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Key Points:

- Disturbance, forest dynamics, and tip-up pools influence carbon accumulation
- Tip-up pools form frequently in peat swamp forests
- Infilled fossil pools dominate the peat deposits of peat domes in Borneo

Correspondence to:

R. Dommain,
rene.dommain@gmx.de

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Forest dynamics and tip-up pools drive pulses of high carbon accumulation rates in a tropical peat dome in Borneo (Southeast Asia)

René Dommain^{1,2}, Alexander R. Cobb³, Hans Joosten¹, Paul H. Glaser⁴, Amy F. L. Chua^{3,5}, Laure Gandois^{3,6,7}, Fuu-Ming Kai³, Anders Noren⁸, Kamariah A. Salim⁹, N. Salihah H. Su'ut¹⁰, and Charles F. Harvey^{3,11}

¹Institute of Botany and Landscape Ecology, University of Greifswald, Greifswald, Germany, ²Now at National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia, USA, ³Singapore-MIT Alliance for Research and Technology, Singapore, Singapore, ⁴Department of Earth Sciences, University of Minnesota, Minneapolis, Minnesota, USA, ⁵Vale Malaysia Minerals Sdn Bhd, Perak, Malaysia, ⁶Université de Toulouse: UPS, INP, EcoLab (Laboratoire Ecologie fonctionnelle et Environnement), ENSAT, Castanet-Tolosan, France, ⁷CNRS, EcoLab, Castanet-Tolosan, France, ⁸National Lacustrine Core Facility, University of Minnesota, Minneapolis, Minnesota, USA, ⁹Biology Programme, Universiti Brunei Darussalam, Bandar Seri Begawan, Brunei Darussalam, ¹⁰Brunei Darussalam Heart of Borneo Centre, Bandar Seri Begawan, Brunei Darussalam, ¹¹Massachusetts Institute of Technology, Parsons Laboratory, Cambridge, Massachusetts, USA

Abstract Peatlands of Southeast Asia store large pools of carbon but the mechanisms of peat accumulation in tropical forests remain to be resolved. Patch dynamics and forest disturbance have seldom been considered as drivers that can amplify or dampen rates of peat accumulation. Here we used a modified piston corer, noninvasive geophysical measurements, and geochemical and paleobotanical techniques to establish the effect of tree fall on carbon accumulation rates in a peat swamp forest dominated by *Shorea albida* in Brunei (Borneo). Carbon initially accumulated in a mangrove forest at over $300 \text{ g C m}^{-2} \text{ yr}^{-1}$ but declined to less than $50 \text{ g C m}^{-2} \text{ yr}^{-1}$ with the establishment of a peat swamp forest. A rapid accumulation pulse of $720\text{--}960 \text{ g C m}^{-2} \text{ yr}^{-1}$ occurred around 1080 years ago as a tip-up pool infilled. Tip-up pools are common in the peatlands of northwest Borneo where windthrow and lightning strikes produce tree falls at a rate of 4 trees ha^{-1} every decade. A simulation model indicates that tip-up pools, which are formed across the entire forested peat dome, produce local discontinuities in the peat deposit, when peat is removed to create a pool that is rapidly filled with younger material. The resulting discontinuities in peat age at the base and sides of pool deposits obscure linkages between carbon accumulation rates and climate and require new approaches for paleoenvironmental reconstructions. Our results suggest that carbon accumulation in tropical peat swamps may be based on fundamentally different peat-forming processes than those of northern peatlands.

1. Introduction

The peatlands of equatorial Southeast Asia contain a globally significant reservoir of over 20 Pg carbon that has been rapidly accumulating over the past several thousand years [Dommain et al., 2011, 2014]. However, rapid carbon accumulation in these tropical peatlands is puzzling because organic matter decomposition normally increases with higher temperature [Trumbore et al., 1996; Davidson et al., 2000; Knorr et al., 2005]. High water tables and recalcitrant woody matter may retard decay [Couwenberg et al., 2010], but the mechanisms that control peat accumulation in tropical peatlands have rarely been studied systematically, unlike those in high-latitude peatlands [e.g., Wieder and Vitt, 2006; Baird et al., 2009].

On the regional scale ($5,000\text{--}100,000 \text{ km}^2$) and over millennial time spans, rates of carbon accumulation in Southeast Asian peatlands seem to be controlled by changes in sea level and hydroclimate, such as long-term shifts in the mean position of the Intertropical Convergence Zone [Dommain et al., 2014]. However, because of the extreme paucity of radiocarbon-dated peat cores [e.g., Supardi et al., 1993; Neuzil, 1997; Page et al., 2004], little is known about variation in carbon accumulation rates on centennial to subcentennial timescales. The drivers behind fluctuations on these timescales need to be identified to improve our mechanistic understanding of the peat accumulation processes as well as predictions of the future carbon balance of tropical peatlands.

Regional temperature and precipitation are believed to exert an overwhelming control on the accumulation of carbon in peatlands by influencing both plant productivity and organic matter decomposition [e.g., *Lottes and Ziegler*, 1994; *Yu et al.*, 2009; *Charman et al.*, 2013]. However, studies in northern peatlands have shown that ecosystem disturbances as well as autogenic peatland processes, such as vegetation change, can also drive variations in carbon accumulation rates in peatlands [e.g., *Kilian et al.*, 2000; *Mauquoy et al.*, 2002; *Turetsky et al.*, 2002; *Couwenberg and Joosten*, 2005]. *Anderson* [1961a, 1983], for example, suggested that peat accumulation in the tropical peatlands of northwest Borneo declines during succession of peat swamp forests because of changing vegetation. Moreover, complex hydrological feedback mechanisms may mitigate the effects of variations in atmospheric moisture supply on ombrotrophic peat swamp forests [*Dommain et al.*, 2010], affecting long-term rates of carbon accumulation [*Dommain et al.*, 2011].

Peat swamp forests in Southeast Asia like northern forested peatlands are strongly influenced by disturbance [*Anderson*, 1961a; *Bruenig*, 1990] and the peat swamp forests dominated by *Shorea albida* in northwest Borneo (Figure 1a) are particularly susceptible to wind throw, lightning damage, insect outbreaks, droughts, tree fires, and mass movements of peat [e.g., *Anderson*, 1961a, 1961b, 1964, 1966; *Brünig*, 1964, 1971, 1973; *Wilford*, 1966] (Figure 2c). High winds, and to some extent lightning, can uproot the generally shallow-rooted trees, which tear a cavity into the peat when they fall, in which a tip-up pool forms [*Yamada*, 1997] (Figure 2a). *Gastaldo and Staub* [1999] proposed that this process creates perennially flooded sites on tropical domed peatlands that provide optimum conditions for the preservation of delicate plant litter. This hypothesis complicates the paradigm that tropical peat swamp forests produce mainly woody peat [*Polak*, 1933] with implications for spatiotemporal patterns of carbon accumulation. However, the direct effects of these processes on carbon accumulation in tropical peatlands have not been investigated.

Insights on how climate, disturbance, and autogenic processes affect carbon accumulation are thus far limited, because the few available peat core records typically suffer from wide sampling intervals for both radiocarbon dates and bulk density, whereas carbon accumulation curves often lack supporting information on the paleovegetation [*Anderson and Muller*, 1975; *Morley*, 1981; *Diemont and Supardi*, 1987; *Supardi et al.*, 1993; *Neuzil*, 1997; *Page et al.*, 2004]. Additional problems are created by the abundance of buried wood in Southeast Asian peat deposits (Figure 2b) that (1) often prevents complete core recovery, (2) lowers the resolution of radiocarbon dating, (3) complicates precise bulk density measurements, and (4) introduces temporal gaps in paleoenvironmental reconstructions such as pollen records [e.g., *Polak*, 1933; *Anderson and Muller*, 1975; *Esterle and Ferm*, 1994; *Shimada et al.*, 2001; *Page et al.*, 2004; *Sumawinata et al.*, 2008; *Wüst et al.*, 2008]. Incomplete recovery of the wood fraction in particular leads to uncertainties in estimating the bulk density and carbon content of peat profiles and directly affects reconstructed rates of carbon accumulation [*Dommain et al.*, 2011].

This study examines the effects of forest succession, disturbance regimes, and pool formation on the long-term accumulation of carbon in tropical peatlands, applying modern nondestructive techniques for geophysical and image analyses of cores with very fine sampling intervals [e.g., *Rothwell*, 2006] to overcome some of the difficulties in measuring cores rich in wood. For more than two decades Southeast Asia has suffered from widespread deforestation that has destroyed most natural peat swamp forests [*Miettinen et al.*, 2012] severely limiting research into the natural dynamics of these unique ecosystems. Brunei offers an unparalleled opportunity for a representative baseline study because it harbors the last intact remnants of domed peat swamps in Southeast Asia.

1.1. Objectives

Here we present the first core record of carbon accumulation rates from a peat swamp forest dominated by *Shorea albida* in Borneo. This study was designed to address four important questions concerning the carbon and ecosystem dynamics of tropical peatlands: (1) what controls rates of carbon accumulation over decadal to centennial timescales? (2) what is the relative importance of external climatic versus internal ecosystem drivers in influencing carbon accumulation at these timescales? (3) which types of ecosystem disturbance have altered rates of carbon accumulation in the past and what is the spatial significance of these disturbance types on the scale of a peat dome? and (4) what is the role of tip-up pools in the carbon dynamics of tropical domed peatlands? In particular, we tested the hypothesis of *Gastaldo and Staub* [1999] that tip-up pools create favorable sites for plant litter deposition and preservation. We addressed the last two questions by

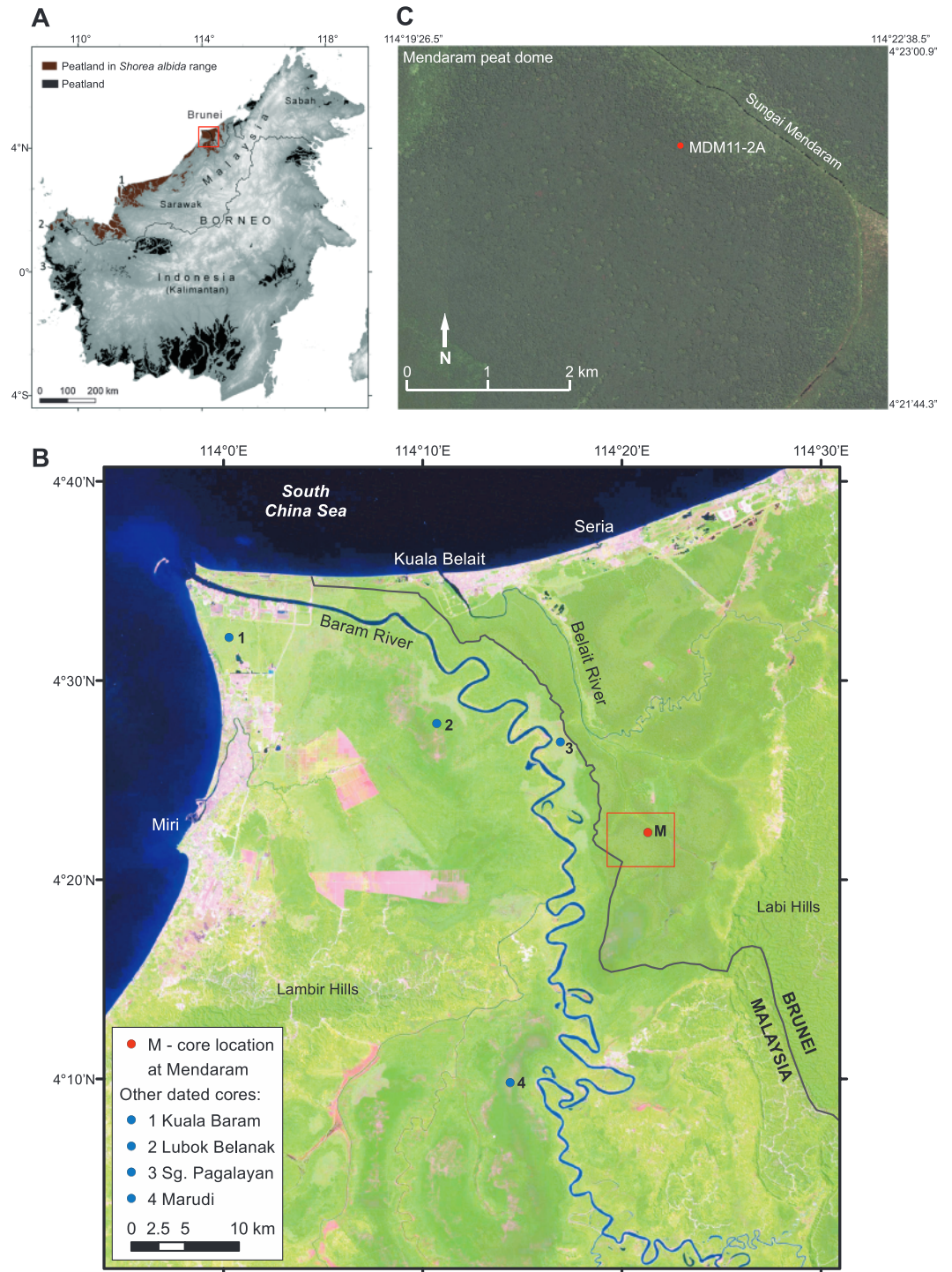


Figure 1. (a) Peatland distribution in Borneo superimposed on a Shuttle Radar Topography Mission-digital elevation model. Brown polygons mark peatlands that are located within the distributional range of *Shorea albida*. Red square marks the area shown in Figure 1b. Numbers denote other peatlands mentioned in the text: (1) Rajang Delta, (2) Teluk Keramat, and (3) Rasau Jaya. (b) The Baram-Belait peatland complex of Brunei and Sarawak (Malaysia) in northwest Borneo with the coring location in the Mendaram peat dome (red dot). Numbers 1–4 mark other peat core locations discussed in the text. Interfluvial, forested peat domes are represented by dark green color. Red square marks the area shown in Figure 1c. Landsat 7 Enhanced Thematic Mapper image from 10 July 2001. (c) High-resolution satellite image of the Mendaram peat dome with the coring location. Bright spots across the dome are canopy gaps. Image taken from Google Earth (Image © 2015 Digital Globe, © 2015 CNES/Astrium).



Figure 2. Photographs of peat swamp forest and forest peat in Brunei. (a) Tip-up pool in the Mendaram peat dome formed from a fallen *Shorea albida* tree. The pool is 8 m across. (b) Peat exposure along a ditch showing the abundance of undecomposed large wood pieces and of smaller roots embedded in the peat. (c) Orthophotograph of *Shorea albida* dominated peat swamp forest on the Mendaram peat dome. Note the up to 100 m wide canopy gaps produced by lightning and wind throw. Photo taken by Brunei Survey Department in 2009.

developing a simulation model of peat accumulation dynamics based on the core record, analysis of aerial photographs, and field observations.

2. Study Area

The Mendaram peatland ($4^{\circ}20'N$ and $114^{\circ}20'E$, Figure 1) lies 30 km south of the coast in the Belait District of Brunei Darussalam in the northwestern part of the equatorial island of Borneo. The peatland is located on the interfluvial divide between the Mendaram and the Baram Rivers (Figure 1) and is one of the last pristine peatlands on Borneo. It covers an area of approximately 40 km^2 and has a surface elevation of only 2.5 to 7 m above sea level. The peatland is part of a 3130 km^2 peatland complex covering the deltas of the Baram and Belait Rivers (Figure 1b), which consists of approximately 30 individual peat domes with peat depths ranging from 1 to 12 m [e.g., Anderson and Muller, 1975; Furukawa, 1988; Tie and Esterle, 1992; Stoneman, 1997]. Late Holocene delta progradation [Caline and Huong, 1992] and progressive seaward expansion of peatlands in this area is indicated by the south to north chronosequence of basal mangrove and peat dates of 4800, 4400, 3900, and 1060 cal years B.P. at Marudi, Sungai Pagalayan, Lubok Belanak, and Kuala Baram, respectively (Figure 1b) [Tie and Esterle, 1992; Woodroffe, 2000].

Brunei has an equatorial-humid-diurnal climate in the sense of Walter [1985] and the coastal belt receives an average annual rainfall of 2880 mm (measured in Seria and Kuala Belait between 1947 and 2004). Monthly rainfall data indicate perhumid conditions: precipitation surpasses potential evapotranspiration (100 mm) [Walter, 1985] in every month. The low seasonality in rainfall can be explained by the overwhelming year-round influence of the Intertropical Convergence Zone over northern Borneo [Cobb et al., 2007]. Typically, rainfall is very localized and falls as heavy convective showers during the afternoon, often associated with thunderstorms. Nearly 200 thunderstorms per year have been recorded at the Bandar Seri Begawan International Airport [James, 1984]. Temperature remains remarkably constant throughout the year with average monthly temperatures fluctuating between 26 and 27°C , with diurnal temperature fluctuations of 7 to 9°C [James, 1984]. The natural vegetation in uplands under such warm and wet climatic conditions is tropical rainforest.

Swamp forest covers the domed peatlands of the Baram-Belait Delta [Anderson and Muller, 1975]. The peat domes show a concentric zonation of up to six so-called phasic communities (P.C. 1–6) [Anderson, 1983]. The shallow margins of these peat domes are covered with species-rich mixed swamp forest (P.C. 1) with *Gonystylus bancanus* and *Dactylocladus stenostachys* as dominant canopy trees. The largest and deeper portions of the peat domes are covered with forest communities (P.C. 2–4) completely dominated by the endemic dipterocarp *Shorea albida* [Anderson, 1963; Ashton, 1964] (Figure 1a). *Shorea albida* trees are between 30 and 70 m tall, can have a stem diameter of up to 2.5 m and possess large buttress roots that extend up to 5 m up the trunk and spread 6–7 m away from the tree [Ashton, 1964; Anderson, 1983; Furukawa, 1988; Yamada, 1997]. Almost pure stands of *Shorea albida* also dominate most of the Mendaram peat dome (Figure 1c), whereas the monocot *Pandanus andersonii* forms a dense understorey up to 3 m high on much of the dome. Nearly circular canopy gaps of 15 to 100 m diameter occur regularly in the peat swamp forest (Figures 1c and 2c).

3. Materials and Methods

Tropical peat deposits present multiple problems for reconstructing long-term records of carbon accumulation and peat accretion. The dense wood layers impose a formidable obstacle for recovering intact peat cores, sampling these cores for various chemical and physical analyses, and finding suitable material for radiocarbon dating. In addition, the dynamic disturbance regime on tropical peat swamps produces tip-up pools that may create gaps in the sedimentary profile and compromise sophisticated age versus depth models that do not account for the patterns of age discontinuities that are created by pool excavation and filling. We therefore used a combination of methods that mitigate these problems to generate reliable reconstructions of peat accumulation for the Mendaram peat dome.

3.1. Coring

Between 31 October and 2 November 2011 several peat cores were recovered from the Mendaram peat dome with a Livingstone piston sampler equipped with a wide (10 cm) diameter core barrel and a serrated cutting edge [Wright *et al.*, 1984]. This type of corer was designed to prevent the problems of previous workers who encountered serious problems penetrating and recovering intact cores from these wood layers, which are abundant in tropical peat domes. The peat sampler was rotated 60° back and forth during the coring process to saw through all sizes of wood, while the wide diameter of the core barrel minimized internal frictional resistance that might prevent dense, woody peat from entering the corer [Wright *et al.*, 1984]. Core compression is minimized if not eliminated by the piston, which prevents pore water from escaping during the coring and extruding operation [Wright *et al.*, 1984; Wright, 1993; Glaser *et al.*, 2012]. The cores were extruded in the field, wrapped in plastic, and sealed in split halves of acrylonitrile butadiene styrene pipe for transport to the National Lacustrine Core Facility (LacCore, University of Minnesota). This study focuses on the longest recovered profile—core MDM11-2A—a 5.81 m long core that reached into basal marine clay and was collected 900 m from the peatland margin (i.e., Mendaram River, Figure 1; 4°22′21.6″N Lat. and 114°21′18.1″ E Long.) in *Shorea albida* forest.

3.2. Core Logging and Processing

At the LacCore facility the intact sections of core MDM11-2A were first scanned with a Geotek Multi-Sensor Core Logger (MSCL) to automatically measure wet bulk density by gamma ray attenuation at 0.5 cm sampling intervals. Each core section was logged 3 times, with the core rotated 45° so that the gamma ray beam passed through different cross-sectional profiles at the same depth interval to account for the heterogeneities within the peat. A mean value of wet density was calculated from the three successive logging runs for every 0.5 cm sampling interval. Wet bulk density is the inverse proportion of the total amount of received gamma rays [e.g., Zolitschka *et al.*, 2001]. The core sections were then split longitudinally with a diamond-bladed band saw. Fresh split core surfaces were imaged with a Geotek MSCL-Core Imaging System with GeoScan IV digital linescan camera at a resolution of 20 pixels per mm for visual core description and subsequent image analysis. In addition, X-ray radiographs, 2 cm wide, were taken along the center of the split core surfaces with an ITRAX X-ray core scanner at the Large Lakes Observatory (University of Minnesota-Duluth).

Table 1. Radiocarbon Dates for the Mendaram Core MDM11-2A

Lab Code	Depth (cm)	Dated Material	$\delta^{13}\text{C}$ (‰ VPDB ^a)	Radiocarbon Age (B.P.)	1 σ Calibrated Age Range (Cal Years B.P.) + (Probability)	2 σ Calibrated Age Range (Cal Years B.P.) + (Probability)	Point Age Estimate (Cal Years B.P.)
OS-106377	25.5–26	wood	–28.9	460 ± 25	503–520 (1.0)	494–534 (1.0)	512
CAMS 158593	42.5–43.5	pollen size concentrate		660 ± 30	565–587 (0.51) and 644–665 (0.49)	558–603 (0.5) and 628–673 (0.5)	615
CAMS 158594	100–101	bracts		> modern	> modern	> modern	> modern
OS-106378	101–102	fossil resin (three pieces)	–29.67	755 ± 25	671–694 (1.0)	667–710 (0.89) and 712–726 (0.11)	689
CAMS 158595	131.5–132.5	pollen size concentrate		1030 ± 35	924–966 (1.0)	804–807 (0.00), 831–853 (0.03), 905–1005 (0.91), and 1027–1051 (0.05)	946
OS-106447	183.5–185	leaf fragments	–30.71	1150 ± 25	984–1033 (0.51), 1047–1082 (0.39), 1114–1117 (0.01), and 1161–1171 (0.09)	980–1098 (0.75), 1101–1149 (0.17), and 1158–1173 (0.08)	1063
OS-106696	237–238	two leaf fragments	–29.25	1160 ± 20	1006–1025 (0.21), 1053–1088 (0.47), 1109–1124 (0.12), 1135–1142 (0.05), and 1160–1172 (0.15)	989–992 (0.01), 996–1030 (0.20), and 1049–1175 (0.79)	1083
CAMS 158596	298.5–300	pollen size concentrate		1445 ± 30	1306–1353 (1.0)	1298–1385 (1.0)	1338
OS-106951	341–342	pollen size concentrate	–23.39	2070 ± 25	1994–2061 (0.89) and 2089–2099 (0.11)	1951–1959 (0.01), 1971–1977 (0.01), and 1986–2121 (0.97)	2042
CAMS 158597	352–353.5	pollen size concentrate		2465 ± 30	2465–2540 (0.38), 2564–2573 (0.04), 2585–2617 (0.18), and 2631–2700 (0.40)	2379–2395 (0.02), 2398–2414 (0.02), and 2421–2713 (0.95)	2563
CAMS 158598	352.5–353.5	seed		2315 ± 40	2212–2219 (0.04) and 2309–2358 (0.96)	2160–2171 (0.01), 2176–2247 (0.18), 2300–2438 (0.80), and 2454–2455 (0.00)	2319
CAMS 158599	399–400	pollen size concentrate		2570 ± 40	2542–2560 (0.11), 2618–2631 (0.08), and 2701–2755 (0.81)	2495–2597 (0.29), 2611–2638 (0.09), and 2684–2762 (0.62)	2667
CAMS 158682	456–457	fern root (cf. <i>Acrostichum</i>)		2655 ± 35	2747–2782 (1.0)	2742–2809 (0.88) and 2813–2844 (0.12)	2776

^aVPDB = Vienna PeeDee Belemnite.

3.3. Lithostratigraphic Core Description

Split cores were described visually with a dissecting scope and by means of smear slide analysis with a petrographic microscope to establish lithostratigraphic units and to record botanical peat composition, degree of humification as well as the general biological components, mineral composition, and charcoal presence. Pollen samples taken from the major lithostratigraphic units were prepared according to standard procedures [Faegri and Iversen, 1989] and the most frequent pollen and nonpollen palynomorphs recorded. Identification and interpretation of microfossils was aided by Anderson and Muller [1975], Maury et al. [1975], van Geel [1976], van Geel et al. [1981], Pals et al. [1980], Simmons et al. [1999], Mao et al. [2012], and E. J. Cushing (personal communication, 2012). A few samples of the basal peat-sediment transition were examined for their mineral content with a Hitachi™ 1000 tabletop scanning electron microscope with an integrated energy dispersive X-ray spectroscopy elemental analyzer.

3.4. Peat and Sediment Geochemistry

Water content and loss-on-ignition were measured on 2 cm³ samples taken at 4 cm intervals. Wet samples were dried in an oven at 100°C overnight, weighed, and then burnt at 550°C in a muffle furnace for 4 h [Dean, 1974]. Samples of 2 cm³ volume were taken for elemental analysis at the same 4 cm intervals from

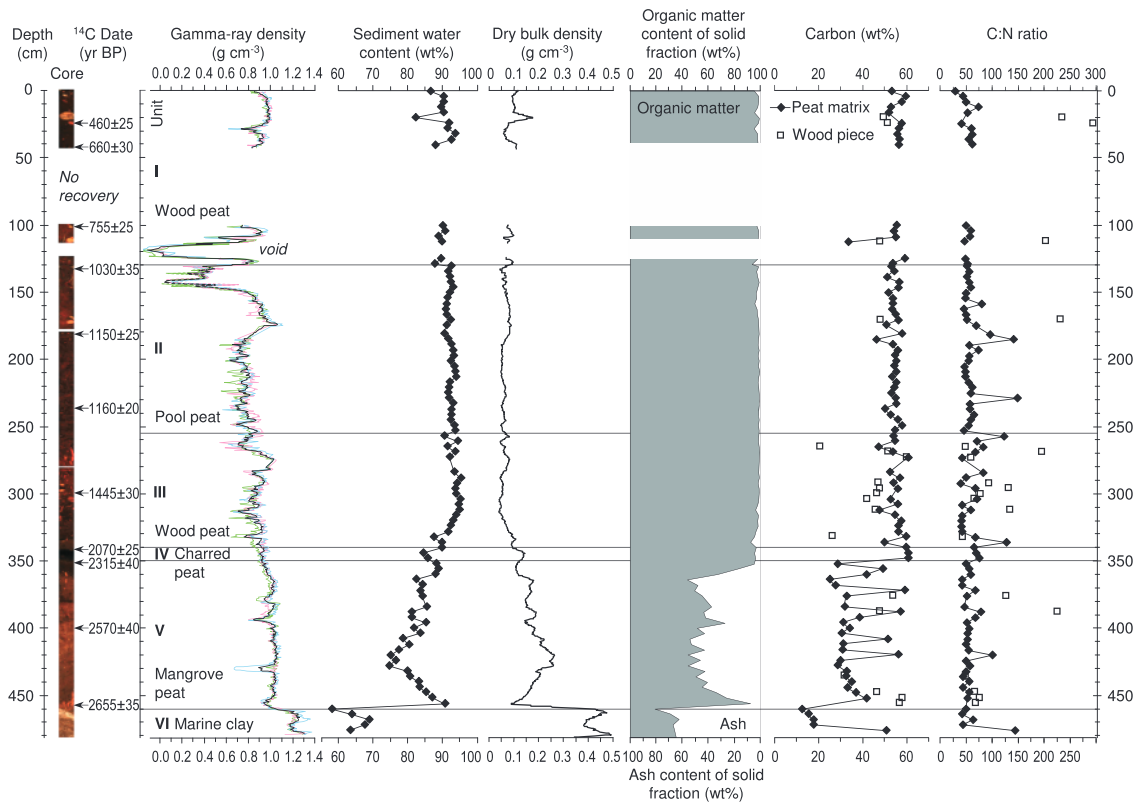


Figure 3. Mendaram core MDM11-2A stratigraphy with physical and geochemical core properties. Roman numbers represent lithostratigraphic units. Original gamma ray density data are shown in green, blue, and pink and the mean values in black. Dotted lines from 131 to 151 cm denote rejected density data due to insufficient core volume. Note the reversed scale for ash content.

the peat/sediment matrix ($n = 98$) or from wood pieces ($n = 19$) as companion samples if wood was also located at the respective sampling interval or if wood filled most of the core tube. The carbon and nitrogen concentrations of freeze-dried and mechanically ground peat/sediment and wood samples were measured with a Vario-EL III CHNOS analyzer at the Institute of Botany and Landscape Ecology (University of Greifswald). Carbon concentrations represent total organic carbon because the peat at Mendaram is acidic with an average pH of 4.0 [Gandois et al., 2014] at which inorganic carbon (CaCO_3) is generally absent [Succow and Stegmann, 2001].

3.5. Image Analysis and Wood Content

From the digital core images we extracted black and white masks of all well-preserved wood pieces larger than 0.2 cm^2 with the image processing software ImageJ version 1.47 [Rasband, 1997; Abràmoff et al., 2004]. The fraction of wood surface area from each successive 1 cm increment of core surface was estimated from the black and white masks in ImageJ. In addition, wood pieces were counted in each 1 cm increment using these images.

3.6. Radiocarbon Dating and Age Model

Most radiocarbon-dated profiles from tropical peatlands are based on the analysis of bulk peat samples [e.g., Anderson and Muller, 1975; Diemont and Supardi, 1987; Supardi et al., 1993; Neuzil, 1997; Page et al., 2004] despite the susceptibility of bulk dates to chronological errors caused by the injection of younger material by roots [Glaser et al., 2012]. This postdepositional contamination by younger carbon may result in bulk dates being several hundred years younger than aboveground plant material deposited contemporaneously with the peat matrix [Wüst et al., 2008] leading to age inversions in densely dated profiles [Page et al., 2004]. We therefore only sampled material that originated from aboveground biomass including selected plant macrofossils (e.g., leaves and seeds), fossil resin, or in their absence concentrates of the pollen size fractions extracted from 1 cm thick peat slices for accelerator mass spectrometry (AMS) radiocarbon dating

Table 2. Physical and Geochemical Core Properties of Core MDM11-2A^a

Physical and Geochemical Core Parameters											
Unit	Depth (cm)	Age (Cal Years B.P.)	Peat/Sediment Type	Gamma Ray Density (g cm ⁻³)	Dry Bulk Density (g cm ⁻³)	Water Content (%)	Ash (Percent of Solid Phase)	Organic Matter (Percent of Solid Phase)	Carbon Content (%) Matrix	Nitrogen Content (%) Matrix	C:N Ratio Matrix
I-IV	0-350	0-2220	Peat	0.845 ± 0.09 (0.530-1.059)	0.072 ± 0.02 (0.039-0.176)	91.9 (82.2-95.1)	1.9 ± 1.4 (0.4-7.2)	98.1 ± 1.4 (92.8-99.6)	54.6 ± 3.9 (34.2-60.9)	1.0 ± 0.3 (0.3-1.5)	60.5 ± 22.2 (28.1-147.8)
I	0-130	0-940	Hemic wood peat	0.886 ± 0.10 (0.530-0.991)	0.092 ± 0.02 (0.057-0.176)	89.9 (82.2-93.5)	2.4 ± 1.6 (0.7-6.2)	97.6 ± 1.6 (93.8-99.3)	54.6 ± 5.9 (34.2-59.9)	1.1 ± 0.3 (0.7-1.9)	51.8 ± 10.1 (28.1-72.4)
II	130-255	940-1150	Fibrous herbaceous peat	0.799 ± 0.09 ^a (0.629-1.059)	0.062 ± 0.01 (0.043-0.090)	92.2 (90.3-93.7)	1.5 ± 0.8 (0.4-4.1)	98.5 ± 0.8 (95.6-99.6)	54.2 ± 2.4 (46.4-57.9)	0.9 ± 0.2 (0.3-1.2)	62.2 ± 24.2 (44.7-147.8)
III	255-340	1150-2020	Hemic wood peat	0.860 ± 0.07 (0.702-1.026)	0.063 ± 0.02 (0.039-0.108)	93.5 (87.4-95.1)	1.9 ± 1.7 (0.4-7.2)	98.1 ± 1.7 (92.8-99.6)	54.5 ± 3.6 (47.4-60.9)	1.0 ± 0.4 (0.4-1.5)	63.9 ± 26.7 (39.1-127.2)
IV	340-350	2020-2250	Sapric, charred peat	0.924 ± 0.01 (0.900-0.945)	0.129 ± 0.01 (0.095-0.144)	85.5 (84.3-89.6)	3.7 ± 0.7 (3.0-4.5)	96.3 ± 0.7 (95.5-97.0)	60.4 ± 0.6 (59.7-60.8)	0.9 ± 0.1 (0.8-0.9)	69.2 ± 4.9 (64.6-74.3)
V	350-460	2250-2780	Peaty clay	1.004 ± 0.04 (0.843-1.064)	0.180 ± 0.05 (0.089-0.427)	83.2 (74.4-90.5)	40.2 ± 13.9 (4.6-55.9)	59.8 ± 13.9 (44.1-95.4)	37.4 ± 9.8 (25.6-59.1)	0.7 ± 0.1 (0.5-1.0)	55.0 ± 12.5 (41.5-100)
VI	460-481	> 2780	Clay/silty clay	1.195 ± 0.08 (0.902-1.302)	0.432 ± 0.04 (0.344-0.491)	63.7 (58.1-68.7)	69.1 ± 7.0 (62.3-80.8)	30.9 ± 7.0 (19.2-37.7)	23.2 ± 15.7 (13.1-51.0)	0.3 ± 0.1 (0.3-0.4)	68.2 ± 42.9 (42.1-143.5)

^aExcludes rejected values from 131 to 151 cm. Values are given as means, standard deviations (in italics), and as ranges (in parentheses). Water content is expressed as median.

(Table 1). Macrofossils were identified by comparison with reference material collected at Mendaram or from the Botanical Garden of Greifswald University. Prior to submission, all macrofossil samples were thoroughly washed in high-purity water. Peat samples for the pollen size fraction were boiled in 10% KOH for 30 min, sieved through an 80 μm screen, and the < 80 μm fraction was sieved again through a 20 μm screen to remove the smallest organic particles. Sieved samples (> 20- < 80 μm) were rinsed with high-purity water to remove dissolved organic compounds, then boiled in 2.5% NaClO for 3 min and again in HCl for 30 min. The pollen size concentrates were inspected for microscopic content and discarded if pollen content was low or nonpollen components dominated. To determine the possible age offsets between the pollen size fraction concentrates and plant macrofossils, we submitted a pair of both materials from the same depth interval (352-353 cm). Thirteen radiocarbon samples were collected along the core at intervals of 10 to 60 cm, including most boundaries between lithological units and submitted for AMS dating to the Center for Accelerator Mass Spectrometry at Lawrence Livermore National Laboratory and the National Ocean Sciences AMS facility at Woods Hole Oceanographic Institution (Table 1). Radiocarbon dates were calibrated into calendar years before present (cal years B.P., where present is 1950) using the IntCal13 calibration curve [Reimer *et al.*, 2013] with the program Calib 7.02 [Stuiver and Reimer, 1993].

The calculation of peat accumulation rates between two radiocarbon dates requires the use of calibrated single years. First, the time span between those single years, which represents the deposition time of a dated peat section, is determined. The peat thickness between two neighboring dates is then divided by its deposition time, which yields rates of peat accretion. In this study single-year age estimates were calculated as the weighted mean of the probability distribution of calibrated age ranges as recommended by Telford *et al.* [2004]. We chose the most parsimonious

Table 3. Paleoenvironmental Data and Rates of Carbon and Peat Accumulation for Core MDM11-2A^a

Paleoenvironmental Data										
Unit	Depth (cm)	Age (Cal Years B.P.)	Peat/Sediment Type	Peat Accumulation Rate (mm yr ⁻¹)	Carbon Accumulation Rate (g C m ⁻² yr ⁻¹)	Mean Wood Cover (%)	Macrofossils	Pollen, Fern, and Algae Spores) and Charcoal	Mineral Content	Reconstructed Ecosystem
I	0–130	0–940	Hemic wood peat	0.80 (0.50–1.68)	40.0 (21.5–106.2)	13.1	Woody roots, resin	<i>Shorea albida</i> type, <i>Pandanus</i> , <i>Ilex</i> , and <i>Asplenium</i>	Absent	<i>Shorea albida</i> peat swamp forest (P.C. 2–3)
II	130–255	940–1150	Fibrous herbaceous peat	6.18 (1.19–26.63)	205.9 (44.6–960.0)	1.9	Leaves (<i>Pandanus</i>), herbaceous roots (cf. <i>Pandanus</i> , cf. <i>Hanguana</i> , and cf. Araceae)	<i>Camposperma</i> , <i>Stemonurus</i> , <i>Pandanus</i> , <i>Garcinia cuspidata</i> , <i>Stenochlaena palustris</i> , <i>Shorea albida</i> type, and <i>Spirogyra</i>	Absent	Tip-up pool in <i>Shorea albida</i> peat swamp forest gap (P.C. 2–3)
III	255–340	1150–2020	Hemic wood peat	0.98 (0.60–2.42)	34.2 (11.5–119.2)	12.1	Woody roots, resin	<i>Eugenia/Tristania</i> type, <i>Camposperma</i> , <i>Shorea albida</i> type, <i>Ilex</i> , and <i>Polypodium</i>	Quartz	Mixed peat swamp forest (P.C. 1)
IV	340–350	2020–2250	Sapric, charred peat	0.43 (0.42–0.60)	33.2 (22.5–39.3)	0.2	Absent	<i>Stenochlaena palustris</i> , and <i>Polypodium</i>	Silicate	Mixed peat swamp forest with local fire impact (P.C. 1)
V	350–460	2250–2780	Peaty clay	1.95 (0.42–5.23)	135.0 (13.6–771.1)	3.4	cf. <i>Acrostichum</i> root pocket, well-decomposed woody roots	<i>Camposperma</i> , <i>Garcinia cuspidata</i> , and abundant charcoal	Halite, Quartz, Feldspar, Pyrite	Coastal freshwater swamp forest, Mangrove forest (until circa 2400 cal years B.P.)
VI	460–481	> 2780	Clay/silty clay	n.d.	n.d.	0.3	Absent	<i>Stenochlaena palustris</i> , <i>Nypa fruticans</i> , <i>Rhizophora stylosa</i> , <i>Acrostichum aureum</i> , and <i>Spirogyra</i>	Pyrite, Quartz	Shallow marine water

^aValues given as means and ranges (in parentheses), n.d. is not determined.

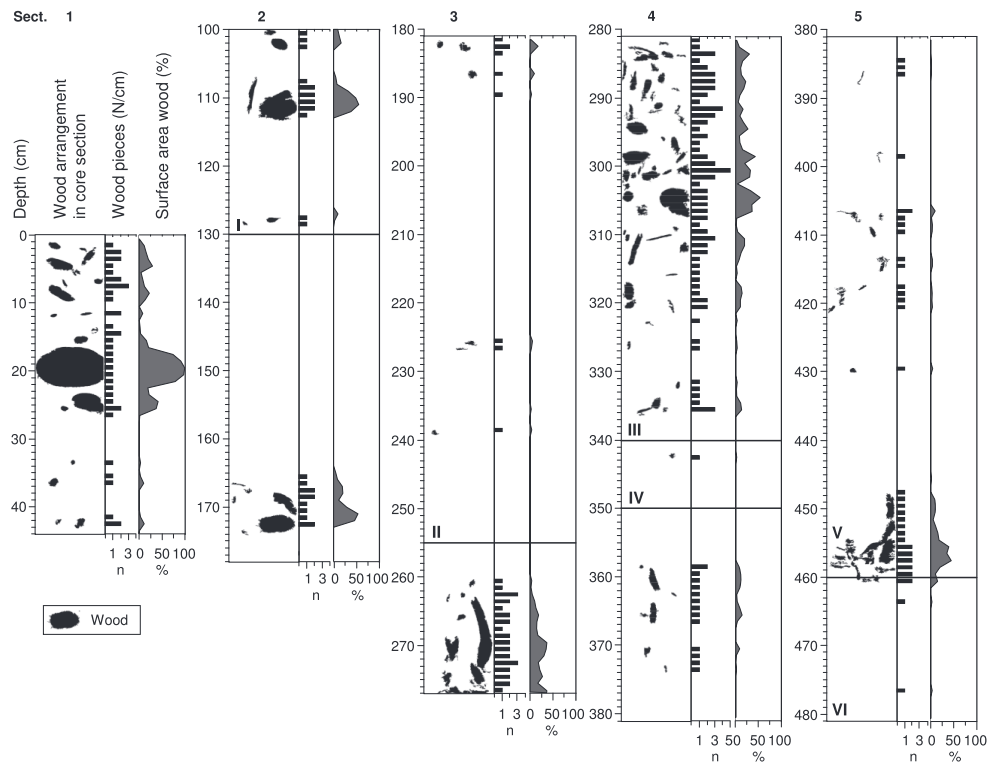


Figure 4. Wood content of core MDM11-2A. Black masks are well-preserved wood pieces larger 0.2 cm^2 taken from the digital core images of each core section (1–5). Next to the black and white images is the frequency of wood pieces in every centimeter core interval (bars) and the percentage of core surface area covered by wood in each centimeter (silhouettes). Note the absence of wood in most of Unit II (section 2 and 3) corresponding to the filled pool stratum.

approach for the construction of an age-depth model by linearly interpolating between the single-year age estimates of neighboring dates. This approach allowed us to make direct comparisons with published age-depth models from Southeast Asian peatlands, which are all based on linear interpolation. Although it is desirable to quantify the age uncertainty between individual dates by using Bayesian age models, the derived uncertainty envelopes are not essential for calculating rates of peat accumulation.

3.7. Rates of Carbon Accumulation

The proportions of wood and peat matrix in each 1 cm increment estimated by image analysis were multiplied by the respective measured or interpolated carbon concentration values of wood and peat to arrive at weighted carbon concentrations in 1 cm intervals for the entire peat profile. Dry bulk density was calculated as the percentage dry mass from the mean wet bulk density. Dry bulk density values of the interval 131–151 cm, in which the core section did not completely fill the storage tube, were measured gravimetrically by analyzing 2.7 cm^3 samples at 1 cm depth intervals. Multiplying peat accumulation rates with dry bulk density and weighted carbon concentration yielded apparent rates of carbon accumulation.

3.8. Tree Fall Dynamics

To assess the spatiotemporal importance of tip-up pools for peat accumulation, the frequency and spatial distribution of recent tree falls within the Mendaram peat swamp forest were determined by comparing georeferenced and orthorectified aerial photographs ($1003.96 \text{ m} \times 1003.96 \text{ m}$; pixel size is 19 cm) from 2002 and 2009 (Figure 2c). The number of tree falls during this 7 year interval was established by counting the number of trees present in the earlier photographs that were absent from the later ones in three square-shaped sampling areas of 25.32 ha in the northern, eastern, and western part of the central peat dome. This analysis is facilitated by the distinct and nonoverlapping canopies of individual *Shorea albida* trees (Figure 2c). In addition, the total number of tree crowns from canopy forming *Shorea albida* trees was also counted in each sample square of the 2009 orthophotographs to determine the tree density in the peat swamp forest.

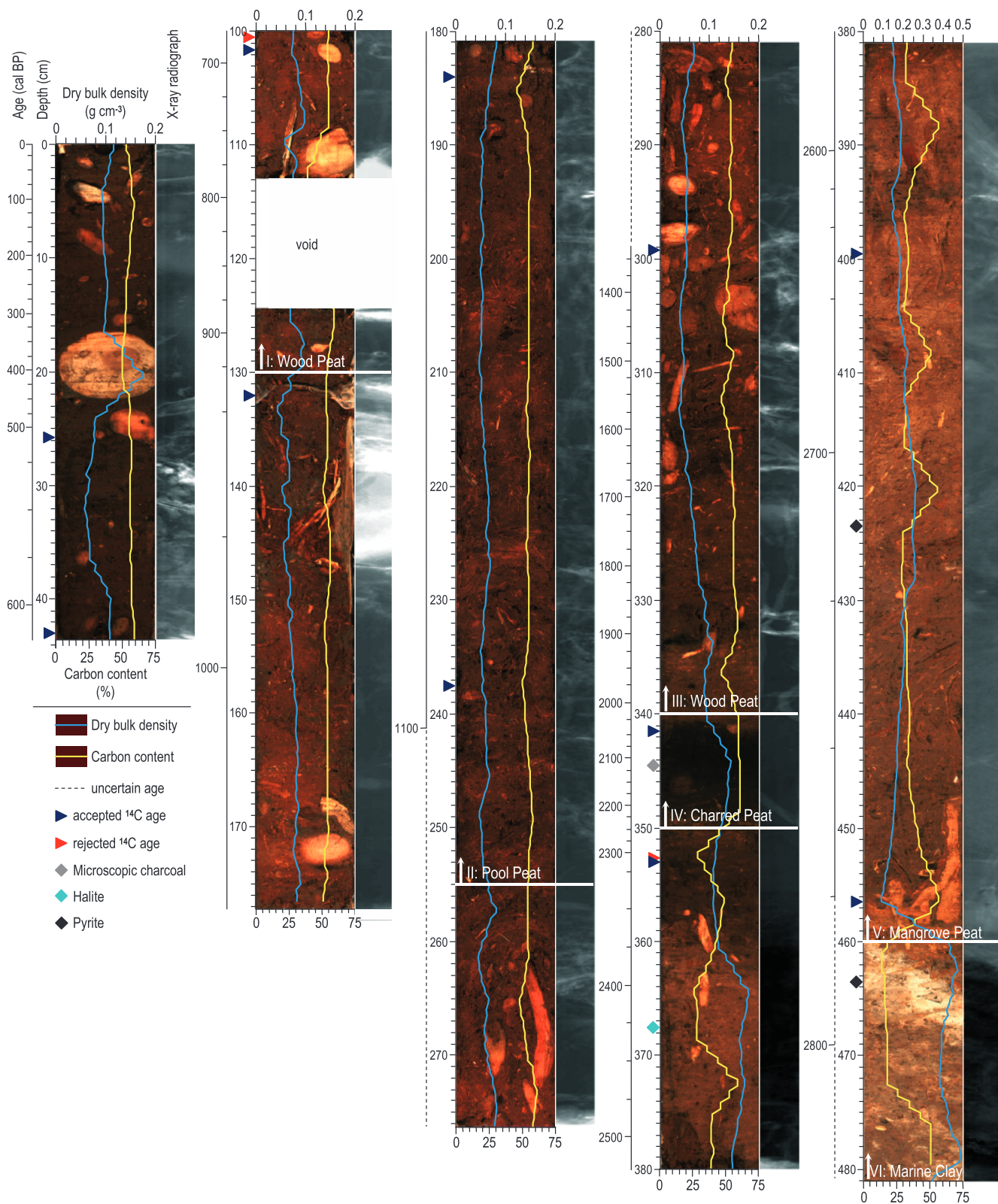


Figure 5. Digital core images with interpolated age scales and superimposed stratigraphies for dry bulk density (blue lines) and weighted carbon content (yellow lines). To the right of each image are 2 cm wide (laterally stretched) X-ray radiographs taken from the center of each split core. White color in the radiographs corresponds to low density and black color to high density. Voids and roots are visible as whitish structures. Note the different scale in dry-bulk density in core section 5 (right side).

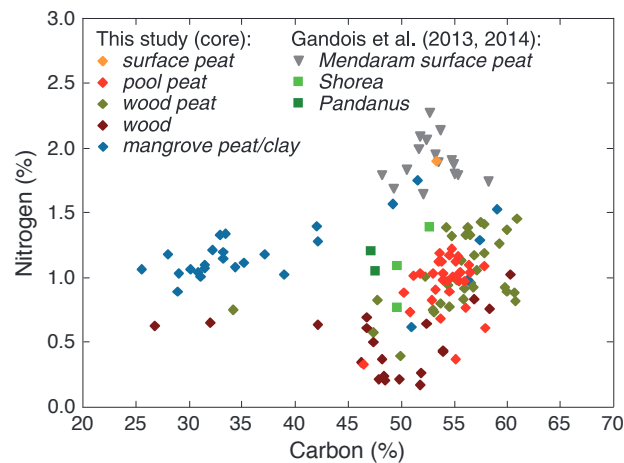


Figure 6. Carbon and nitrogen concentration of peat, sediment, and wood samples of core MDM11-2A (diamonds), of surface peat (upper 15 cm) at different locations of Mendaram (triangles) and of living plant material (squares). The latter two data sets are from Gandois *et al.* [2013, 2014].

237 cm depth with *Pandanus* leaf fragments at the latter location. The top of this unit, from 131 to 151 cm, is very fibrous, dominated by vertically oriented herbaceous roots. This unit contains wood pieces, which are generally smaller than in Unit I (Figure 4). Unit III from 255 to 340 cm consists of well-decomposed, hemic woody peat with numerous embedded wood fragments. This unit contains several wood lenses at 257–277 cm and at 281–320 cm with the largest piece measuring 4.5 × 4.2 cm (Figure 4). The wood content declines in the bottom of this unit, where the peat is more humified and grades abruptly into Unit IV (340–350 cm). This basal peat layer is mostly composed of charred, sapric (strongly decomposed) peat, which is rich in microscopic charcoal (Figure 5). Unit V (350–460 cm) below consists of grey peaty clay with pyrite and halite minerals, few small pieces of woody remnants and strongly humified organic material. The base of this unit is composed of an agglomeration of fern roots (*cf. Acrostichum* sp., Figure 5). A sharp contact forms the transition to the basal Unit VI (460–481 cm), which consists of marine clay and silty clay of whitish to grey color and contains abundant pyrite (Figure 5). The results of pollen and mineral analyses indicate that these six lithostratigraphic units fit a typical successional sequence from a basal-inundated marine environment, to a coastal mangrove forest, then a freshwater swamp forest, and finally a peat swamp forest stage (Table 3).

4.2. Physical and Chemical Core Properties of the Deposits

The largest changes in the physical and geochemical properties of the core occur at the transition from underlying marine sediment to the peaty clay (Unit V) at 460 cm and at the transition from the peaty clay layer to peat (Unit IV) at 350 cm (Figure 3). Out of 2257 individual wet bulk density measurements from three logging runs, 751 mean values of wet density were calculated in 0.5 cm intervals corresponding to an estimated temporal resolution of 0.2 to 12 years. Wet bulk density ranges from 0.53 to 1.30 g cm⁻³ with a mean wet bulk density of 0.85 g cm⁻³ of the peat layers (Units I–IV) and 1.00 g cm⁻³ of the peaty clay sediment (Unit V) (Table 2 and Figure 3). Because the water content of the peat is around 92% (Table 2 and Figure 3), wet density values of less than 0.9 g cm⁻³ imply that portions of the peat core contain up to 5% gas.

The dry bulk density of the peat layer ranges from 0.034 to 0.176 g cm⁻³ with the lowest values obtained from the herbaceous peat layer (Unit II; 0.062 g cm⁻³) and from the void-rich woody peat of Unit III (0.063 g cm⁻³; Table 2 and Figures 3 and 5). The largest recovered wood piece at 20 cm depth has the highest value for dry bulk density (0.176 g cm⁻³; Figure 5), whereas the highest values of the matrix peat are from well-decomposed peat layers of Unit I (0.092 g cm⁻³) and Unit IV (0.130 g cm⁻³). The entire peat layer (Units I–IV) has a mean dry bulk density of 0.072 g cm⁻³, whereas the peaty clay sediment of Unit V is more than twice as dense (0.180 g cm⁻³ Table 2). The ash content of the peat layer (Units I–IV) is 1.9% and that of the peaty clay layer (Unit V) 40.2% on average (Table 2).

4. Results

4.1. Lithostratigraphy

Core MDM11-2A can be divided into six lithostratigraphic units (Figure 3 and Tables 2 and 3). Unit I from 0 to 130 cm consists of well-humified (hemic) woody peat with generally vertically oriented woody and herbaceous rootlets and several hardwood layers. The wood pieces are well preserved and often larger than 2 cm in diameter with the largest piece being 5 × 9.5 cm. Unit II extends from 130 to 255 cm and is composed of well-preserved, fibrous peat with abundant herbaceous rootlets, rhizomes, and fine roots (< 2 mm) as well as horizontal layers of well-preserved leaves embedded in an organic, muddy matrix. Conspicuous leaf litter lenses occur at around 130 cm, 184 cm, and

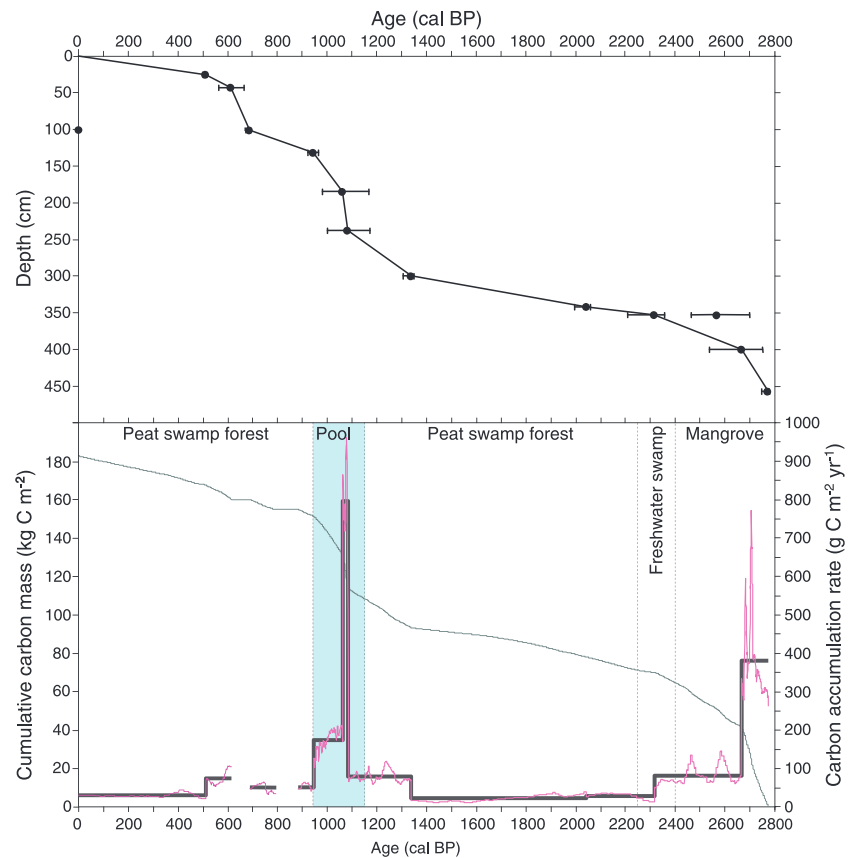


Figure 7. (top) Age-depth model of core MDM11-2A based on linear interpolation between calibrated point age estimates (with 1σ calibrated age ranges) of accepted dates (see text). (bottom) Record of carbon accumulation: the bold gray line shows average carbon accumulation rates between dates and the thin pink line the detailed record based on bulk density data. Cumulative carbon mass accumulation over time is represented by the thin gray line.

The X-ray radiographs reveal the internal structure of the core and show that the peat contains abundant macropores, voids, and root channels visible as white structures (i.e., low density) (Figure 5). Root channels are perceptible as bright, narrow, vertically oriented structures (e.g., from 103 to 110, 181 to 220, and 321 to 333 cm).

In general, both carbon and nitrogen concentrations are higher in the peat matrix than in embedded wood pieces (Figures 3 and 6). The matrix of the peat (0–350 cm; $n = 68$) has a mean carbon concentration of 54.6%, a mean nitrogen concentration of 1.0%, and a mean C:N ratio of 60.5 (Table 2), whereas the respective values for wood samples ($n = 21$) are 48.5%, 0.5%, and 125.1. Combining carbon concentrations from peat matrix and wood yields a weighted mean carbon content of 54.4% for the entire peat layer. The peaty clay layer (Unit V) shows highly varying concentrations of carbon ($n = 30$) ranging from 25.6 to 59.1% and on average a distinctly lower value (37.4%) than the peat layer above (Figure 3 and Table 2). The carbon and nitrogen content of the freshwater peat phase did not vary significantly down core (Figure 3). However, the nitrogen content within the core was lower ($< 1.5\%$) from that reported for near-surface (0–15 cm) samples across the peat dome [Gandois *et al.*, 2013, 2014], whereas the carbon content was higher than values reported for living plants (Figure 6).

4.3. Wood Content

The wood content in the core varies considerably with some portions dominated by numerous hardwood pieces, whereas wood is completely absent from other portions (Figure 4). Wood pieces $> 0.2 \text{ cm}^2$ cover 7.7% of the surface of the split cores on average in Units I–IV (peat strata). The woody peat layers of Unit I and Unit III have wood contents of about 13% and 12% respectively, including a peak value of 100% at 20 cm (Unit I)

and a maximum of 54% for Unit III at 304 cm (Figure 4). The near absence of wood in the herbaceous peat of Unit II is reflected in an average wood abundance of only 1.9% (Table 3).

4.4. Radiocarbon Dating and Age Model

The age-depth model based on dated macrofossils and pollen size concentrates shows a consistent sequence of progressively older ages down core with the exception of one age reversal at 100 cm (Figure 7). At this depth a modern date was obtained from macrofossils (i.e., bracts; Table 1), which were likely dragged from the forest floor when the corer was inserted into the bore hole for the second drive. We reject this modern date because it falls out of the sequence of adjacent radiocarbon dates that indicate a much older sediment age at this depth. The radiocarbon dates of the companion pollen size concentrate and macrofossil samples from 352 to 353 cm show that the pollen size concentrate is 150 ^{14}C years older than the macrofossil (Table 1). This finding is in line with that of *Wüst et al.* [2008] who showed that dated pollen concentrates from tropical peats were consistently older than macrofossils deposited contemporaneously with the peat. In principle, pollen should also provide useful dates [Brown et al., 1992], but in practice, the pollen size concentrate is obtained on the basis of its size alone and may contain other material of unknown age, such as fungal spores and fragments of fungal hyphae. We rejected the older date from the pollen size concentrate because of the potential contamination by older carbon from fragments of saprophytic fungi and consequently used the macrofossil date for building the age-depth model (Figure 7).

The basal date of the mangrove sediment indicates that organic matter accumulation at Mendaram started at circa 2780 cal years B.P., whereas freshwater peat accumulation began at circa 2250 cal years B.P. (Figure 5). The age-depth model is characterized by a stepwise pattern with relatively long phases of steady, slow accretion interrupted by brief and rapid accretion pulses derived from the mangrove sediment and the herbaceous peat layers (Unit II, Figure 7). Rates of peat accretion ranged from 0.4 to 26.6 mm yr^{-1} with the highest rate reconstructed from the herbaceous peat. The mean accretion rate from the base of the peaty clay layer to the core top is 1.5 mm yr^{-1} and that of the entire peat layer is 1.4 mm yr^{-1} .

4.5. Carbon Accumulation Rates

A mean rate of carbon accumulation of 53.5 $\text{g C m}^{-2}\text{yr}^{-1}$ was reconstructed for the entire peat layer (0–350 cm). This rate increases to 70.0 $\text{g C m}^{-2}\text{yr}^{-1}$ by including the basal mangrove sediment (0–460 cm). At the coring site a total cumulative mass of 180 kg C m^{-2} accumulated since circa 2800 cal years B.P. and 110 kg C m^{-2} since the beginning of peat accumulation at around 2250 cal years B.P. (Figure 7). Two short pulses of high carbon accumulation rates punctuate the otherwise low-accumulation history of generally less than 50 $\text{g C m}^{-2}\text{yr}^{-1}$. An initial pulse with an average rate of over 300 $\text{g C m}^{-2}\text{yr}^{-1}$ occurred during the early mangrove phase (Unit V) at circa 2800–2700 cal years B.P. and a second and even stronger pulse with around 800 $\text{g C m}^{-2}\text{yr}^{-1}$ during the peat swamp phase (Unit II) from circa 1080–1060 cal years B.P. (Figure 7).

4.6. Tree Fall Dynamics

The Mendaram peat dome is marked by numerous canopy gaps created by tree falls that range in area from 150 to 6000 m^2 . An analysis of aerial photographs from the year 2009 indicates that the total number of trees in the three 25.32 ha large sampling areas was 1367, 1567, and 1657, respectively, giving an average density of emergent *Shorea albida* trees of 60.4 trees per hectare. The tree fall totals between 2002 and 2009 for each counted sampling area were 50, 75, and 93, giving an average rate of tree fall of 0.4 trees $\text{ha}^{-1}\text{yr}^{-1}$.

5. Discussion

Peatlands are dynamic ecosystems governed by both external drivers such as climate and by internal ecosystem processes. Insights on peatland development can be gleaned with paleoecological techniques, but the reliability and value of these records strongly depend on the completeness of the recovered peat profile, the depth resolution of the sampling intervals, and a precise chronology. When rates of peat and carbon accumulation are to be determined, the resolution and accuracy of the bulk density record are also critical [Glaser et al., 2012]. These methodological issues have not been adequately addressed in previous analyses of tropical peat cores with high wood content, which create substantial sampling and analytical difficulties. Core MDM11-2A yielded a 2800 year long record of carbon accumulation at very fine temporal

resolution, a result that could only be achieved through the application of targeted AMS dating and nondestructive density measurements with very narrow sampling intervals.

5.1. Methodological Challenges

The abundance of undecomposed wood layers in the deposits of tropical swamp forests (Figure 2b) presents a major challenge for proper sampling. Numerous studies from Southeast Asian peatlands report that coring from a single borehole could not be completed due to the presence of dense wood layers [e.g., Furukawa, 1988; Esterle and Ferm, 1994; Shimada *et al.*, 2001]. This study demonstrates, however, that the Livingstone piston corer with a wide diameter core barrel and a serrated cutting edge can fully recover relatively intact sections of peat that are rich in dense tropical hardwoods. Several challenges remain with regard to having deeper penetration blocked by the probability of hitting a buried tree trunk (> 1 m), implying some bias against sampling the densest parts of the peat deposits. However, tropical wood peats have variable density because the dense wood layers often contain an array of gas- or water-filled voids [Sumawinata *et al.*, 2008]. Only coring devices with a large sampling volume such as the piston corer are able to capture this void space sufficiently. The suitability of this sampler in recovering and not compressing those features is demonstrated by the abundance of voids and macropores as visible in the radiographs (Figure 5). The piston corer appears to provide the most reliable cores for determining bulk density based on its ability to cut through all but the largest masses of wood while avoiding core compression.

Moreover, this study also shows that gamma ray attenuation logging provides a significant advantage over conventional destructive methods for measuring wet bulk density of wood peat. This noninvasive approach was able to capture the contributions from both voids and dense wood at fine spatial resolution (0.5 cm; Figures 3 and 5) when the cores were scanned at three different cross-sectional orientations. The resulting mean dry bulk density of the peat is relatively low (0.072 g cm^{-3} ; Table 2), although the core is rich in dense wood. The low density is the result of the frequent occurrence of macropores and voids and also related to the fibrous herbaceous peat layer that constitutes 35% of the peat profile (Table 2). Hardwood is clearly an important component of tropical peat deposits as shown by its average content of up to 13% in woody peat layers of the core (Table 3). However wood is also completely absent over core intervals of up to 70 cm (Figures 4 and 5), suggesting that significant proportions of tropical swamp forest peats may originate from herbaceous, rather than woody, plant material.

The average dry bulk density of 0.072 g cm^{-3} of the peat is nearly midway within the range of average values (0.066 to 0.084 g cm^{-3}) derived from dated cores of coastal Sumatran and Bornean peatlands [Cameron *et al.*, 1989; Neuzil, 1997] and corroborates the mean dry bulk density of 0.076 g cm^{-3} estimated for Southeast Asian coastal peatlands by Dommain *et al.* [2011]. However, the mean bulk density is substantially lower than that reported for peatlands from Indonesian Borneo that range from 0.11 to 0.29 g cm^{-3} [Wahyunto *et al.*, 2004].

5.2. The Development of the Mendaram Peat Dome

Long-term vegetation succession and local patch dynamics had an important influence on the rates of carbon accumulation in the Mendaram peat dome. The development of Mendaram follows the general pathway described for Southeast Asian coastal peatlands: an initial marine and/or mangrove environment is succeeded by a transitional freshwater swamp and finally by peat swamp forest [e.g., Anderson and Muller, 1975; Anderson, 1983; Staub and Esterle, 1994; Dommain *et al.*, 2011].

Marine sedimentation dominated at Mendaram until circa 2800 cal years B.P. The marine influence decreased during the ensuing mangrove forest phase that lasted from about 2800 to 2400 cal years B.P., as is indicated by spores of the mangrove fern *Acrostichum* and pollen of *Nypa* palm and the mangrove tree *Rhizophora stylosa* (Table 3). The subsequent occurrence of pollen of the swamp forest trees *Camposperma* and *Lophopetalum multinervium* and of spores of the fern *Stenochlaena palustris* at around 2400 cal years B.P. (Table 3) likely represents the *Camposperma*-*Cyrtostachys-Zalacca* transitional phase between mangrove and mixed peat swamp forest [Anderson, 1963, 1983; Anderson and Muller, 1975; Bruenig, 1990]. The generally large inorganic fraction of Unit V (Figure 3) shows that carbon accumulation in both the mangrove and freshwater swamp forest was associated with a regular influx of clastic sediments, which induced rapid rates of vertical sediment accretion of up to 5 mm yr^{-1} .

At around 2250 cal years B.P. the final ombrotrophic peat swamp forest stage began as inferred from the abrupt increase in organic matter content from less than 70% to 96% and the corresponding increase in carbon content from 30% to 60% (Figure 3). Charcoal in Unit IV indicates that in its early stage the domed peatland was locally influenced by fire, which left a 10 cm thick layer of thermally altered charred peat. Lightning has been observed to cause local tree fires even during heavy rainfall [Anderson, 1966] and such tree fires can apparently penetrate onto a desiccated forest floor. The spatial extent of the identified fire event was, however, small as this charcoal rich layer was not found in other cores.

The following peat swamp forest phase that lasted from about 2020 to 1150 cal years B.P. was characterized by *Eugenia* or *Tristania*, *Shorea albida* and *Camposperma* trees. This peat swamp forest steadily deposited peat with a wood fraction of over 10% at a rate of 1 mm yr^{-1} (Table 3). The abrupt transition from the slowly accumulating woody peat to the rapidly accumulating herbaceous peat layer above implies a rapid transformation of the local depositional environment. We interpret this new developmental phase, from circa 1150–950 cal years B.P., as an infilled fossil tip-up pool that had formed by a falling tree similar to the mechanism described by *Gastaldo and Staub* [1999]. The uprooted tree would have excavated a layer of woody peat forming a tip-up mound, whereas a tip-up pool formed in the excavated hole (as in Figure 2a). This pool rapidly filled up with contemporary deposited material causing a pulse in local peat accumulation. However, a temporal gap must exist between the top the underlying woody peat layer and the bottom of the pool sediments.

This reconstruction based on tree fall and subsequent pool infilling is supported by four lines of stratigraphic evidence: (1) The thickness of this herbaceous peat layer is 125 cm, which is typical of the depth range (approximately 70 to 150 cm) of modern pools in Mendaram. (2) The preservation of leaf litter lenses within this sequence indicates permanently flooded conditions, an interpretation supported by the regular occurrence of spores of *Spirogyra* (Table 3), a group of aquatic algae that require stagnant open water bodies [Pals et al., 1980; van Geel et al., 1981]. Leaf litter normally decomposes rapidly within 0.5 to 2 years on the floors of dipterocarp rain forests [Anderson et al., 1983; Burghouts et al., 1992; Baillie et al., 2006] and within 1.5 to 3 years in mixed peat swamp and *Shorea albida* forests [Tie, 1990]. Leaf litter only survives consumption by detritivores and microbial decomposition when deposited in permanently standing water [Esterle and Ferm, 1994; Gastaldo and Staub, 1999] in which loss rates are significantly lower [Yule and Gomez, 2009]. (3) The dates on leaf fragments within this layer that are 50 cm apart in depth differ by only 20 years demonstrating a very rapid peat accretion of over 26 mm yr^{-1} . Such rapid upward accretion could not have been associated with large-scale rising water levels because such rise would have soon killed the buttress roots of *Shorea albida* trees, which are restricted to the aerobic zone above the water table [Furukawa, 1988]. (4) Finally, the general low abundance of *Shorea albida* pollen and the high frequency of *Camposperma* pollen within the pool assemblage (Table 3) suggest a gap in the canopy, because *Camposperma coriaceum* is a long-lived pioneer species that thrives in disturbance gaps on deeper peat [Whitmore, 1975; Yule and Gomez, 2009].

The frequent herbaceous roots and rhizomes that constitute the structural skeleton of the pool deposit must have grown into the pool from the sides but could also have penetrated into previously deposited litter and detritus from floating mats that extended over the pool's surface. The roots and rhizomes were probably derived from nonwoody monocotyledonous peat-forming plants, such as *Pandanus andersonii* (Pandanaceae; Table 3), *Alocasia longiloba* (Araceae, or other species of this family), and *Hanguana malayana* (Hanguanaceae), which grow in and around pools of Mendaram (personal observation) and other Baram-Belait peatlands [Anderson, 1961a, 1963].

By around 950 cal years B.P. the pool was completely filled in and trees such as *Shorea albida* and *Ilex* became reestablished on site. This new *Shorea albida*-*Pandanus* peat swamp forest community seems to have persisted for over 900 years until the present forming an uppermost peat layer with a hardwood content of 13%.

5.3. Rates and Drivers of Carbon Accumulation

In general, the Mendaram record shows that vegetation changes, patch dynamics and ecosystem disturbances controlled local rates of carbon accumulation during the development of this peat dome. Rapid pulses of sedimentation were largely responsible for the very high rates of carbon accumulation (initially

> 300 g C m⁻² yr⁻¹) during the approximately 400 year long mangrove forest phase. However, mangrove forests in prograding deltaic settings such as the Baram-Belait Delta are ephemeral coastal environments that persist for only a few hundred years before being succeeded by peat swamp forests [Anderson and Muller, 1975; Staub and Esterle, 1994; Woodroffe, 2000]. Nevertheless, the mangrove-freshwater swamp forest stage accounts for nearly 40% (70 kg C m⁻²) of the total accumulated soil carbon at Mendaram (Figure 7). Similar soil carbon densities have been reported for modern Indo-Pacific mangroves [Donato et al., 2011].

The peat swamp forest stage in contrast is marked by generally lower and more steady rates of carbon accumulation but is also punctuated by a major pulse associated with the infilling phase of the tip-up pool. During the first approximately 1000 year long peat swamp forest phase the rate of carbon accumulation was initially at around 20–30 g C m⁻² yr⁻¹ and then increased to over 60–100 g C m⁻² yr⁻¹.

After formation of the tip-up pool carbon accumulation increased abruptly to maximum values of over 800 g C m⁻² yr⁻¹ as the lower portion of the pool was filled. These high rates are derived from herbaceous peat and leaf litter and demonstrate that wood is not necessary to produce high carbon accumulation rates in tropical peatlands as previously thought [Dommain et al., 2011]. This rapid pulse in carbon accumulation apparently lasted for only a few decades and was followed by a decline from 200 to 100 g C m⁻² yr⁻¹ over about the next hundred years (Figure 7). This decline in carbon accumulation probably occurred as the tip-up basin approached its capacity to hold and preserve plant detritus.

Once the pool was filled and overgrown the rate of carbon accumulation stabilized at approximately 60 g C m⁻² yr⁻¹ under the *Shorea albida* forest stand that ultimately became established at the coring location. During the past 500 years this forest type accumulated carbon at a steady rate of 30 g C m⁻² yr⁻¹.

The two peat swamp forest phases that existed at the coring site from 2250 to 1150 cal years B.P. and from 950 to 0 cal years B.P. deposited woody peat at a relatively low rate of 35 g C m⁻² yr⁻¹ on average. Together these two phases of wood peat deposition accumulated a total mass of 70 kg C m⁻² over a circa 2000 year long time span. In contrast, herbaceous peat and plant litter accumulated a total of 40 kg C m⁻² in a tip-up pool in only 200 years. This tip-up pool therefore stored 35% of the total peat-carbon pool that accumulated at the coring site in 10 times less time, which emphasizes the significance of tip-up pools as local hot spots for carbon accumulation within peat swamp forests.

The average rate of carbon accumulation that integrates both these depositional settings is 53.5 g C m⁻² yr⁻¹ for the entire peat swamp forest stage, a value that is similar to the long-term rate of 56.2 g C m⁻² yr⁻¹ of the inland Sebangau peat dome in southern Borneo [Page et al., 2004], but lower than the long-term rate of 86 g C m⁻² yr⁻¹ of the coastal Teluk Keramat peat dome in western Borneo [Neuzil, 1997], and also somewhat lower than the mean rates of 64 and 68 g C m⁻² yr⁻¹ estimated for the past two millennia of Indonesian coastal peatlands [Dommain et al., 2014].

5.4. Significance of Pool Deposits in Influencing Carbon Accumulation Rates

Tree fall and associated pool formation are inherent features of the patch dynamics in peat swamp forests because of their regular disturbance by wind throw and lightning [Anderson, 1964; Bruenig, 1990]. Wind throw can affect areas of up to 100 ha [Anderson, 1964], whereas lightning typically creates circular canopy gaps with an average size of about 0.25 ha [Brünig, 1964] (Figure 2c). Lightning gaps alone take up 0.1–3% of the area in *Shorea albida* forests [Brünig, 1973], where a single lightning strike may kill more than 50 trees [Anderson, 1964]. These important disturbance agents lead to frequent tree falls and creation of tip-up pools, which implies that associated shifts in the rates of carbon accumulation should be observed in other forested peatlands of Southeast Asia.

Although the extremely high local rates of past carbon accumulation associated with the tip-up pool stratum in our core may seem exceptional, similar centennial-scale pulses in carbon accumulation greater than 200 to 530 g C m⁻² yr⁻¹ have been reconstructed for the peatlands of Bengkalis Island and Siak Kanan (Sumatra) with correspondingly high rates of vertical peat accretion of 10–12 mm yr⁻¹ [Diemont and Supardi, 1987; Supardi et al., 1993; Neuzil, 1997; Dommain et al., 2014]. These high rates were previously interpreted as either climatically induced or considered artifacts of dating errors [Dommain et al., 2011]. However, they may be attributed to the dynamics of local pool deposits—an interpretation supported by the similarly low bulk density (0.05 g cm⁻³) and depth span (120 cm) of a high-accumulation section from the Siak Kanan core of

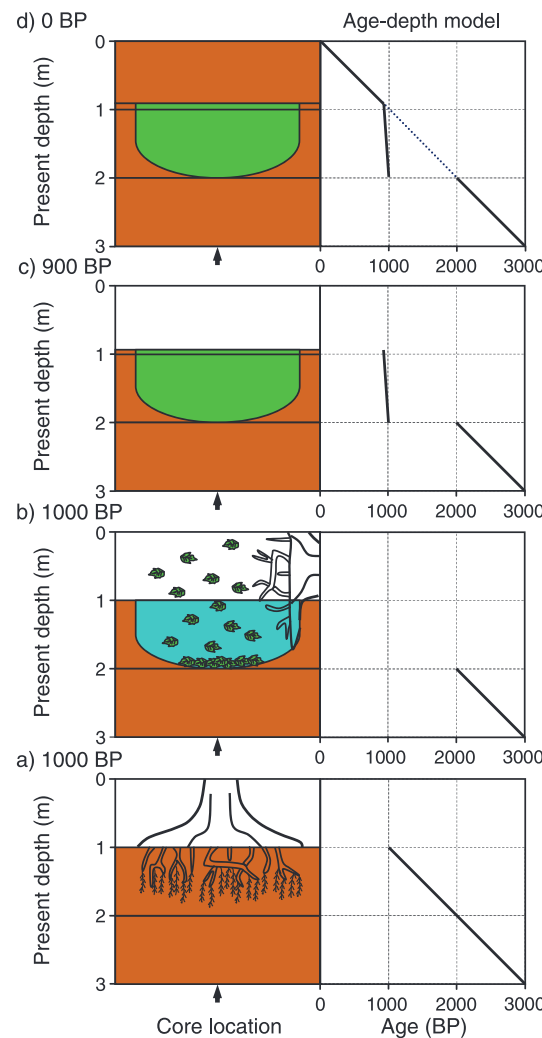


Figure 8. Conceptual model illustrating the formation of a tip-up pool and its effects on an age-depth model. (a) Until 1000 B.P.: wood peat accumulation under a forest floor at a rate of 1 mm yr^{-1} resulted in a 2 m thick wood peat deposit (brown color). (b) In 1000 B.P. a tree falls and excavates a 1 m deep hole in which a tip-up pool forms (blue color). The result is the removal of a 1000 year long age interval. Leaf litter is immediately deposited in the pool, (c) 900 B.P., after 100 years of rapid accumulation at 10 mm yr^{-1} the tip-up pool has completely filled (green color), whereas the peat dome has grown by another 10 cm. The result is a steep increase in the age-depth curve after a temporal gap (hiatus) of 1000 years. (d) 0 B.P., the tip-up pool deposit is overgrown by 90 cm of wood peat at a rate of 1 mm yr^{-1} . The dotted blue line illustrates the trajectory without tip-up pool formation (i.e., peat dome scale accumulation).

Diemont and Supardi [1987]. That the pool deposit mechanism reported here is not an atypical feature of this core is supported by the presence of a 3 m layer of well-preserved herbaceous peat with monocotyledonous roots, abundant *Pandanus* pollen, and fully preserved moss remains in a peat core from Marudi (Figure 1b) [Anderson and Muller, 1975] and also by a recovered thick lens of leaf litter from a peat swamp in the Rajang Delta (Figure 1a) [Gastaldo and Staub, 1999].

The exceptionally high carbon accumulation rates of up to $800 \text{ g C m}^{-2} \text{ yr}^{-1}$ of the pool deposit can partly be explained by the constantly high rates of litterfall in Bornean dipterocarp forests that range from 440 to $790 \text{ g C m}^{-2} \text{ yr}^{-1}$ [Proctor et al., 1983; Burghouts et al., 1992; Saner et al., 2012; Kho et al., 2013]. In the Sebangau peat swamp in southern Borneo monthly litterfall rates are 61.6 and $76.4 \text{ g dry mass m}^{-2}$ (66 and 70% by leaves), yielding an annual production of 828 and $917 \text{ g dry mass m}^{-2} \text{ yr}^{-1}$ [Sulistiyanto et al., 2002]. Somewhat lower annual rates of litterfall of 717 and $623 \text{ g dry mass m}^{-2} \text{ yr}^{-1}$ (74%–78% by leaves) were measured in a mixed peat swamp and a *Shorea albida* forest in the Marudi peat dome [Tie, 1990; Tie and Esterle, 1992]. These high rates of litterfall together with the substantial proportion of root biomass allocated by herbaceous plants surrounding or invading the pool are responsible for the high carbon accumulation rates in tip-up pools. In addition, pools can also preserve falling branches and logs.

The pulses of high carbon accumulation rates reported for the Mendaram (this study) and other peat domes [e.g., Neuzil, 1997; Dommain et al., 2014] are too high to be driven by short-term climatic fluctuations alone. Considering that the coastal Bornean climate is already very favorable for peat accumulation because of high monthly rainfall (150–370 mm), which induces frequent waterlogging, and constantly high temperatures (26–27°C), which favor high ecosystem productivity, shifts in climate

could neither enhance productivity nor suppress decomposition sufficiently to produce significantly higher rates of carbon accumulation. The major climate control on the carbon balance of tropical peatlands seems to be rainfall variability, largely related to variations in the El Niño–Southern Oscillation (ENSO) [Dommain et al., 2014]. Variability in ENSO causes substantial interannual fluctuations in net ecosystem exchange of peat swamp forests but has not been shown to produce massive net carbon gains during wetter La Niña years [Hirano et al., 2012]. Moreover, the occurrence of the major peak in carbon accumulation at around 1080–950 cal years B.P. falls into the so-called Medieval Warm Period (1200–800 cal years B.P.) that in

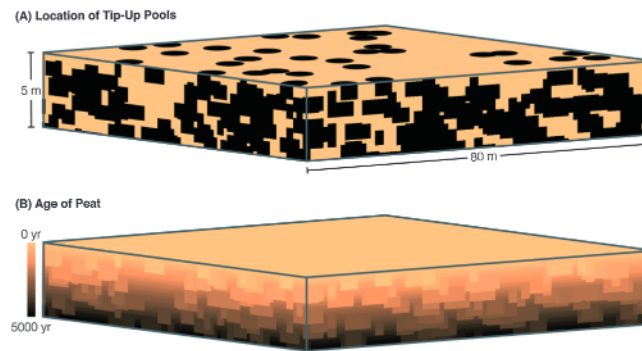


Figure 9. (a) Three-dimensional model simulation of idealized peatland growth with pool formation and infilling (black squares) after a 5000 year simulation run. Landscape-scale peat accumulation is 10 cm in 100 years, pools are 1 m deep and 6 m in diameter and fill at a rate of 100 cm/100 years. Pool formation is set at 40 new pools per 100 years. (b) Age distribution from bottom to top of the simulated peatland (dark brown—oldest layer, yellow youngest (surface) layer). Note that material in filled pools is always younger than adjacent peat.

equatorial Southeast Asia was characterized by El Niño-like conditions and reduced rainfall [Yan *et al.*, 2011]. If local rates of carbon accumulation were controlled primarily by climate, accumulation rates should have decreased during this period. Conversely, the core record shows reduced carbon accumulation rates during the Little Ice Age (600–150 cal years B.P.), when wet La Niña-like conditions prevailed in Southeast Asia [Yan *et al.*, 2011]. In general, the high variability of ENSO during the past 2000 years [e.g., Conroy *et al.*, 2008] is not reflected by synchronous variations in rates of carbon accumulation that were reconstructed from the Mendaram

core. The Mendaram record therefore suggests that decadal to centennial-scale climate variability only had a minor impact on local rates of carbon accumulation in comparison to peat swamp forest dynamics and disturbance events.

5.5. Implications of Tip-Up Pools for the Spatial Pattern of Peat Radiocarbon Ages

The sequence of cartoons in Figure 8 illustrates the effect of a single tip-up event on the age-depth curve of a peat core. In regions where the peat did not accumulate in a pool, the peat age increases linearly, i.e., according to the prevailing rate of accumulation. The tip-up event generates a temporal gap (hiatus) and a subsequent rapid increase in the apparent accumulation rate. The slope of the age-depth curve of a core corresponds to the landscape-scale accumulation rate only in the portions of the core never affected by tip-up events. Tip-up pools create sharp local perturbations in age gradients that do not correspond to regional changes in peat accumulation rates.

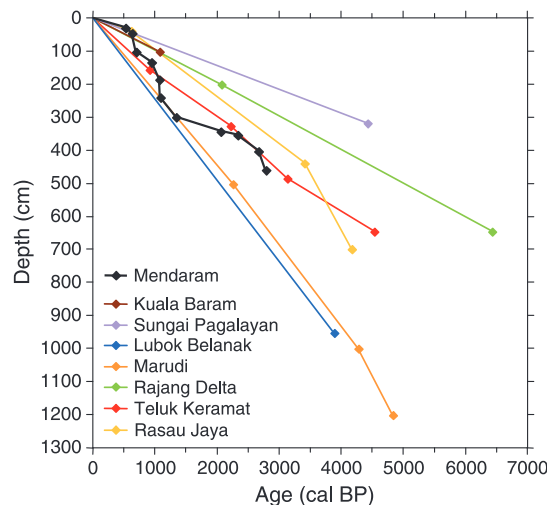


Figure 10. Comparison of age-depth models from coastal peat domes of western Borneo. The core locations of Mendaram to Marudi are shown in Figure 1b and those of the Rajang Delta, Teluk Keramat, and Rasau Jaya in Figure 1a. Note the generally large dating intervals and possibly smoothed accumulation records in comparison to core MDM11-2A. Data sources are Tie [1990] and Dommain *et al.* [2011].

To explore the effects of many tree falls over time, causing multiple tip-up events, we constructed a simple simulation of peat accumulation (Figure 9) to reproduce the processes illustrated in Figure 8 in three dimensions. To match the approximate rate of peat growth of the Mendaram peat, a 5000 year old peatland was simulated by adding 10 cm layers of peat over 50 time steps of 100 years each. Forty new tip-up pools were created at random locations across the 1 ha domain in each 100 year time step to match the estimated frequency of tree falls (0.4 trees ha⁻¹ yr⁻¹) and hence pool formation. The shape of each pool was 6 m in diameter and 1 m deep, within the size range of modern pools of Mendaram. The simulated peat comprises former pools that were filled in at some point and regions where

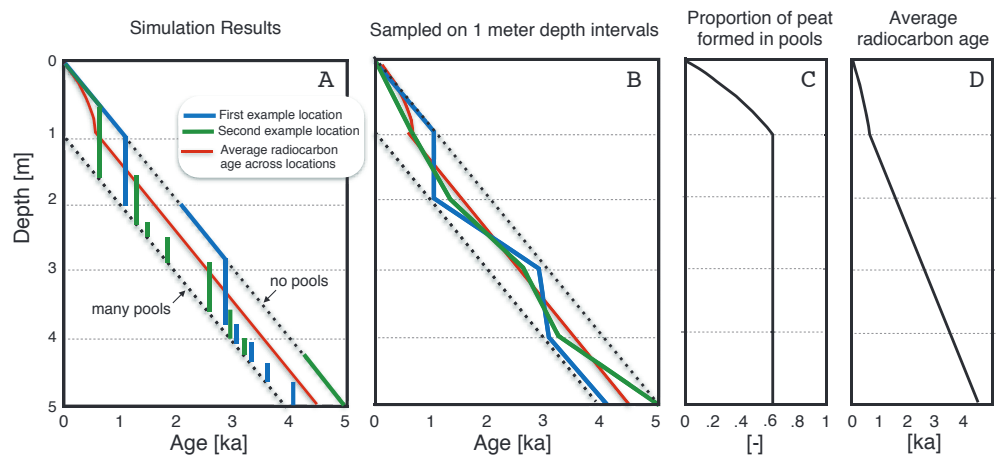


Figure 11. Results of the model simulation. (a) Age-depth curves (green, blue) derived from two simulated cores extracted from arbitrary locations of the model domain. Vertical lines represent rapid infilling of pools. Tree fall causes temporal gaps in the curves. (b) Interpolated age-depth curves for the same cores but dated in 1 m intervals. Pool formation and infilling events become invisible at this dating interval. (c) Average proportion of peat formed in pools and (d) vertical age distribution integrated over the entire peat dome.

no pool ever existed in the 5000 year development of the peatland (Figure 9a). In the regions never affected by tip-up events, radiocarbon ages increase linearly with depth, but elsewhere, the overlapping influence of former pools leads to abrupt steps in radiocarbon age both vertically and horizontally even though age increases with depth at all locations (Figure 9b). Below, we consider how these patterns can affect the interpretation of individual cores and how this spatial heterogeneity affects the radiocarbon ages across the peatland.

Most available dated peat cores from coastal Borneo are dated at large depth intervals (Figure 10). Here we consider the combined effects of this limited dating resolution and the presence of tip-up pools on the interpretation of core data. For two hypothetical cores extracted from our simulated peatland, we compare the age-depth profiles constructed by interpolating age values collected at 1 m intervals (Figure 11b) to the continuous age-depth functions (Figure 11a). The continuous age-depth curves (Figure 11a) have nearly constant ages in pool deposits (vertical lines) that form a lower bound on the peat age and a smooth diagonal relationship where pools never existed as an upper bound. The interpolated age-depth curves (Figure 11b) lack the discontinuities at the bottom of pools where there is an apparent hiatus in accumulation. This discontinuity accompanies every rapid infilling but simply cannot be resolved by interpolating across sample depths unless dates were measured at very fine depth intervals along the core. The interpolated age-depth curves smooth away the different submeter discontinuities in each core.

The simulation model also provides a tool for considering the average age of peat across an elevation or, in other words, the average age-depth curve for many cores from the same peatland. At the peatland surface, the gradient in age (Figure 11d) matches the accumulation rate because there are no pools. Below the surface, age increases more slowly with depth because the peat has been penetrated by more pools (Figure 11c), in which young material is deposited, down to the depth of 1 m, where new pools can no longer penetrate. At 1 m depth, the average age of peat is less than 1000 years, the time to accumulate one meter of peat at the average rate, because many pools have penetrated into the peat profile over the course of 1000 years replacing older peat with younger material (Figure 9). Below 1 m (the maximum pool depth) the average age of peat increases linearly at the rate of peat accumulation because the proportion of peat formed in pools remains constant (Figure 11d).

The frequent formation of tip-up pools over time across a peat dome has important implications for interpretation of core records from tropical peatlands. Apparent hiatuses in peat accumulation and abrupt increases in the local apparent rate of peat accumulation after tip-up events should be a common feature in cores from peatlands supporting large-statured trees. Dating cores at depth intervals of 1 m or larger likely results in smoothed local accumulation records that fail to capture the full range in variations of carbon

accumulation rates in these highly dynamic systems (Figure 10). The apparent peat accumulation rates observed in core MDM11-2A span almost the entire range of apparent rates from cores in coastal Borneo (Figure 10), because its narrow dating interval captures pulses of both slow and rapid accumulation phases. The removal of peat when trees fall and its rapid replacement in tip-up pools, together with the accumulation of hardwoods in tropical peat, makes the inference of climatic signals deeply challenging. Both larger numbers of cores and finer depth intervals for radiocarbon dates than are currently the norm will be required before tropical peat cores can be confidently used to estimate landscape-scale variations in past rates of carbon accumulation.

6. Conclusions

Tropical peatlands present many challenges for reconstructing their past carbon dynamics because of inherent difficulties in field access, core recovery, radiocarbon dating, and analytical measurements. However, by applying more advanced and noninvasive methods, it was possible to resolve fine-scale variations in the rates of carbon accumulation over the past 2800 years for a domed *Shorea albida* peatland in Brunei (Borneo). Local rates of carbon accumulation were largely controlled by local disturbance events, forest-patch dynamics, and vegetation changes. Forest disturbance leads to variations in local rates of carbon accumulation that can be an order of magnitude higher on multidecadal to centennial timescales than those previously reported by interannual- or millennial-scale moisture changes [Hirano *et al.*, 2012; Dommain *et al.*, 2014]. Local tip-up pools strongly control the local carbon accumulation history derived from a single peat core. Deciphering the climatic influence on landscape-scale carbon accumulation rates is therefore limited to long timescales (i.e., millennia) and will require the analysis of a range of peat cores to reduce local accumulation signals.

The Mendaram core confirms the hypothesis of *Gastaldo and Staub* [1999] that pools permit not only rapid litter deposition and preservation but also permanent wood burial. Hence, tip-up pools create localized carbon accumulation hot spots in which aboveground plant biomass is rapidly transferred into the soil carbon reservoir. The carbon dynamics of these tropical tip-up pools are therefore fundamentally different from that of pools in northern peatlands, which function as important sources of atmospheric carbon [e.g., *Hamilton et al.*, 1994; *Pelletier et al.*, 2014]. The creation of pools through tree falls and their rapid infilling is a newly recognized mechanism for peat formation characteristic of the peat domes of Southeast Asia and explains their extremely heterogeneous peat deposits that are rich in dense wood layers. This peat accumulation mechanism is likely to be common in other equatorial forested peatlands elsewhere.

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