controlled largely by the position of the water-table level (WL) in the peat profile, determines the dominance of either faster aerobic decomposition (in oxic conditions) or anaerobic decomposition (in water-saturated anoxic conditions) (Clymo 1984, Vasander & Kettunen 2006). Land-use change and drainage lead to permanent WL drawdown and thus create a thicker oxic peat layer within which aerobic decomposition is favoured. The predominantly aerobic decomposition under drained conditions generally facilitates more efficient release of C from the peat than the anaerobic decomposition processes that dominate in water-saturated peat (e.g., Jauhiainen *et al.* 2005, 2008). Simultaneously, however, several other processes shape the physical and chemical properties of the peat.

Peat subsidence starts with the onset of drainage, due to loss of water from surface-peat pores and the

shrinkage that accompanies drying; and continues with increasing dominance of biological decomposition, leading to increased bulk density (BD; dry mass per fresh volume) and reduced porosity (volume of air space between particles) (Minkinen & Laine 1998, Kurnain *et al.* 2001, Hooijer *et al.* 2012, Couwenberg & Hooijer 2013, Moore *et al.* 2013). Drainage and land-use change may further affect nutrient concentrations in the peat directly *via* leaching and indirectly *via* changes in nutrient cycling arising from changes in vegetation (e.g., Radjagukguk *et al.* 1998, Laiho *et al.* 1999, Westman & Laiho 2003). Furthermore, the number and severity of wildfires increases in drained and deforested areas; and fire events can, within a few days, expose peat layers that were previously at depths of several decimetres (Page *et al.* 2002, Hoscilo *et al.* 2011). This undoubtedly has potential impacts on the physical and chemical properties of both the surface peat and vertical peat profiles.

Although several processes modify peat properties in reclaimed areas, there is still little information on the magnitude of the changes even under common stabilised land uses. In particular, systematic studies on the changes in peat properties that occur under long-term land uses that differ in terms of management intensity have been lacking. The main objective of this study was to compare

physical (bulk density; particle size distribution; porosity) and chemical (pH; ash content; C, N, P, K, Ca, Mg, Mn, Zn, Na, Al, Fe, S and Si concentrations) properties of peat under four land-use types that clearly differ in management intensity. By studying these key properties under selected land uses, in profiles from the surface down to normally water-saturated peat, we assess a continuum of conditions; and this enables us to discern the major changes in peat physical and chemical properties that occur after land-use change.

We hypothesised that: (i) long-term use of peatland leads to changes in the physical and chemical properties of peat; (ii) the changes in peat properties occur in the peat layers that are not normally water-saturated; and (iii) land-use-specific changes in peat properties are more extreme when both vegetation and WL depth are affected, i.e., in open sites as compared to forested sites.

## METHODS

### Study area

The study area was on lowland peat in a catchment basin of the Sebangau River ( $2^{\circ} 12' 36''$  S,  $113^{\circ} 55' 12''$  E) in the province of Central Kalimantan, Indonesia (Figure 1). For the period

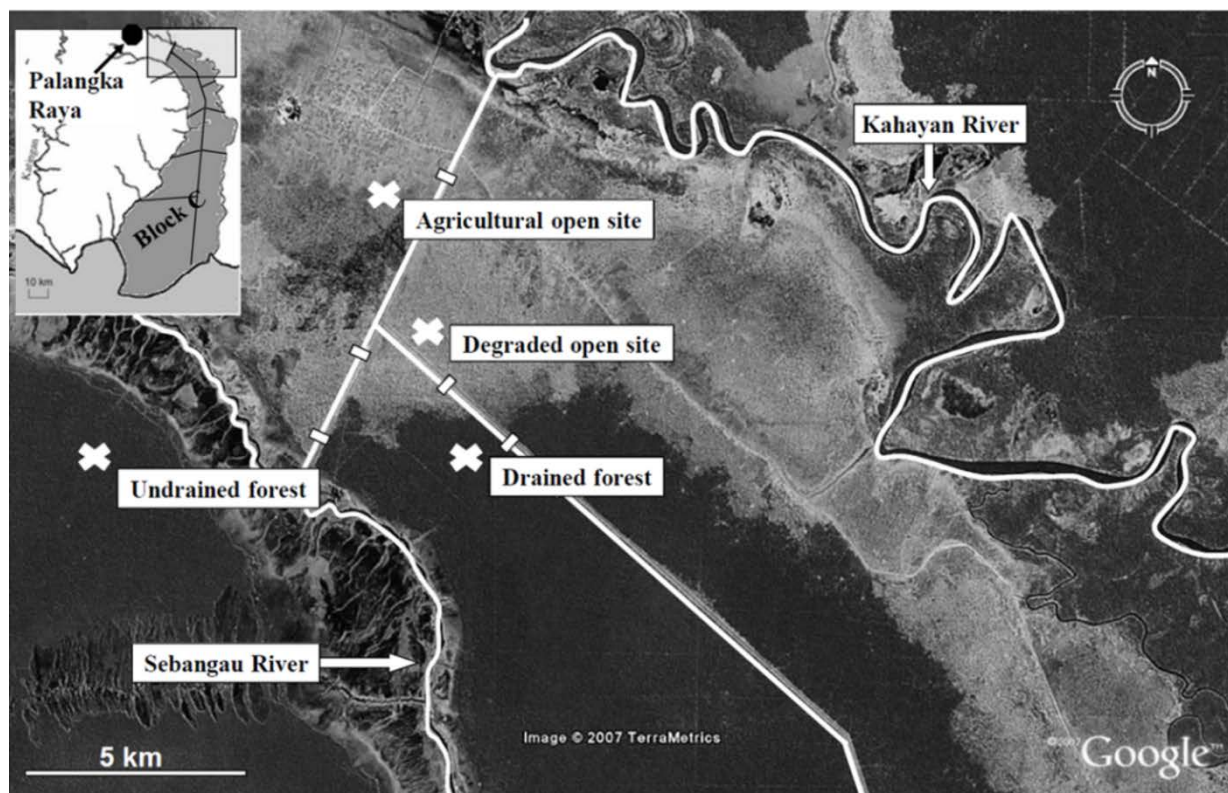


Figure 1. Locations of the study sites in undrained forest and Block C of the ‘mega rice project’ (MRP) area in Central Kalimantan, Indonesia.

2002–2010, average annual rainfall in the region was  $2540 \pm 596$  mm yr<sup>-1</sup> and mean annual air temperature was  $26.2 \pm 0.3$  °C (Sundari *et al.* 2012). There are clear wet and dry seasons, with the wettest period between December and February and the driest months being August and September.

### Study sites

In the past, the river basin containing the four closely-located study sites was covered by swamp forest on thick (> 3 m) ombrotrophic peat. The sites selected for this study in 2009 differed in terms of their vegetation characteristics and/or hydrological conditions as a result of human-induced changes at three of the sites several decades ago. In order of increasing management intensity, the study sites are described as: (i) undrained peat swamp forest (UF) and (ii) drained peat swamp forest (DF), which were characterised by forest vegetation; (iii) drained,

degraded open peatland (DO) and (iv) drained open peatland in settled agricultural use (AO), which were clear-felled and affected by fire (Figure 1, Table 1).

The vegetation of both of the forested sites was close to steady-state forest despite former selective and illegal logging activities (Page *et al.* 1999; Jauhiainen *et al.* 2005, 2008). On the floor of the undrained forest, microtopographical features ranged from an open peat surface forming the base level to vegetated ‘hummocks’ some decimetres high. Surface features were less pronounced in the drained forest. Hydrologically, the undrained forest site was close to intact, and large portions of the base-level surface were flooded during the wet season (Figure 2). The drained forest site was located within an area drained by a canal measuring 25 m wide and 3–4 m deep, which was dug in 1997–1998. The degraded open peatland site was influenced by the same canal.

Table 1. Descriptions of the study sites.

Land use	Undrained forest (UF)	Drained forest (DF)	Degraded open peatland (DO)	Agricultural open peatland (AO)
Location	02° 19' 16.96" S 113° 53' 54.29" E	02° 20' 43.24" S 114° 02' 07.02" E	02° 20' 00.43" S 114° 01' 12.99" E	02° 17' 38.22" S 114° 01' 04.69" E
Land-use history	selective and illegal logging (1990–2000)	drained (1996→), selective logging (1996–1998)	clear-cut and drained (1996→), several fires	clear-cut and drained (1987→), then cultivated
Peat thickness (m)	3	4	4	4
Primary vegetation type	swamp forest	swamp forest	ferns	seasonal crops
Sampling depths (cm below soil surface)	10–15 40–45 80–85	10–15 40–45 80–85 110–115	10–15 40–45 80–85 110–115	10–15 40–45 80–85 110–115
Long-term median water table depth (cm)	-10.30	-38.60	-16.75	-21.98
Water table depth during sampling (cm)	-100	> -115	> -115	> -115

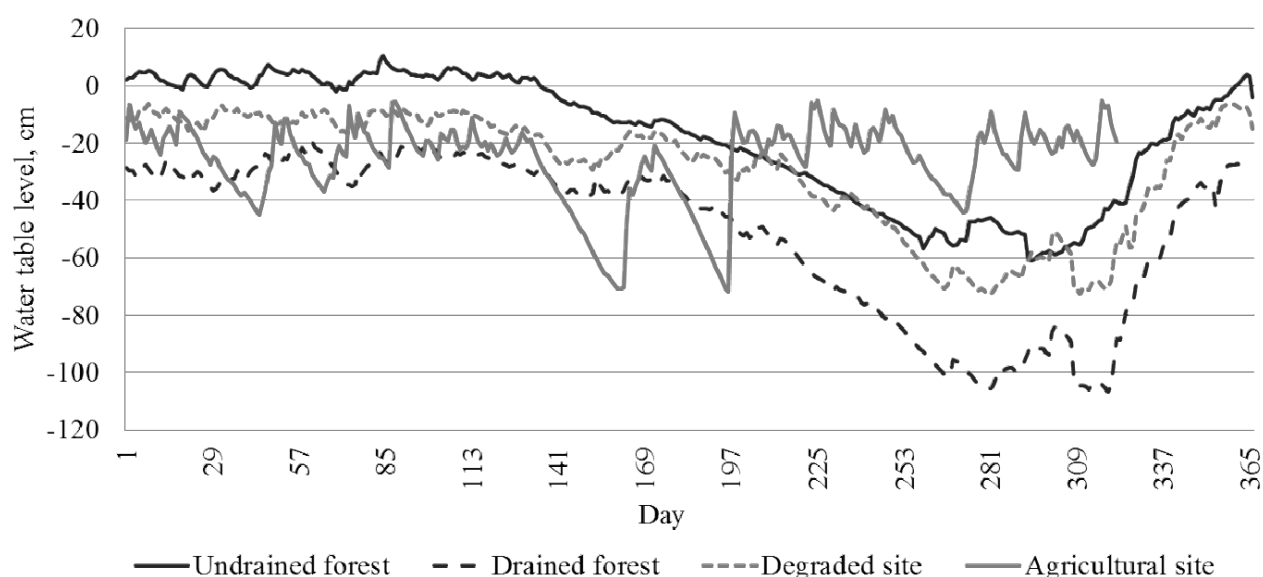


Figure 2. Daily mean water table depths for the four study sites: undrained forest (1997–2006); drained forest (2004–2007); degraded peatland (2004–2008); and agricultural peatland (2001–2003).

The degraded open peatland site, referred to as ‘the degraded site’ hereafter, was drained and clear-felled (deforested) in 1997–1998. Subsequently, the vegetation and surface peat were affected by fires in 1997, 1999, 2002 and 2006; it has been estimated that more than 0.5 m of the topmost peat has been lost in multiple wildfires (Page *et al.* 2002, Hoscilo *et al.* 2011). During our study the dominant vegetation type was composed of ferns (primarily *Stenochlaena palustris*) and some scattered trees (primarily *Compretocarpus rotundatus*) which were ~4 m tall. The soil surface was relatively flat. Since the 1980s, the agricultural open peatland site, hereafter called ‘the agricultural site’, has been under shallow drainage with the water table always below the surface, and has been cultivated seasonally for smallholder cropping (e.g., maize, cassava, beans). It was flat, bare fallow land during sampling. Annual management practices have included shallow tilling, and amelioration with industrial fertilisers and ash from burning a mixture of peat, dung and plant residues. Thus, the agricultural site can also be regarded as fire-impacted, even though deep peat-consuming fires have not occurred.

### Sampling

Peat was sampled close to the end of the dry season in September 2009, when water tables in the area were at their deepest (Figure 2). The samples were taken from base-level surfaces at the forest sites;

from parts of the surface where fern cover was low at the degraded site; and on bare fallow peat surface at the agricultural site. If present, recently deposited loose litter (such as leaves and branches) was removed before sampling. At each sampling location, the soil surface was set as the starting depth (0 cm).

A 100 cm square pit, 150 cm deep and thus reaching below the deepest typical water table (Table 1), was excavated at each site. Samples were collected from one wall of the pit at three or four depths, to include surface peat that is typically unsaturated during dry seasons (10–15 cm) and peat layers that are either temporarily (45–50 cm and 80–85 cm) or permanently (110–115 cm) water-saturated during a typical year (Table 1, Figure 2). In the undrained forest, the deepest sampling depth was 80 cm because the deepest typical WL depth was approximately 60 cm. Augers were not used for sampling, in order to avoid the associated possibilities of compressing peat structures and selectively excluding roots and wood (Pitkänen *et al.* 2011). Instead, a sharp knife and volume-exact rectangular steel frame (10 × 10 × 5 cm) were used to cut six 500 cm<sup>3</sup> peat samples from each sampling depth immediately after the pit wall had been excavated to that level. Thus, 90 samples in total were collected from the four sites. The samples were sealed into plastic bags to avoid drying, and taken to a laboratory where they were stored in a refrigerator (4 °C) for up to one week before further treatments.

### Measurements and calculations

Living roots (diameter > 0.5 mm) were separated from each sample, dried at 70 °C and weighed. Then, for one sample from each site and depth, the pH of a mixture of peat and deionised water (v/v = 1/2) was measured using a WinLab Data Line meter (peat pH).

Three samples from each sampling depth were dried at 70 °C and weighed, and their dry bulk density (BD, g cm<sup>-3</sup>) was calculated. These samples (n = 45) were named 'non-fractioned' samples. The remaining three samples from each depth were individually fractioned, by washing them (with water) through two sieves (0.15 mm and 1.5 mm mesh diameter), into two classes: 'fibric fraction' (particle size 0.15–1.5 mm) and 'woody fraction' (particle size > 1.5 mm). The sieved fractions were dried at 70 °C and weighed. The smallest particles (< 0.15 mm) were washed away, but the mass of material lost was estimated by summing the masses of woody and fibric material retained from each fractioned sample, and subtracting the total from the average mass of all (parallel) non-fractioned samples taken from the same site and sampling depth. This smallest fraction was named the 'amorphic fraction'. Thus, the woody, fibric and amorphic fractions together accounted for 100 % of the original sample. The mass of each fraction per sample volume (i.e., density of fraction, g cm<sup>-3</sup>) was calculated.

Loss-on-ignition (*LOI*) and ash content (*ash*) were determined from the mass change during combustion of 1–2 g of dry peat from the three non-fractioned samples per site/depth, which were first combined and mixed (4 hours at 550 °C; three laboratory replicates). Total pore space (*TPS*, %) was derived as:

$$TPS = [(D_s - BD)/D_s] \times 100 \quad [1]$$

where  $D_s$  is the density of solids in the peat (g cm<sup>-3</sup>), calculated as:

$$D_s = [(LOI \times D_p) + (ash \times D_a)]/100 \quad [2]$$

where  $D_p$  is the density of solids for peat and  $D_a$  is the density of solids for ash. *LOI* and *ash* are expressed as % of dry mass,  $D_a$  is 2.56 g cm<sup>-3</sup> and  $D_p$  for tropical peat is 1.43 g cm<sup>-3</sup> (Driessen & Rochimah 1976).

Total nutrient concentrations were also determined from the three pooled non-fractioned samples per site/depth. Total C and N concentrations were measured using a Leco CHN-600 Elemental Analyzer, and total concentrations of P, K, Ca, Mg, Mn, Zn, Na, Al, Fe, S and Si were determined by Inductively Coupled Plasma Mass Spectrometry (EPA Method 3051) using Perkin Elmer ELAN 6000 ICP-MS equipment. All analyses were performed on three replicate subsamples. Results for nutrient

concentrations were calculated both per unit dry mass (mg g<sup>-1</sup>) and per unit volume of the non-fractioned samples (g cm<sup>-3</sup>). In each case, the volume-based value was calculated by multiplying the mass-based concentration by the average BD of peat from the same sampling depth and site. The mass-based data (only) are presented here because the two approaches did not lead to differences in the statistical results.

### Data analysis

Each management type was represented by just one site. Thus, we assume that differences between the sites arise from their different management intensities. Variation amongst the measured physical and chemical properties of samples collected from each site reflects within-site variation only. All sites were located in the same catchment basin, within less than 10 km of one another, had similar peat thickness and, as far as we know, were formerly covered by similar peat swamp forest. Even though we cannot completely rule out random site effects, we are confident that our assumption is valid insofar as our data analysis reveals true management effects.

General patterns in the chemical and physical properties of peat were analysed using ordination techniques. Peat properties were used as response variables, and site and sampling depth as explanatory variables, after conversion to binary form. Principal component analysis (PCA) was first used to explore the variation in peat properties and their relationships with site and depth. Redundancy analyses (RDA) were then used to test whether any site (management) and sampling-depth effects on peat properties were statistically significant. The first hypothesis (the effect of site on peat properties) was tested using depth as covariate; i.e., the potential effect of depth was removed prior to analysis of the site effect. RDA was also used as one of two approaches. The second hypothesis (concerning the effect of depth on peat properties) was tested in the same way, using site as covariate. A Monte Carlo permutation test with 999 permutations was applied to evaluate the significance of the canonical axes; permutations were constrained by the covariates. All ordination analyses were made using Canoco 5 for Windows. The tests of both the first hypothesis and the second hypothesis were complemented by testing the differences in each measured peat property amongst sites and sampling depths by a two-way analysis of variance followed by Tukey's post hoc test. These analyses were made using the Multicomp package R-cran 2.15.0 for Windows at significance level  $p < 0.05$ . The third hypothesis could also be supported or rejected using the outcomes of the RDAs (separation of sites in the results) and ANOVAs (based on the post hoc tests).

## RESULTS

The PCA detected two main gradients in the soil properties, related to site and depth (Figure 3). The first principal component, PC1 (X-axis) explained 29.7 %, and PC2 (Y-axis) explained 20.4 % of the total variation in peat chemical and physical properties, respectively. The strongest gradient, captured by PC1, separated the deepest peat layers of the two forest sites and the degraded site from the upper two layers of the degraded site and all layers of the agricultural site. Ash content, pH, base cation concentrations and C correlated with PC1. Ash, pH and base cations increased towards the agricultural site and the upper two layers of the degraded site, and correlated negatively with C. PC2 separated the upper peat layers at the two forest sites (10–15 and 40–45 cm for UF, 10–15 cm for DF) from the deepest peat layer of the undrained forest and the upper two layers of the degraded site as well as all layers of the

agricultural site. The density of woody and fibric fractions and the peat N, P and Si concentrations correlated with the PC2 axis, increasing towards the topmost layers in the forest sites (Figure 3). Furthermore, peat N, P and Si concentrations correlated negatively with C. Both site and sampling depth alone had a significant ( $p < 0.001$ ) impact on the physical and chemical properties of the peat. Site explained 39.4 %, and depth 31.1 % of the variation in peat properties, supporting our first and second hypotheses. With some exceptions, the forest sites showed rather similar patterns that differed from those of the open sites, thus partially supporting our third hypothesis. The upper two layers, especially, of the forest and open sites showed different patterns.

ANOVA confirmed the results of the ordination analyses described above. The main differences in peat properties between the four sites were in the upper two layers (Table 2). In general, the lowest-BD and highest-porosity surface (10–15 cm) peat was in

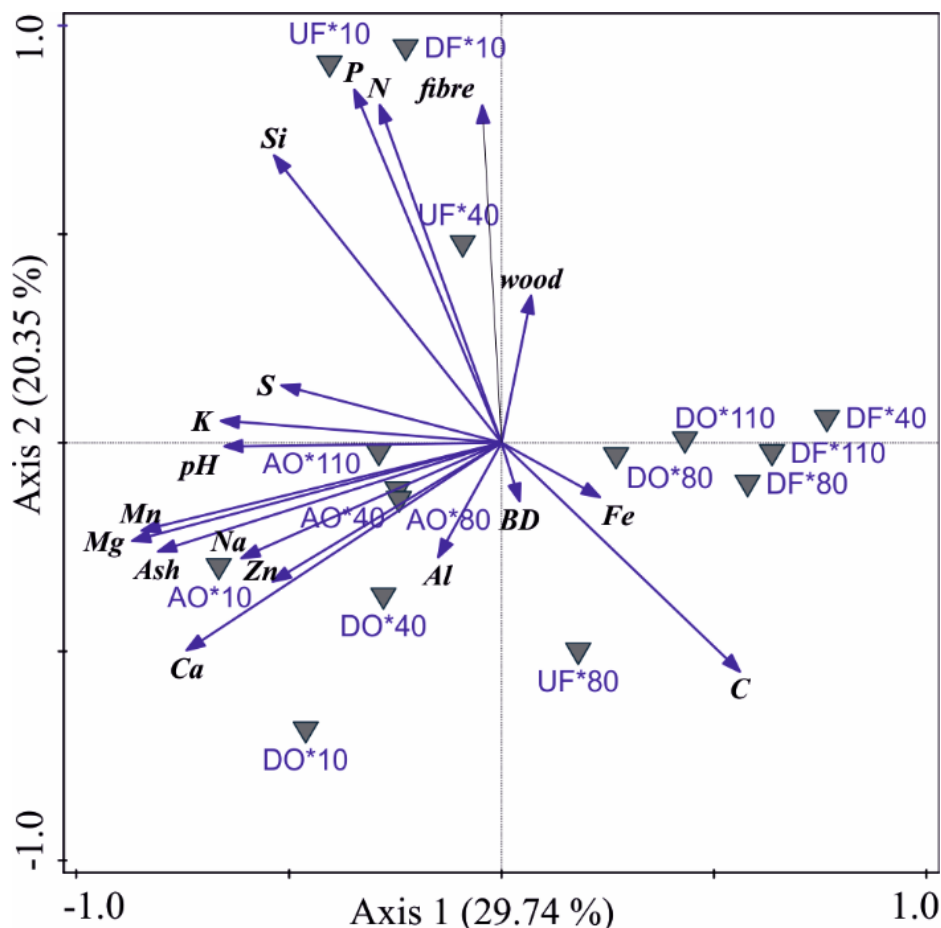


Figure 3. Ordination diagram from principal component analysis (PCA) summarising the variation in peat properties. The first and second axes account for 29.74 % and 20.35 % of the total variation, respectively. UF = undrained forest; DF = drained forest; DO = degraded, open peatland; AO = agricultural, open peatland; number following asterisk indicates sampling depth (e.g., UF\*10 = 10 cm below the soil surface in undrained forest).

Table 2. Physical properties of peat collected from different sampling depths at the four study sites, calculated on sample volume basis. Mean  $\pm$  standard deviation is provided in each case. Analyses were carried out on three of the six field replicate samples collected from each depth and site, after removing roots. Statistically significant differences between the respective sites and depths are indicated by superscript indices which denote the significantly different site: a = undrained forest; b = drained forest; c = degraded open peatland; d = agricultural open peatland). Statistically significant differences with  $p < 0.01$  are indicated by lowercase letters, and those with  $0.01 < p < 0.05$  are indicated by uppercase letters.

Land use	Sampling depth (cm)	Bulk density (g cm <sup>-3</sup> )	Total pore space (%)	Root (g)	Woody fraction (g cm <sup>-3</sup> )	Fibric fraction (g cm <sup>-3</sup> )	Amorphous fraction (g cm <sup>-3</sup> )
Undrained forest (UF) a	10–15	0.13 $\pm$ 0.01 <sup>c</sup>	90.9 $\pm$ 0.6 <sup>c</sup>	3.97 $\pm$ 4.04	0.030 $\pm$ 0.005 <sup>C</sup>	0.064 $\pm$ 0.011 <sup>bc</sup>	0.040 $\pm$ 0.010 <sup>cd</sup>
	40–45	0.14 $\pm$ 0.01 <sup>b</sup>	90.5 $\pm$ 0.8 <sup>b</sup>	6.63 $\pm$ 9.43	0.008 $\pm$ 0.002	0.063 $\pm$ 0.004 <sup>b</sup>	0.067 $\pm$ 0.006
	80–85	0.15 $\pm$ 0.03	89.2 $\pm$ 1.6	-	0.009 $\pm$ 0.003	0.024 $\pm$ 0.004	0.113 $\pm$ 0.006
Drained forest (DF) b	10–15	0.17 $\pm$ 0.03	88.1 $\pm$ 2.1	1.93 $\pm$ 1.45	0.016 $\pm$ 0.003	0.111 $\pm$ 0.016 <sup>acd</sup>	0.043 $\pm$ 0.015 <sup>cd</sup>
	40–45	0.22 $\pm$ 0.03 <sup>ac</sup>	85.0 $\pm$ 2.1 <sup>ac</sup>	2.37 $\pm$ 3.41	0.004 $\pm$ 0.002	0.106 $\pm$ 0.020 <sup>acd</sup>	0.107 $\pm$ 0.023
	80–85	0.15 $\pm$ 0.02	89.8 $\pm$ 1.0	-	0.010 $\pm$ 0.007	0.039 $\pm$ 0.003	0.097 $\pm$ 0.006
	110–115	0.12 $\pm$ 0.01	91.5 $\pm$ 0.5	-	0.023 $\pm$ 0.010	0.045 $\pm$ 0.007	0.050 $\pm$ 0.010
Degraded open peatland (DO) c	10–15	0.20 $\pm$ 0.03 <sup>a</sup>	86.2 $\pm$ 1.6 <sup>a</sup>	0.17 $\pm$ 0.06	0.005 $\pm$ 0.004 <sup>A</sup>	0.028 $\pm$ 0.001 <sup>abc</sup>	0.167 $\pm$ 0.006 <sup>abd</sup>
	40–45	0.12 $\pm$ 0.04 <sup>b</sup>	91.7 $\pm$ 2.1 <sup>b</sup>	-	0.014 $\pm$ 0.002	0.041 $\pm$ 0.002 <sup>b</sup>	0.063 $\pm$ 0.006
	80–85	0.14 $\pm$ 0.02	90.4 $\pm$ 1.4	-	0.006 $\pm$ 0.020	0.042 $\pm$ 0.009	0.070 $\pm$ 0.026
	110–115	0.15 $\pm$ 0.02	89.7 $\pm$ 0.9	-	0.022 $\pm$ 0.009	0.045 $\pm$ 0.005	0.083 $\pm$ 0.006
Agricultural open peatland (AO) d	10–15	0.18 $\pm$ 0.01	87.9 $\pm$ 0.7	-	0.008 $\pm$ 0.004	0.066 $\pm$ 0.002 <sup>bc</sup>	0.107 $\pm$ 0.006 <sup>abc</sup>
	40–45	0.17 $\pm$ 0.01	88.2 $\pm$ 0.5	-	0.017 $\pm$ 0.002	0.063 $\pm$ 0.007 <sup>b</sup>	0.107 $\pm$ 0.038
	80–85	0.13 $\pm$ 0.01	90.7 $\pm$ 0.1	-	0.009 $\pm$ 0.003	0.043 $\pm$ 0.007	0.077 $\pm$ 0.006
	110–115	0.13 $\pm$ 0.00	90.9 $\pm$ 0.4	-	0.023 $\pm$ 0.016	0.042 $\pm$ 0.013	0.067 $\pm$ 0.006



the undrained forest and the highest-BD and lowest-porosity peat was in the degraded site (Table 2). The BD of surface peat was 54 % higher in the degraded site and 31–38 % higher in the drained forest and agricultural sites than in the undrained forest ( $0.13 \text{ g cm}^{-3}$ ). At 40–45 cm depth in the drained forest, BD was notably (29–88 %) higher and porosity was 4–8 % lower than at the same depth in the other sites. The deeper peat layers at the four sites were more similar to one another, with BD in the range  $0.12\text{--}0.15 \text{ g cm}^{-3}$  and porosity 89.2–91.5 % at the two deepest sampling depths in all sites (Table 2).

The density of woody fraction in the surface (10–15 cm) peat at the undrained forest site was double that in the drained forest, and up to six times that on the open sites (Table 2); whereas the density of this fraction in the 40–45 cm layer was highest at the open sites. The density of fibric fraction in the surface peat (10–15 cm) was highest in the drained forest, where it was also quite high at 40 cm depth. The density of this fraction at the top two sampling depths was clearly lowest at the degraded site. The density of amorphous fraction in the top two peat layers was highest at the open sites; for the agricultural site more than double, and for the degraded site nearly three times the corresponding values for the two forest sites. At greater sampling depths, differences between the sites were less clear. Living roots were found at the upper two sampling depths only, their mass proportions being 1.9–6.6 % in the forest sites and 0–0.17 % in the open sites (Table 2).

The peat pH was very low (2.68–3.74) and showed some distinct patterns; most notably, it was relatively high in all of the peat layers sampled at the agricultural site (Appendix 1). There were two clear trends in total nutrient concentrations in the upper two peat layers: cation (Mg, Ca, Zn, Mn) and ash concentrations were higher at the open sites; and N and P concentrations were higher at the forest sites (Figure 3, Appendix 1). Peat C concentration tended to increase with depth at the forest sites, but was relatively invariable with depth at the open sites. However, C concentration peaked at 40–45 cm depth in the drained forest. Drained-forest peat at 40–45 cm depth displayed lower C/N quotient and lower N and P concentrations than undrained-forest peat from the same depth, and in this regard was more similar to peat from the same depth in the open sites (Figure 3 and Appendix). At the agricultural site, Ca, Mg and K concentrations were higher than at the other sites (Appendix). At the undrained forest site, the Fe concentration in the shallowest (10–15 cm) peat was around half that at the other sites. There were no clear differences in concentrations of Al, S and Na between the four land-use types.

## DISCUSSION AND CONCLUSIONS

The physical and chemical properties of peat generally differed between land uses. We interpret the differences as reflections of change that occurred at our three disturbed study sites after conversion from undrained peat swamp forest, in line with our first hypothesis. The most distinct differences between undrained forest and altered sites were in the uppermost two peat layers (10–15 cm and 40–45 cm depths), in accordance with our second hypothesis. However, while the properties of the upper layers of peat at the open sites could be linked with typical water table levels as in the forest sites, they had been additionally modified by repeated fires and by tilling in the agricultural site. Thus, the effects of land use on peat properties were clearest at the open sites, where both water table level and vegetation type differed substantially from those in undrained forest. This accords with our third hypothesis, although the main contributing processes (discussed later) are not similar at all of the study sites.

The observed differences in peat properties can be interpreted in terms of peat breakdown processes. Peat breakdown can be divided into biological decomposition leading to gaseous or waterborne C losses, and physical processes that modify and reposition materials. Especially after drainage enhancements, processes including peat shrinkage, compaction and consolidation result in an increase in peat BD (Minkinen & Laine 1998, Laiho *et al.* 1999, Kurnain *et al.* 2001, Kool *et al.* 2006, Hooijer *et al.* 2012, Couwenberg & Hooijer 2013). Accordingly, peat BD was higher at our drained sites than in the undrained forest. The high BD we observed in drained forest may result from particulate organic matter being flushed out of surface peat (Moore *et al.* 2013) and concentrated close to the average water table (at 50 cm depth), alongside compaction arising from aerobic decomposition of the deeper layers of unsaturated peat and compression by the mass of the tree stand.

Due to peat loss in fires and other disturbance of surface peat at the open sites, the processes affecting peat properties in forest and open sites are not fully comparable. In the severely fire-affected degraded site and the actively managed agricultural site, the observed characteristics of surface peat may be significantly influenced by peat combustion. Smouldering, which often occurs at high temperatures during peat combustion (Usup *et al.* 2004), is similar to the pyrolysis process that is used to produce biochar (Lehman & Joseph 2009). The apparent changes in surface peat at our open sites (increased BD and concentrations of base cations,



ash, Fe and C; decreased N concentration and particle size) resemble the outcome of biochar pyrolysis of organic matter (Certini 2005, Dikici & Yilmaz 2006, Hadden *et al.* 2013). The aged, finer-particled and largely vegetation-free peats exposed at the surfaces of the open sites are further prone to the effects of high temperatures and erosion. Wind and water can move fine particles so that they eventually fill empty spaces (larger pores, cracks and cavities) in lower-lying peat surfaces. It is likely that the high BD of surface peat at the open sites can be attributed, in part, to this physical process.

In our forested study sites, the highest concentrations of N, P, K and Si were in the topmost peat of the rhizosphere, which in this ombrotrophic system is the main location of litter deposition and organic matter turnover. In forested ombrotrophic peatlands, the highest organic matter decomposition rates are observed in the topmost peat, which encloses most of the recently deposited litter and is most often exposed to oxic conditions (Clymo 1984). The more advanced decomposition status of deeper peat layers in forested sites is expressed as a decrease in N, P and K and an increase in C/N quotient. An increase in C/N quotient with depth is also reported in several other studies from ombrotrophic peatlands (Kurnain *et al.* 2001, Takakai *et al.* 2006, Anshari *et al.* 2010, Lampela *et al.* 2014).

In the open study sites, fires and repeated biomass removal have influenced surface peat chemistry in three ways: i) older peat is exposed at the surface, offering a substrate of advanced decomposition status that would otherwise be found only in deeper peat layers; ii) peat properties change during combustion and agricultural soil management (tilling, fertilisation); and iii) readily soluble elements in the peat may become depleted if vegetation and litter turnover replenish them less rapidly than they are lost by leaching. Volatilisation of N during peat combustion and biomass removal, continued decomposition of recalcitrant peat, and additions of low-lability C and N to the peat from fresh litter of non-peatland species, may all have contributed to the smaller N concentration and larger C/N quotient detected in surface peat at the open sites. Thus, the chemical properties of the topmost peat at the open sites resemble those found only at or below 80–85 cm depth in the forested sites. Additions of ash to the surface peat during fires has led to enrichment with cations (Ca, Mg, Mn, Fe, Na and Zn) at both open sites, as observed in several other tropical peatlands (Andriesse 1988, Kurnain *et al.* 2001, Dikici & Yilmaz 2006, Takakai *et al.* 2006). At the agricultural site, soil preparation (tilling) and water filtering through the surface peat may have widely distributed

K from mineral fertilisers within the peat profile. Generally, it has been observed that K in organic soils cannot compete for cation exchange sites against ions which have stronger electric charges (e.g.,  $H^+$ ,  $Ca^{2+}$ ,  $Mg^{2+}$ ), so that it will leach if not retained in the biological cycle by vegetation (Laiho *et al.* 1999).

It has generally been noted that nutrient status changes less if the change in type and volume of vegetation that accompanies land-use change remains low. For example, the primary purpose of drainage in boreal peatland forests is to improve the growth of original forest vegetation; in this case, nutrient cycling is largely sustained and nutrient reserves in the peat are mostly rather stable (Laiho *et al.* 1999, Westman & Laiho 2003). In contrast, during land reclamation in the tropics, natural forest vegetation is usually replaced with planted vegetation types (plantations, smallholder crops, *etc.*), and the ecosystem's nutrient cycling alters more dramatically as a result (McGrath *et al.* 2001, Anshari *et al.* 2010).

The result of the greater changes in physical and chemical properties of surface peat that we observed at the open sites is that, as compared with forest sites, they offer more compacted and nutrient-impovertised substrates for plants. Compaction is known to reduce the hydraulic conductivity of peat (Päivänen 1973), which might increase flooding, but also increase water retention in the peat. The reduced concentrations of N and P in surface peat at open sites mean that fertilisation is likely to be a necessity for maintaining land production capacity (Andriesse 1988, Rieley & Page 2005). Adding nutrients to the well-decomposed (high C/N) peat at open sites can be expected to enhance decomposition and lead to increased rates of peat loss and greenhouse gas emissions (Jauhiainen *et al.* 2014). If ombrotrophic peat swamp forest is reclaimed, we cannot avoid changes in peat physical characteristics. However, the management options chosen can influence the magnitude of changes in peat properties that follow. To provide sustainable-use guidelines aiming to minimise losses of accumulated thick peat from storage, further improvements to our understanding of decomposability and decomposition processes in peat under different land management regimes will be needed.

## ACKNOWLEDGEMENTS

We thank Dr. Hidenori Takahashi and Dr. Takashi Inoue for providing the data we used to calculate average water table depths at the study sites. We thank the Center for International Cooperation in Sustainable Management of Tropical Peatland

(CIMTROP) for providing their facilities and help during field sampling. We also acknowledge Marjut Wallner for her help and expertise. This research was conducted as part of the RETROPEAT project (Restoration Impact on Tropical Peat Carbon and Nitrogen Dynamics, Decision 253933), funded by the Academy of Finland, with additional contributions from University of Helsinki Peatlanders prize money and the Jenny and Antti Wihuri Foundation.

## REFERENCES

- Andriesse, J.P. (1988) *Nature and Management of Tropical Peat Soils*. FAO Bulletin 59, Food and Agriculture Organization of the United Nations, Rome, 165 pp.
- Anshari, G.Z., Afifudin, M., Nuriman, M., Gusmayanti, E., Arianie, L., Susana, R., Nusantara, R.W., Sugardjito, J. & Rafiastanto, A. (2010) Drainage and land use impacts on changes in selected peat properties and peat degradation in West Kalimantan Province, Indonesia. *Biogeosciences*, 7, 3403–3419.
- Certini, G. (2005) Effects of fire on properties of forest soils: a review. *Oecologia*, 143, 1–10.
- Clymo, R.S. (1984) The limits to peat bog growth. *Philosophical Transactions of the Royal Society of London B*, 303(1117), 605–654.
- Comeau, L.-P., Hergoualc’h, K., Smith, J.U. & Verchot, L. (2013) Conversion of intact peat swamp forest to oil palm plantation: Effects on soil CO<sub>2</sub> fluxes in Jambi, Sumatra. Working Paper 110, CIFOR, Bogor, Indonesia, 8 pp.
- Couwenberg, J. & Hooijer, A. (2013) Towards robust subsidence-based soil carbon emission factors for peat soils in south-east Asia, with special reference to oil palm plantations. *Mires and Peat*, 12(01), 1–13.
- Dikici, H. & Yilmaz, C.H. (2006) Peat fire effects on some properties of an artificially drained peatland. *Journal of Environmental Quality*, 35(3), 866–70.
- Driessen, P.M. & Rochimah, L. (1976) The physical properties of lowland peats from Kalimantan, Indonesia. In: *Peat and Podzolic Soils and Their Potential for Agriculture in Indonesia*. Proceedings ATA Midterm Seminar, Tugu, Soil Research Institute, Bogor, Indonesia, Bulletin 3, 56–73.
- Hadden, R., Guillermo, R. & Belcher, C. (2013) Study of the competing chemical reactions in the initiation and spread of smouldering combustion in peat. *Proceedings of the Combustion Institute*, 34, 2547–2553.
- Hooijer, A., Page, S., Canadell, J., Silvius, M., Kwadijk, J., Wösten, H. & Jauhiainen, J. (2010) Current and future CO<sub>2</sub> emissions from drained peatlands in Southeast Asia. *Biogeosciences*, 7, 1505–1514.
- Hooijer, A., Page, S., Jauhiainen, J., Lee, W.A., Idris, A. & Anshari, G. (2012) Subsidence and carbon loss in drained tropical peatlands. *Biogeosciences*, 9, 1053–1071.
- Hoscilo, A., Page, S., Tansey, K. & Rieley, J. (2011) Effect of repeated fires on land-cover change on peatland in southern Central Kalimantan, Indonesia, from 1973 to 2005. *International Journal of Wildland Fire*, 20, 578–588.
- Jauhiainen, J., Kerojoki, O., Silvennoinen, H., Limin, S. & Vasander, H. (2014) Heterotrophic respiration in drained tropical peat is greatly affected by temperature - a passive ecosystem cooling experiment. *Environmental Research Letters*, 9(10), 18 pp.
- Jauhiainen, J., Limin, S., Silvennoinen, H. & Vasander, H. (2008) Carbon dioxide and methane fluxes in drained tropical peat before and after hydrological restoration. *Ecology*, 89(12), 3503–3514.
- Jauhiainen, J., Takahashi, H., Heikkinen, J., Martikainen, P. & Vasander, H. (2005) Carbon fluxes from a tropical peat swamp forest floor. *Global Change Biology*, 11, 1788–1797.
- Kool, D.M., Burman, P. & Hoekman, D.H. (2006) Oxidation and compaction of a collapsed peat dome in Central Kalimantan. *Geoderma*, 137, 217–225.
- Kurnain, A., Notohadikusomo, T., Radgajuguk, B. & Hastuti, S. (2001) Peat soil properties related to degree of decomposition under different land use systems. *International Peat Journal*, 11, 67–78.
- Laiho, R., Sallantausta, T. & Laine, J. (1999) The effect of forestry drainage on vertical distributions of major plant nutrients in peat soils. *Plant and Soil*, 207, 169–181.
- Lampela, M., Jauhiainen, J. & Vasander, H. (2014) Surface peat structure and chemistry in a tropical peat swamp forest. *Plant and Soil*, 382, 329–347.
- Lehman, J. & Joseph, S. (eds.) (2009) *Biochar for Environmental Management: Science and Technology*, Earthscan, London, 448 pp.
- McGrath, D., Smith, K., Gholz, H. & de Assis Oliveira, F. (2001) Effects of land-use change on soil nutrient dynamics in Amazonia. *Ecosystems*, 4, 625–645.
- Miettinen, J. & Liew, S. (2010) Status of peatland degradation and development in Sumatra and Kalimantan. *Ambio*, 39, 394–401.
- Minkinen, K. & Laine, J. (1998) Effect of forest drainage on the peat bulk density of pine mires in

- Finland. *Canadian Journal of Forest Research*, 28, 178–186.
- Moore, S., Evans, C., Page, S., Garnett, M., Jones, T., Freeman, T., Hooijer, A., Wiltshire, A., Limin, S. & Gauci, V. (2013) Deep instability of deforested tropical peatlands revealed by fluvial organic carbon fluxes. *Nature*, 493, 660–663.
- Page, S.E., Rieley, J.O. & Banks, C.J. (2011) Global and regional importance of the tropical peatland carbon pool. *Global Change Biology*, 17, 798–818.
- Page, S.E., Rieley, J.O., Shotyk, W. & Weiss, D. (1999) Interdependence of peat and vegetation in a tropical peat swamp forest. *Philosophical Transactions of the Royal Society of London B*, 354(1391), 1885–1897.
- Page, S.E., Siegert, F., Rieley, J.O., Boehm, H.-D.V., Jaya, A. & Limin, S. (2002) The amount of carbon released from peat and forest fires in Indonesia during 1997. *Nature*, 420(7), 61–65.
- Päivänen, J. (1973) Hydraulic conductivity and water retention in peat soils. *Acta Forestalia Fennica*, 129, 1–70.
- Pitkänen, A., Turunen, J. & Simola, H. (2011) Comparison of different types of peat corers in volumetric sampling. *Suo*, 62(2), 51–57.
- Radjagukguk, B., Nishizaki, Y., Yazawa, Y. & Yamaguchi, T. (1998) Characteristics of tropical peat and its possible uses as a soil ameliorant. *International Peat Journal*, 8, 107–112.
- Rieley, J. & Page, S. (eds.) (2005) *Wise Use of Tropical Peatlands: Focus on South East Asia*. ALTERRA - Wageningen University and Research Center and the EU INCO - STRAPEAT and RESTORPEAT Partnerships, 237 pp.
- Sundari, S., Hirano, T., Yamada, H., Kusin, K. & Limin, S. (2012) Effect of groundwater level on soil respiration in tropical peat swamp forests. *Journal of Agricultural Meteorology*, 68, 121–134.
- Takakai, F., Morishita, T., Hashidoko, Y., Darung, U., Kuramochi, K., Dohong, S., Limin, S. & Hatano, R. (2006) Effects of agricultural land-use change and forest fire on N<sub>2</sub>O emission from tropical peatlands, Central Kalimantan, Indonesia. *Soil Science and Plant Nutrition*, 52, 662–674.
- Usup, A., Hashimoto, Y., Takahashi, H. & Havasaka, H. (2004) Combustion and thermal characteristics of peat fire in tropical peatland in Central Kalimantan, Indonesia. *Tropics*, 14(1), 1–19.
- Vasander, H. & Kettunen, A. (2006) Carbon in boreal peatlands. In: Wieder, R.K. & Vitt, D.H. (eds.) *Boreal Peatland Ecosystems*, Ecological Studies 188, Springer-Verlag, Heidelberg, 165–194.
- Westman, C.J. & Laiho, R. (2003) Nutrient dynamics of peatland forests after water-level drawdown. *Biogeochemistry*, 63, 269–298.

Submitted 05 Jly 2015, revision 18 Sep 2015

Editor: Olivia Bragg

Author for correspondence:

Mari Könönen, Department of Forest Sciences, University of Helsinki, P.O. Box 27, Latokartanonkaari 7, FI-00014 University of Helsinki, Finland. Tel: +358-40-7780292; E-mail: mari.kononen@helsinki.fi

## Appendix

Table A1. pH, ash content, total nutrient concentrations (C, N, P, K), C/N and N/P in peat collected from different sampling depths at the four study sites, calculated on dry mass basis. Mean  $\pm$  standard deviation is provided in each case. Analyses were carried out on the three non-fractionated field replicate samples collected from each depth and site, after pooling. Statistically significant differences between the respective sites and depths are indicated by superscript indices which denote the significantly different site: a = undrained forest; b = drained forest; c = degraded open peatland; d = agricultural open peatland). Statistically significant differences with  $p < 0.01$  are indicated by lowercase letters, and those with  $0.01 < p < 0.05$  are indicated by uppercase letters.

Land use	Sampling depth (cm)	pH	ash (%)	C (%)	N (%)	P (mg g <sup>-1</sup> )	K (mg g <sup>-1</sup> )	C/N	N/P
Undrained forest (UF) a	10–15	3.40	0.60 $\pm$ 0.04 <sup>d</sup>	55.53 $\pm$ 0.24 <sup>cd</sup>	1.60 $\pm$ 0.02 <sup>bcd</sup>	0.156 $\pm$ 0.007 <sup>cd</sup>	0.24 $\pm$ 0.01 <sup>D</sup>	34.8 $\pm$ 0.60 <sup>cd</sup>	13.4 $\pm$ 1.5 <sup>cd</sup>
	40–45	3.74	0.36 $\pm$ 0.31 <sup>D</sup>	57.30 $\pm$ 0.51 <sup>B</sup>	1.59 $\pm$ 0.03 <sup>bcd</sup>	0.106 $\pm$ 0.004 <sup>bcd</sup>	0.13 $\pm$ 0.02 <sup>d</sup>	36.1 $\pm$ 0.98 <sup>bcd</sup>	20.4 $\pm$ 2.0 <sup>d</sup>
	80–85	2.98	0.63 $\pm$ 0.03 <sup>C</sup>	61.49 $\pm$ 0.18 <sup>Bc</sup>	0.86 $\pm$ 0.04	0.028 $\pm$ 0.001	0.09 $\pm$ 0.04 <sup>Cd</sup>	72.0 $\pm$ 3.52	46.6 $\pm$ 10.0
Drained forest (DF) b	10–15	3.1	0.61 $\pm$ 0.08 <sup>d</sup>	55.46 $\pm$ 0.46 <sup>cd</sup>	1.88 $\pm$ 0.13 <sup>acd</sup>	0.149 $\pm$ 0.005 <sup>cd</sup>	0.17 $\pm$ 0.01 <sup>D</sup>	29.6 $\pm$ 1.86 <sup>cd</sup>	21.4 $\pm$ 3.9 <sup>d</sup>
	40–45	2.68	0.39 $\pm$ 0.02	63.76 $\pm$ 0.48 <sup>acd</sup>	0.89 $\pm$ 0.03 <sup>a</sup>	0.059 $\pm$ 0.001 <sup>acd</sup>	0.07 $\pm$ 0.00 <sup>d</sup>	71.3 $\pm$ 3.19 <sup>a</sup>	32.6 $\pm$ 3.6
	80–85	2.92	0.43 $\pm$ 0.04	59.25 $\pm$ 0.29 <sup>A</sup>	0.86 $\pm$ 0.10	0.036 $\pm$ 0.001 <sup>c</sup>	0.06 $\pm$ 0.001 <sup>cd</sup>	68.2 $\pm$ 9.18	33.8 $\pm$ 3.2
	110–115	3.13	0.32 $\pm$ 0.06	60.40 $\pm$ 0.58	0.73 $\pm$ 0.02	0.024 $\pm$ 0.002 <sup>d</sup>	0.04 $\pm$ 0.002	82.8 $\pm$ 3.03	37.1 $\pm$ 2.6 <sup>cd</sup>
Degraded open peatland (DO) c	10–15	3.57	0.88 $\pm$ 0.01	58.74 $\pm$ 0.99 <sup>ab</sup>	0.85 $\pm$ 0.06 <sup>ab</sup>	0.038 $\pm$ 0.001 <sup>ab</sup>	0.13 $\pm$ 0.011 <sup>Ad</sup>	69.4 $\pm$ 4.92 <sup>ab</sup>	44.4 $\pm$ 7.5 <sup>b</sup>
	40–45	3.30	0.73 $\pm$ 0.03	58.52 $\pm$ 0.05 <sup>b</sup>	0.80 $\pm$ 0.03 <sup>a</sup>	0.032 $\pm$ 0.001 <sup>ab</sup>	0.15 $\pm$ 0.031 <sup>d</sup>	72.8 $\pm$ 2.44 <sup>a</sup>	29.9 $\pm$ 8.7
	80–85	2.96	0.22 $\pm$ 0.01 <sup>AD</sup>	58.82 $\pm$ 0.29 <sup>a</sup>	0.75 $\pm$ 0.02	0.022 $\pm$ 0.006 <sup>bd</sup>	0.19 $\pm$ 0.026 <sup>Abd</sup>	78.2 $\pm$ 2.95	49.8 $\pm$ 8.2
	110–115	3.35	0.23 $\pm$ 0.01	57.86 $\pm$ 1.07	0.70 $\pm$ 0.04	0.014 $\pm$ 0.002 <sup>d</sup>	0.15 $\pm$ 0.016	83.2 $\pm$ 2.93	73.2 $\pm$ 5.7 <sup>bd</sup>
Agricultural open peatland (AO) d	10–15	3.30	1.10 $\pm$ 0.05 <sup>b</sup>	58.62 $\pm$ 0.91 <sup>ab</sup>	0.88 $\pm$ 0.06 <sup>ab</sup>	0.046 $\pm$ 0.002 <sup>ab</sup>	0.28 $\pm$ 0.028 <sup>Bc</sup>	66.5 $\pm$ 3.05 <sup>ab</sup>	33.8 $\pm$ 4.7 <sup>a</sup>
	40–45	3.37	0.75 $\pm$ 0.04 <sup>A</sup>	58.31 $\pm$ 1.67 <sup>b</sup>	0.77 $\pm$ 0.03 <sup>a</sup>	0.031 $\pm$ 0.007 <sup>ab</sup>	0.37 $\pm$ 0.092 <sup>abc</sup>	76.1 $\pm$ 5.26 <sup>a</sup>	44.3 $\pm$ 12.4 <sup>a</sup>
	80–85	3.38	0.62 $\pm$ 0.36 <sup>C</sup>	59.58 $\pm$ 0.58	0.88 $\pm$ 0.03	0.035 $\pm$ 0.005 <sup>c</sup>	0.39 $\pm$ 0.029 <sup>abc</sup>	67.5 $\pm$ 3.07	33.9 $\pm$ 5.9
	110–115	3.47	0.60 $\pm$ 0.02	58.24 $\pm$ 0.87	0.68 $\pm$ 0.16	0.077 $\pm$ 0.001 <sup>bc</sup>	0.36 $\pm$ 0.023	89.6 $\pm$ 22.86	11.4 $\pm$ 2.8 <sup>bc</sup>

Table A2. Total nutrient concentrations (Ca, Mg, Mn, Zn, Na, Al, Fe, S, Si) in peat collected from different sampling depths at the four study sites, calculated on dry mass basis. Mean  $\pm$  standard deviation is provided in each case. Analyses were carried out on the three non-fractionated field replicate samples collected from each depth and site, after pooling. Statistically significant differences between the respective sites and depths are indicated by superscript indices which denote the significantly different site: a = undrained forest; b = drained forest; c = degraded open peatland; d = agricultural open peatland). Statistically significant differences with  $p < 0.01$  are indicated by lowercase letters, and those with  $0.01 < p < 0.05$  are indicated by uppercase letters.

Land use	Sampling depth (cm)	Ca (mg g <sup>-1</sup> )	Mg (mg g <sup>-1</sup> )	Mn (mg g <sup>-1</sup> )	Zn (mg g <sup>-1</sup> )	Na (mg g <sup>-1</sup> )	Al (mg g <sup>-1</sup> )	Fe (mg g <sup>-1</sup> )	S (mg g <sup>-1</sup> )	Si (mg g <sup>-1</sup> )
Undrained forest (UF) a	10–15	0.17 $\pm$ 0.01 <sup>cd</sup>	0.59 $\pm$ 0.02 <sup>D</sup>	0.005 $\pm$ 0.000 <sup>c</sup>	0.004 $\pm$ 0.001 <sup>c</sup>	0.051 $\pm$ 0.006	0.549 $\pm$ 0.026 <sup>cd</sup>	0.194 $\pm$ 0.005 <sup>bcd</sup>	0.912 $\pm$ 0.078	0.045 $\pm$ 0.007 <sup>D</sup>
	40–45	0.11 $\pm$ 0.03 <sup>cd</sup>	0.36 $\pm$ 0.01 <sup>c</sup>	0.001 $\pm$ 0.000 <sup>cd</sup>	0.006 $\pm$ 0.001 <sup>bD</sup>	0.058 $\pm$ 0.018	0.573 $\pm$ 0.007 <sup>bd</sup>	0.204 $\pm$ 0.003 <sup>c</sup>	0.925 $\pm$ 0.103 <sup>b</sup>	0.024 $\pm$ 0.003
	80–85	0.11 $\pm$ 0.02 <sup>d</sup>	0.55 $\pm$ 0.02 <sup>bc</sup>	0.003 $\pm$ 0.000	0.005 $\pm$ 0.000	0.060 $\pm$ 0.021	0.992 $\pm$ 0.017 <sup>bcd</sup>	0.290 $\pm$ 0.013 <sup>bcd</sup>	0.782 $\pm$ 0.116	0.017 $\pm$ 0.002
Drained forest (DF) b	10–15	0.17 $\pm$ 0.01 <sup>cd</sup>	0.44 $\pm$ 0.01 <sup>d</sup>	0.005 $\pm$ 0.001 <sup>c</sup>	0.004 $\pm$ 0.000 <sup>c</sup>	0.053 $\pm$ 0.016	0.487 $\pm$ 0.010 <sup>cd</sup>	0.377 $\pm$ 0.011 <sup>a</sup>	0.788 $\pm$ 0.053	0.040 $\pm$ 0.007
	40–45	0.08 $\pm$ 0.01 <sup>cd</sup>	0.15 $\pm$ 0.01 <sup>cd</sup>	-	0.002 $\pm$ 0.000 <sup>ac</sup>	0.024 $\pm$ 0.002	0.267 $\pm$ 0.005 <sup>ac</sup>	0.217 $\pm$ 0.004 <sup>c</sup>	0.531 $\pm$ 0.020 <sup>a</sup>	0.021 $\pm$ 0.005
	80–85	0.06 $\pm$ 0.01 <sup>d</sup>	0.20 $\pm$ 0.00 <sup>D</sup>	-	0.002 $\pm$ 0.000 <sup>a</sup>	0.030 $\pm$ 0.002 <sup>d</sup>	0.615 $\pm$ 0.007 <sup>acd</sup>	0.752 $\pm$ 0.008 <sup>acd</sup>	0.727 $\pm$ 0.013	0.018 $\pm$ 0.003
	110–115	0.07 $\pm$ 0.01 <sup>d</sup>	0.11 $\pm$ 0.00 <sup>D</sup>	-	0.003 $\pm$ 0.000	0.030 $\pm$ 0.002	0.372 $\pm$ 0.017 <sup>d</sup>	0.698 $\pm$ 0.021 <sup>cd</sup>	0.728 $\pm$ 0.067	0.016 $\pm$ 0.002
Degraded open peatland (DO) c	10–15	1.62 $\pm$ 0.09 <sup>ab</sup>	0.69 $\pm$ 0.02	0.011 $\pm$ 0.000 <sup>abd</sup>	0.007 $\pm$ 0.001 <sup>ab</sup>	0.066 $\pm$ 0.019	0.750 $\pm$ 0.018 <sup>abd</sup>	0.364 $\pm$ 0.008 <sup>a</sup>	0.688 $\pm$ 0.095	0.021 $\pm$ 0.004
	40–45	0.97 $\pm$ 0.08 <sup>ab</sup>	0.77 $\pm$ 0.01 <sup>ab</sup>	0.007 $\pm$ 0.000 <sup>ab</sup>	0.008 $\pm$ 0.002 <sup>bd</sup>	0.064 $\pm$ 0.024	0.626 $\pm$ 0.019 <sup>bd</sup>	0.388 $\pm$ 0.015 <sup>abd</sup>	0.773 $\pm$ 0.112	0.019 $\pm$ 0.006
	80–85	0.13 $\pm$ 0.03 <sup>c</sup>	0.20 $\pm$ 0.01 <sup>aD</sup>	-	0.004 $\pm$ 0.000	0.067 $\pm$ 0.029	0.354 $\pm$ 0.017 <sup>ab</sup>	0.085 $\pm$ 0.008 <sup>abd</sup>	0.812 $\pm$ 0.156	0.015 $\pm$ 0.001
	110–115	0.10 $\pm$ 0.02 <sup>d</sup>	0.10 $\pm$ 0.00 <sup>D</sup>	-	0.003 $\pm$ 0.001	0.066 $\pm$ 0.014	0.413 $\pm$ 0.009 <sup>d</sup>	0.058 $\pm$ 0.001 <sup>bd</sup>	0.846 $\pm$ 0.119	0.018 $\pm$ 0.004
Agricultural open peatland (AO) d	10–15	2.08 $\pm$ 0.08 <sup>ab</sup>	0.91 $\pm$ 0.02 <sup>Ab</sup>	0.007 $\pm$ 0.000 <sup>c</sup>	0.005 $\pm$ 0.001	0.085 $\pm$ 0.027	0.340 $\pm$ 0.006 <sup>abc</sup>	0.336 $\pm$ 0.074 <sup>a</sup>	0.897 $\pm$ 0.139	0.032 $\pm$ 0.004 <sup>A</sup>
	40–45	0.94 $\pm$ 0.47 <sup>ab</sup>	0.56 $\pm$ 0.22 <sup>b</sup>	0.004 $\pm$ 0.001 <sup>ab</sup>	0.002 $\pm$ 0.000 <sup>Ac</sup>	0.080 $\pm$ 0.033	0.317 $\pm$ 0.066 <sup>ac</sup>	0.177 $\pm$ 0.027 <sup>c</sup>	0.860 $\pm$ 0.264	0.024 $\pm$ 0.004
	80–85	0.78 $\pm$ 0.51 <sup>abc</sup>	0.48 $\pm$ 0.26 <sup>aBC</sup>	0.004 $\pm$ 0.002	0.003 $\pm$ 0.001	0.101 $\pm$ 0.011 <sup>b</sup>	0.354 $\pm$ 0.019 <sup>ac</sup>	0.190 $\pm$ 0.011 <sup>abc</sup>	0.926 $\pm$ 0.145	0.024 $\pm$ 0.002
	110–115	0.85 $\pm$ 0.01 <sup>bc</sup>	0.41 $\pm$ 0.01 <sup>BC</sup>	0.007 $\pm$ 0.000	0.004 $\pm$ 0.000	0.071 $\pm$ 0.009	0.540 $\pm$ 0.010	0.278 $\pm$ 0.005 <sup>bc</sup>	0.870 $\pm$ 0.150	0.026 $\pm$ 0.005