VOLUME 79, ISSUE 2, 15 NOVEMBER 2009 ISSN 0341-8162

ELSEVIER

CATENA

AN INTERDISCIPLINARY JOURNAL OF
SOIL SCIENCE -
HYDROLOGY - GEOMORPHOLOGY
FOCUSING ON
GEOECOLOGY AND LANDSCAPE EVOLUTION

founded by H. Rohdenburg

A Cooperation Journal of the International Union of Soil Science

Catena 79 (2009) 140–145

Contents lists available at ScienceDirect

Catena

journal homepage: www.elsevier.com/locate/catena

Amazonian floodplains harbour minerotrophic and ombrotrophic peatlands

Outi Lähteenoja [a,*], Kalle Ruokolainen [a], Leif Schulman [b], José Alvarez [c]

[a] Department of Biology, University of Turku, FI-20014 Turku, Finland
[b] Finnish Museum of Natural History, Botanic Garden, P.O.Box 44, FI-00014 University of Helsinki, Finland
[c] Instituto de Investigaciones de la Amazonía Peruana (IIAP), Av. José A. Quiñones km 2.5, Apartado Postal 784, Iquitos, Perú

ARTICLE INFO

Article history:
Received 24 June 2009
Accepted 26 June 2009

Keywords:
Minerotrophy
Mire ecosystem
Ombrotrophy
Peat
Peruvian Amazonia
Raised bog

ABSTRACT

In tropical lowlands, ecosystems with peat strata are commonly reported from Southeast Asia, but hardly at all from Amazonia. In this paper, we quantify the horizontal distribution of four important plant nutrients (Ca, Mg, K and P) in five peatland sites located in Peruvian Amazonia and the vertical distribution of these nutrients in one of the sites. With this data as well as topography measurements of the peat deposit from one of the sites, we showed that minerotrophic and ombrotrophic peatlands can be detected in Amazonian floodplains. The nutrient-poor ombrotrophic bogs receive nutrients only from atmospheric deposition because of their thick peat layer and convex topography, while the minerotrophic swamps are periodically covered by nutrient-rich floodwater and/or receive nutrient input from surface waters or from groundwater with capillary rise. The existence of such peatlands in the Amazonian lowlands increases the regional habitat diversity and availability of palaeoecological information and probably has implications also for the hydrological dynamics, water quality, and carbon dynamics of the area.

1. Introduction

In waterlogged soils, anoxic conditions cause partly decomposed organic matter to accumulate as peat. Ecosystems featuring this process, generally termed mires or peatlands, are mostly located in boreal and temperate regions, but extensive and varied tropical mire ecosystems also exist particularly in Southeast Asia (Morley, 1981; Anderson, 1983; Page et al., 1999, 2002; Weiss et al., 2002; Rieley and Page, 2005). In contrast, our knowledge on Amazonian peatland ecosystems seems to be restricted to some sporadic observations in different ecological studies (Junk, 1983; Suszczynski, 1984; Shier, 1985; Andriesse, 1988; Kahn and Mejia, 1990; Kahn and Granville, 1992; Dubroeucq and Volkoff, 1998; Batjes and Dijkshoorn, 1999; Schulman et al., 1999; Ledru, 2001; Ruokolainen et al., 2001; Guzmán Castillo, 2007). Nevertheless, in a recent study covering 17 floodplain wetland sites in Peruvian lowland Amazonia, we observed up to 5.9 m thick peat deposits in 16 of the sites (Lähteenoja et al., 2009). These peatlands can play a role in the global carbon cycle as carbon sinks and sources, especially under the future changing climate (Lähteenoja et al., 2009). Furthermore, these findings are interesting also from other points of view than the carbon cycle: the existence of peatlands in the Amazonian floodplains can affect, i.a., the hydrological dynamics and water quality of water systems, local microclimate, availability of palaeoecological records, as well as regional habitat diversity and species distribution (Maltby and Immirzi, 1993; Maltby and Proctor, 1996).

Mire ecosystems can be divided in minerotrophic peat swamps and ombrotrophic peat bogs (see e.g., Heinselman, 1970; Verhoeven, 1986; Bridgham and Richardson, 1993; Gerdol et al., 1994; Page et al., 1999; Bragazza et al., 2003; Clarkson et al., 2004; Bragazza et al., 2005; Muller et al., 2006). This division is based on the origin of nutrient input. Minerotrophic mires are typically formed in depressions and floodplains and receive mineral nutrients with incoming surface or groundwater. These waters are in contact with mineral soil, and therefore minerotrophic mires reflect the nutrient levels of the soil. In contrast, the only nutrient and water input of ombrotrophic mires is from wet and dry atmospheric deposition. No surface or groundwater can enter ombrotrophic mires because the peat forms a convex dome that forces waters to run off the bog. Ombrotrophic mires can be formed on level terrain or represent the late successional stage of minerotrophic mires. Because of the hydrological difference, the nutrient levels are often higher in minerotrophic mires than in ombrotrophic bogs. Peat Ca content is the best indicator of ombrotrophic conditions because of its limited input in ombrotrophic peats (Verhoeven, 1986; Laine et al., 2002; Muller et al., 2006), and the Ca/Mg ratio of ombrotrophic bogs usually resembles that of rainwater (Weiss et al., 1997, 2002; Muller et al., 2006). If the peat Ca/Mg ratio exceeds that of the local rainwater, the peatland must have an additional (minerotrophic) source of Ca (Weiss et al., 1997, 2002; Muller et al., 2006). Minerotrophic and ombrotrophic mire types typically have specific species compositions, and the coexistence of these types contributes to the regional diversity of ecosystems and habitats (e.g., Heinselman, 1970; Bridgham and Richardson, 1993; Gerdol et al., 1994; Page et al., 1999; Wheeler and Proctor, 2000; Bayley and Mewhort, 2004; Clarkson et al., 2004; Bragazza et al., 2005; Hájek et al., 2006).

* Corresponding author.
E-mail address: outi.lahteenoja@utu.fi (O. Lähteenoja).

0341-8162/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.catena.2009.06.006

Amazonian peatlands are apparently mostly located on river floodplains (Ruokolainen et al., 2001; Lähteenoja et al., 2009). The logical first assumption is therefore that they are minerotrophic. As far as we know, ombrotrophic mires have never been reported from Amazonia, and their existence in the area has only been speculated upon (Richards, 1952). In this paper, we quantify the horizontal distribution of four important plant nutrients (Ca, Mg, K and P) in five peatland sites that were studied for their carbon stocks by Lähteenoja et al. (2009) in Peruvian Amazonia. With these data as well as topography measurements of the peat deposit and the vertical distribution of nutrients in one of the sites, we study whether these sites can be divided in minerotrophic and ombrotrophic ecosystems.

2. Materials and methods

The study was realized in northern Peruvian lowland Amazonia in July–September 2006 and in July 2008 (Fig. 1). The climate of the study area is hot and humid, and shows very little seasonal variation (average yearly temperature 26 °C, annual precipitation *c*. 3100 mm; Marengo, 1998). The study area is characterized by extensive floodplains, on which the study sites were located. No maps of wetland types were available for the area, but there are observations suggesting that different wetlands have different spectral values in Landsat TM satellite images (Mäki and Kalliola, 1998; Instituto de Investigaciones de la Amazonía Peruana, 2004). On this basis, we selected five accessible study sites (Fig. 1) that were assumed to be wetland sites and represented an as wide range of spectral signatures as possible. In this way the selection of field study sites follows the principle of gradsect sampling (Austin and Heyligers, 1989). We delimited each site visually in hard copies of satellite images (Mäki and Kalliola, 1998; Instituto de Investigaciones de la Amazonía Peruana, 2004), and established a straight transect line from the edge of the site to its centre (in the sites Buena Vista, Charo, Quistococha and Riñón), or in a representative part of an extensive peatland area (the site San Jorge). We collected peat samples at every 300 m along the transect with a Russian peat sampler (50 cm × 5 cm × 2.5 cm; Jowsey, 1965). The samples were dried in the laboratory at 105 °C.

Two hermetically closed peat samples per site (from two different study points) representing the most superficial meter of peat were analysed for their nutrient content (Ca, K, Mg, P) by inductively coupled plasma optical emission spectrometer (ICP-OES, Thermo Jarrel Ash IRIS Advantage with CID detector) with the HNO3–HClO4–HF method. In the San Jorge mire, the nutrient analysis included nine superficial peat samples and six peat samples collected from one complete peat profile (one peat sample from the lower 50 cm of each meter of peat until the mineral subsoil was reached). The uncertainty of each measurement was ±5%. The sampling depths are shown in Table 1. We compared the peat Ca/Mg mass ratio to that of the Amazonian rainwater (Furch and Junk, 1997) and global average of continental rainwater (Berner and Berner, 1996 in Weiss et al., 2002), because this is a common method used to determine whether a peatland is ombrotrophic or not (Weiss et al., 1997, 2002; Muller et al., 2006).

On the 10th of July 2008, we levelled the transect of the San Jorge mire (and the path from the village of San Jorge to the beginning of the transect) using a 35-m-long hose filled with water. We placed firmly along the transect (beginning from the Amazon River) two wooden stakes and bound each end of the hose to one of the stakes. We measured the difference between the river water level and the water level in stake 1 and marked the same water level to stake 2. Next we moved the starting end of the hose to a third stake, marked the new water level in both stakes (2 and 3) and measured the difference between the two marks in stake 2. This way we were able to establish in the stakes a reference altitude that was always at known altitude above the level of the river on the 10th of July 2008. At each stake we measured the distance from the reference altitude to the soil surface in order to depict the topography of the studied transect. The distance from the river bank to the end of the transect in San Jorge mire involved 202 altitude measurements of differences in water level along the height of the stake. At each measurement point, there is some error involved, but these errors are not likely to be systematically biased up- nor downwards. Therefore the resulting topographical line for the transect should be very accurate. We compared the difference in the Amazon River water level measured in Iquitos, some 50 km downstream from San Jorge, between the 10th of July 2008 and the absolute maximum since 1907 (data obtained from Servicio Nacional de Meteorología y Hidrología del Perú, SENAMHI, 2008 and Dirección Agraria Regional de Loreto, 2008) in order to deduce

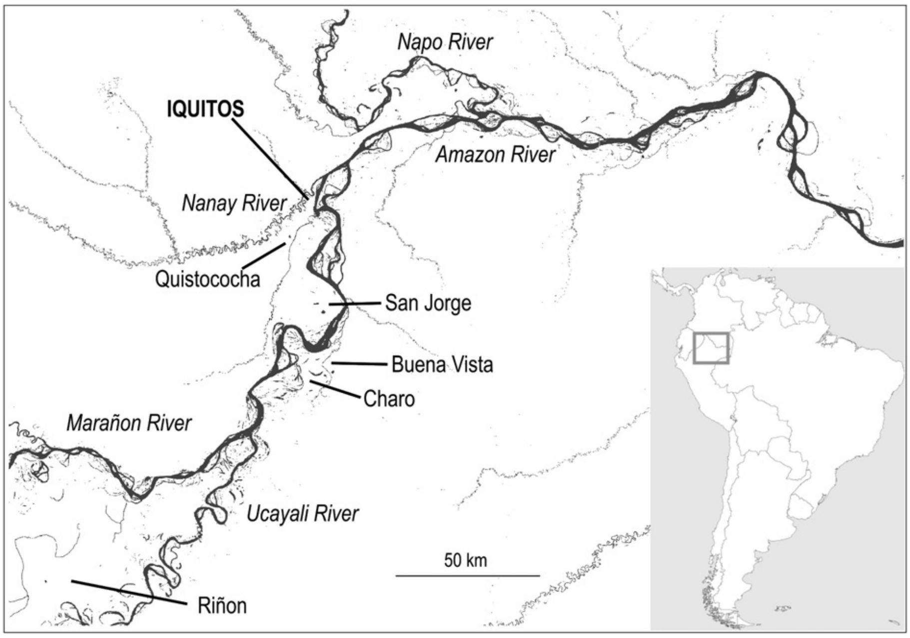

Fig. 1. Location of the study sites and the city of Iquitos (03°44′5″ S, 073°14′3″ W).

Table 1
Description of the study sites and results of the nutrient analyses.

Study site (range of peat thickness*)	Vegetation	Number of samples (sampling depth)	Ca (g kg^{-1} dry peat) average (range)	K (g kg^{-1} dry peat) average (range)	Mg (g kg^{-1} dry peat) average (range)	P (g kg^{-1} dry peat) average (range)	pH
Buena Vista (0–300 cm)	Forested	2 (60–64 cm; 50–54 cm)	17.40 (17.14–17.66)	2.13 (1.89–2.37)	1.73 (1.65–1.81)	0.39 (0.36–0.41)	–
Charo (0–210 cm)	Mixed palm swamp	2 (70–74 cm; 92–96 cm)	16.77 (16.46–17.08)	2.06 (1.92–2.19)	1.39 (1.34–1.43)	0.42 (0.40–0.43)	–
Quistococha (0–490 cm)	*M. flexuosa* palm swamp and forested	2 (70–80 cm; 90–100 cm)	1.46 (1.27–1.64)	0.18 (0.10–0.25)	0.14 (0.14–0.14)	0.18 (0.13–0.23)	–
Riñón (300–390 cm)	Open savanna	2 (20–30 cm; 90–100 cm)	1.33 (0.25–2.4)	0.66 (0.36–0.95)	0.29 (0.11–0.46)	0.21 (0.12–0.30)	–
San Jorge (0–590 cm)	*M. flexuosa* palm swamp and forested	9 (10 for pH) (1 × 30–40 cm; 5 × 70–80 cm; 3 × 80–90 cm)	0.37 (0.18–1.04)	0.89 (0.15–1.72)	0.30 (0.09–0.75)	0.37 (0.21–0.59)	3.8 (3.5–4.5)

The pH was determined in the surface peat water in the San Jorge mire. The uncertainty of each measurement is ± 5%. * indicates data on peat thickness from Lähteenoja et al. (2009).

whether the San Jorge mire is periodically covered by floodwaters. In addition, we measured the pH of the surface peat water with a field meter and the water table depth of the study points.

3. Results

The sites can be divided into two groups according to their nutrient content: the nutrient-rich sites (Buena Vista and Charo) and the nutrient-poor sites (Quistococha, Riñón, and San Jorge; Table 1). The biggest difference between the two groups was observed for Ca content. In the nutrient-rich sites, it was about 10-fold higher than in Quistococha and Riñón, and ca. 40-fold higher than in San Jorge. The smallest difference in nutrient content between the two groups was observed for P. The Ca/Mg mass ratios of all the samples from San Jorge and Riñón (also the deeper samples from the entire analyzed profile from San Jorge) were similar to that of global average of continental rainwater and Amazonian rainwater, while the Ca/Mg ratio of Quistococha, Charo and Buena Vista was clearly higher (Fig. 2). Here again the study sites could be divided into two clearly separate groups, but this time Quistococha belonged to the same group with Buena Vista and Charo.

According to our levelling measurements, the peat surface of the San Jorge mire had a convex shape (Fig. 3A) and the peat surface of the central part lied about 8 m higher up than the water level of the Amazon River on the 10th of July 2008. The corresponding difference for the edge of the mire was about 6.5 m. These differences were larger than the 6.49 m difference in the Amazon River water level between the 10th of July 2008 (112.39 masl) and the absolute maximum since 1907 (118.88 masl) (data obtained from SENAMHI, 2008 and Dirección Agraria Regional de Loreto, 2008).

Between km 1.2 and 1.5 of the San Jorge transect, a sharp decrease in the nutrient content of the superficial peat was observed (Fig. 3B). In the analyzed entire peat profile of the San Jorge mire (Fig. 3C), the contents of base cations were relatively low in the two most superficial samples at depths of 75 cm and 175 cm (slightly higher at 75 cm than at 175 cm), but below them the contents increased abruptly to manifold levels. Phosphorus had about the same concentration at all depths. The water table was closer to the peat surface in the edge than in the centre of the mire (Fig. 3D). The pH of surface peat water of the San Jorge mire varied from 3.5 to 4.5 (Table 1).

4. Discussion

According to nutrient concentration, we can divide the study sites between nutrient-rich (Buena Vista and Charo) and nutrient-poor mires (Quistococha, Riñón, and San Jorge). Because of the striking difference (especially in the Ca content), we interpret that Buena Vista and Charo get their nutrients from the periodical floodwaters, and are thus minerotrophic (Weiss et al., 1997, 2002; Muller et al., 2006). This is confirmed by the Ca/Mg ratios of these mires, which clearly exceed that of the global and Amazonian rainwater.

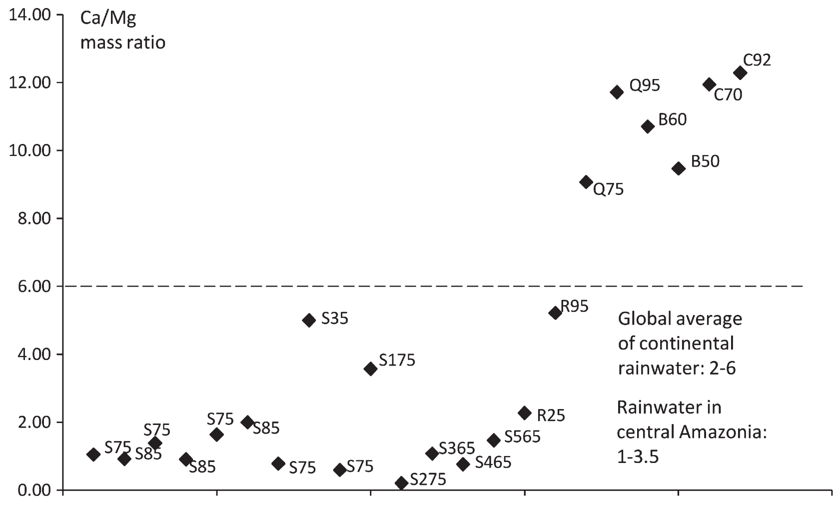

Fig. 2. The Ca/Mg mass ratio of all the peat samples analyzed for their nutrient content. S = San Jorge, R = Riñón, Q = Quistococha, B = Buena Vista, C = Charo, the number following each letter indicate the average depth of each sample. The dashed line indicates the maximum Ca/Mg ratio of the global average of continental rainwater (rainwater data from central Amazonia from Furch and Junk, 1997, data on global average of continental rainwater from Berner and Berner, 1996 in Weiss et al., 2002). If the peat Ca/Mg ratio exceeds that of the rainwater, the peatland must have an additional (minerotrophic) source of Ca (Weiss et al., 1997, 2002; Muller et al., 2006).

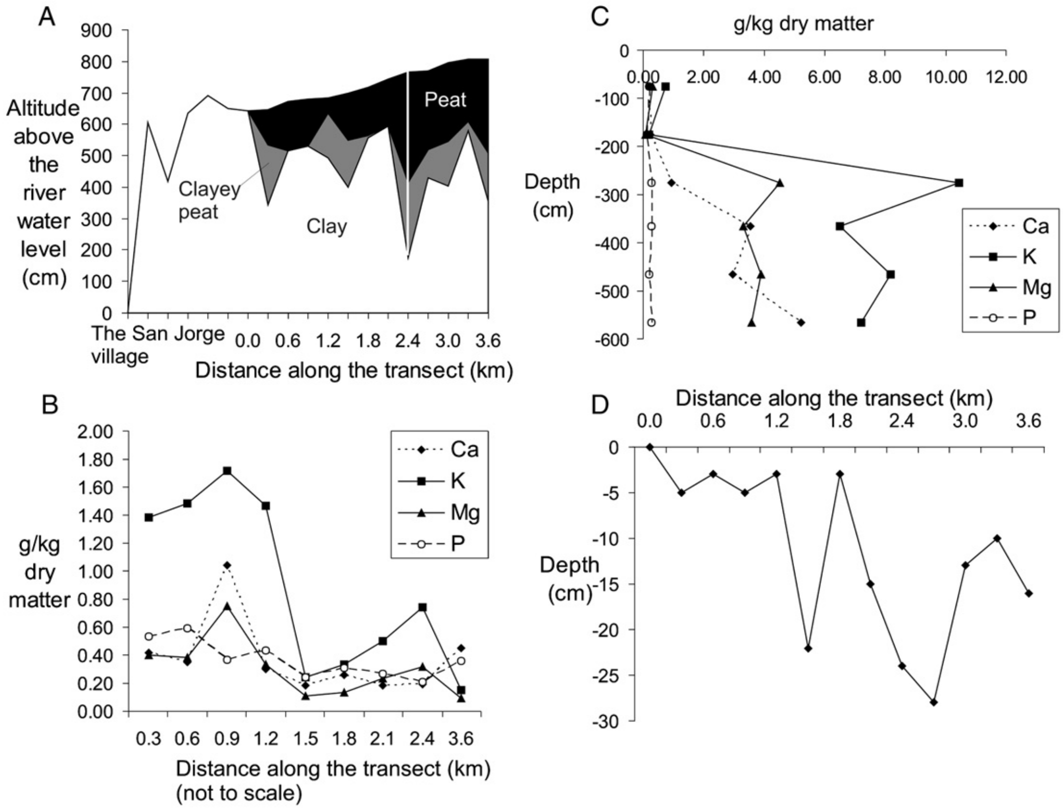

Fig. 3. The San Jorge mire: A) topography and soil profile (data on peat thickness from Lähteenoja et al., 2009), the vertical line indicates the location of the peat profile presented in C, B) nutrient content of the superficial peat, C) nutrient content of the entire peat profile, D) water table depth. The uncertainty of each nutrient content measurement is ±5%.

Our levelling measurements revealed that the San Jorge mire has a convex shape typical of raised ombrotrophic bogs, and that its surface has not been covered by flood water at least since 1907. These observations suggest that San Jorge is an ombrotrophic bog, though they cannot yet fully prove it. Young and relatively thin convex peat deposits can receive nutrients also from the underlying mineral soil and groundwater with the capillary rise of water and nutrients in the peat pores (Hill and Siegel, 1991; Waniek et al., 2000). Furthermore, it is also possible that there are infrequently massive floods that do rise even to the highest areas of the San Jorge bog and bring significant nutrient input to the system. However, our chemical analyses of the peat showed that at least the central part of the San Jorge bog has levels of base cations and phosphorus, as well as values of pH, that are typical for ombrotrophic bogs in the tropics (Anderson, 1983; Page et al., 1999; Muller et al., 2006; Troxler, 2007; Table 2) as well as for ombrotrophic bogs in other climatic zones around the world (Bragazza et al., 2003; Table 2). Therefore, the capillary rise of nutrients in the peat pores, if existent, must be minimal. Also the peat Ca/Mg ratio of San Jorge is very close to that of rainwater. Consequently, we interpret that the central part of the San Jorge mire is an ombrotrophic bog. We do not have levelling nor floodwater data from the Riñón mire, but the low peat nutrient content comparable to other ombrotrophic mires together with the peat Ca/Mg ratio very close to that of rainwater suggest that also the Riñón mire is an ombrotrophic bog. The high Ca/Mg ratio of the Quistococha mire suggests that the mire has a minerotrophic source of Ca, but the peat nutrient content in the Quistococha mire is considerably lower than that of the Buena Vista and Charo mires. Consequently, Quistococha is probably a nutrient-poor minerotrophic peatland.

The sharp decrease in the nutrient content of the superficial peat in the San Jorge mire between 1.2 km and 1.5 km along the transect implies that the marginal part of this mire is influenced by groundwater and/or surface runoff waters, and is, hence, a peripheral minerotrophic lagg of the otherwise ombrotrophic bog (cf. Gerdol et al., 1994). This is probably due to the relatively thin peat layer of the marginal part. However, the nutrient content is still relatively low in comparison to that of the Buena Vista and Charo mires, which suggests that the marginal part of the San Jorge mire is above the highest floods (even if unusually massive floods may reach it). This is supported by the very low Ca/Mg ratio (comparable to that of rainwater) of the marginal part of the San Jorge mire.

In the analyzed entire profile of the San Jorge mire, the sharp increase in the nutrient content from the depth of 175 cm to 275 cm indicates the vertical limit between what we interpret as ombrotrophic and minerotrophic conditions. At least there is no other logical explanation for such a sharp change in nutrient content in a peat profile (Page et al., 1999; Weiss et al., 2002; Muller et al., 2006).

Table 2
Peat nutrient content in other tropical and extratropical ombrotrophic bogs.

Study	Sample depth (cm)	Ca (g kg^{-1})	Mg (g kg^{-1})	K (g kg^{-1})	P (g kg^{-1})	pH
Muller et al. (2006), Australia	50–100	ca. 4.0	ca. 2.7	–	–	–
Anderson (1983), Malaysia	Surface	0.33 (0.12)	0.92 (0.18)	0.30 (0.10)	0.37 (0.12)	3.40 (0.09)
Page et al. (1999), Indonesia	30–90	0.165	0.401	0.149	0.115	3.6
Bragazza et al. (2003), Italian Alps	Surface	1.95 (0.58)	0.54 (0.13)	0.56 (0.28)	0.23 (0.12)	–
Bragazza et al. (2003), Sweden	Surface	1.31 (0.56)	0.46 (0.16)	0.68 (0.32)	0.40 (0.12)	–

The pH was determined in the surface peat water. Values in parenthesis indicate standard deviation. The Australian bog is rather special as it is situated in a crater of an old volcano.

Interestingly, the Ca/Mg ratio of all the peat samples from the entire profile was comparable to that of the rainwater, even that of the deepest parts. Nevertheless, the deepest parts of the San Jorge mire cannot be ombrotrophic, because clay was observed inside the peat and the nutrient levels were well above those of ombrotrophic bogs (Table 2). We interpret the slightly higher nutrient content at the depth of 75 cm in comparison to 175 cm in the San Jorge mire as a result of bioaccumulation of plant nutrients in the superficial peat due to continuous nutrient uptake and cycling by the vegetation (Page et al., 1999; Weiss et al., 2002; Muller et al., 2006).

Our observations come from relatively few mires in a geographically restricted area, but despite this, they are enough to show that the world's largest continuous area of tropical rainforest biome, Amazonia, harbours two previously unreported ecosystem types: minerotrophic peat swamps and ombrotrophic peat bogs. This variation of peatlands has several different implications for our understanding on the Amazonian lowlands as well as global distribution of ecosystems. First, the existence of these ecosystems increases the regional habitat diversity, and, consequently, further research should be targeted to clarify what kind of vegetation the different peatlands support, and how the existence of nutrient-rich and nutrient-poor peatland soils affect the regional distribution patterns of species (Heinselman, 1970; Bridgham and Richardson, 1993; Gerdol et al., 1994; Page et al., 1999; Wheeler and Proctor, 2000; Bayley and Mewhort, 2004; Clarkson et al., 2004; Bragazza et al., 2005; Hájek et al., 2006). In the geoecological map of the region of Iquitos, based on Landsat TM satellite images (Mäki and Kalliola, 1998), the ombrotrophic centre and the minerotrophic lagg of the San Jorge mire harbour visually different vegetation types. Interestingly, in the ombrotrophic part of the San Jorge mire we observed species of Melastomataceae (*Clidemia epibaterium*, *Tococa macrosperma*), pteridophytes (*Selaginella producta*, *Trichomanes martiusii*), and other plant groups (*Doliocarpus dentatus*, *Euterpe catinga*, *Pachira brevipes*) typical of the so called Amazon caatinga, *campina-rana*, *varillal* or white-sand forest that grows on unflooded terrain on extremely nutrient-poor quartz sand soils (Anderson, 1981; Encarnación, 1985; García Villacorta et al., 2003). Also, the physiognomy of the vegetation appeared to be similarly characterised by slender trees as are the forests of white-sand soils. In addition, one of us (JA) registered in the central part of the San Jorge mire three near-obligate white-sand forest specialist bird species (*Neopipo cinnamomea*, *Attila citriniventris*, and *Heterocercus aurantiivertex*), four facultative white-sand forest users (*Galbula dea*, *Megastictus margaritatus*, *Hypocnemis hypoxantha*, and *Dixiphia pipra*) (Alvarez and Whitney, 2003), and three additional species associated with white-sand or sandy-belt forests in other Amazonian countries (*Hylocharis cyanus*, *Piaya melanogaster*, and *Campephilus rubricollis*) (Hilty and Brown, 1986; Stotz et al., 1996). Future research should clarify whether the nutrient-poor mires in general are suitable habitats for white-sand forest species, and thereby extend the very restricted habitat range of these specialized species.

Second, ombrotrophic bogs are especially good archives of information in detecting the past changes in climate, atmospheric deposition and vegetation (Weiss et al., 1997, 2002; Muller et al., 2006), and therefore palynological studies of them can reveal important palaeoecological details of Amazonian rainforest biome. Third, ombrotrophic peatlands affect the water quality and hydrological dynamics of the surrounding areas by storing a considerable amount of water in the peat and by affecting the directions of the surface water flow (e.g. McNamara et al., 1992). Fourth, the peat and carbon stock reserved in ombrotrophic bogs is very vulnerable to changes in climate because of their direct dependence on the atmospheric water input. Consequently, drought events can have severe consequences in tropical ombrotrophic peatlands, as observed for example in Indonesia during the El Niño event in 1997 (Page et al., 2002). The relevance of these considerations in lowland Amazonia naturally depends on the abundance and distribution of ombrotrophic bogs in the area, which future studies should clarify.

Acknowledgements

We thank Yully Rojas Reátegui, Peruvian rainforest villagers, and the Peruvian Amazon Research Institute (IIAP) for help in the field work, Jyrki Jauhiainen and Harri Vasander for assistance in planning the field work, Janeth Braga, Professor Jorge Marapara and Marjut Wallner for laboratory facilities, Tuuli Toivonen for help in GIS, and Hanna Tuomisto, Noam Shany, and Victor Vargas. The study was funded by the Finnish Cultural Foundation, Kone Foundation, the Finnish Concordia Fund and Societas Biologica Fennica Vanamo, and supported also by the Faculty of Biosciences (University of Helsinki) and by the Peruvian Amazon Research Institute (IIAP).

References

Alvarez, J., Whitney, B., 2003. Eight new bird species for Peru and other distributional records from white-sand forests of northern Peruvian Amazon, with implications for biogeography of northern South America. Condor 105, 552–566.

Anderson, A.B., 1981. White-sand vegetation of Brazilian Amazonia. Biotropica 13, 199–210.

Anderson, J.A.R., 1983. The tropical peat swamps of western Malesia. In: Gore, A.J.P. (Ed.), Ecosystems of the world 4B. Mires: swamp, bog, fen and moor. Elsevier, Amsterdam, pp. 181–199.

Andriesse, J.P., 1988. Nature and management of tropical peat soils. FAO Soils Bulletin, vol. 59. Food and Agriculture Organization of the United Nations, Rome, Italy.

Austin, M.P., Heyligers, P.C., 1989. Vegetation survey design for conservation: gradsect sampling of forests in north-east New South Wales. Biological Conservation 50, 13–32.

Batjes, N.H., Dijkshoorn, J.A., 1999. Carbon and nitrogen stocks in the soils of the Amazon Region. Geoderma 89, 273–286.

Bayley, S.E., Mewhort, R.L., 2004. Plant community structure and functional differences between marshes and fens in the southern boreal region of Alberta, Canada. Wetlands 24, 277–294.

Berner, E.K., Berner, R.A., 1996. Global Environment: Water, Air and Geochemical Cycles. Prentice Hall, NJ.

Bragazza, L., Gerdol, R., Rydin, H., 2003. Effects of mineral and nutrient input on mire biogeochemistry in two geographical regions. The Journal of Ecology 91 (3), 417–426.

Bragazza, L., Håkan, R., Gerdol, R., 2005. Multiple gradients in mire vegetation: a comparison of a Swedish and an Italian bog. Plant Ecology 177, 223–236.

Bridgham, S.D., Richardson, C.J., 1993. Hydrology and nutrient gradients in North Carolina peatlands. Wetlands 13, 207–218.

Clarkson, B.R., Schipper, L.A., Lehmann, A., 2004. Vegetation and peat characteristics in the development of lowland restiad peat bogs, North Island, New Zealand. Wetlands 24, 133–151.

Dubroeucq, D., Volkoff, B., 1998. From oxisols to spodosols and histosols: evolution of the soil mantles in the Río Negro Basin (Amazonia). Catena 32, 245–280.

Encarnación, F., 1985. Introducción a la flora y vegetación de la Amazonía peruana: estado actual de los estudios, medio natural y ensayo de una clave de determinación de las formaciones vegetales en la llanura amazónica. Candollea 40, 237–252.

Furch, K., Junk, W.J., 1997. Physicochemical conditions in floodplains. In: Junk, W.J. (Ed.), The central Amazon floodplain: ecology of a pulsing system. Ecological Studies, vol. 126. Springer, pp. 69–108.

García Villacorta, R., Ahuite Reátegui, M., Olórtegui Zumaeta, M., 2003. Clasificación de bosques sobre arena blanca de la zona reservada Allpahuayo-Mishana. Folia Amazónica 14, 17–33.

Gerdol, R., Tomaselli, M., Bragazza, L., 1994. A floristic-ecologic classification of 5 mire sites in the montane-sub-alpine belt of South Tyrol (South Alps, Italy). Phyton-Annales Rei Botanicae 34 (1), 35–56.

Guzmán Castillo, W., 2007. Valor económico del manejo sostenible de los ecosistemas de aguaje (Mauritia flexuosa). In: Feyen, J., Aguirre, L.F., Moraes, M. (Eds.), International Congress on Development, Environment and Natural Resources: Multi-level and Multi-scale Sustainability, volumen III. Publication of the Universidad Mayor San Simón, Cochabamba, Bolivia, pp. 1513–1521.

Hájek, M., Horsák, M., Hájková, P., Dítě, D., 2006. Habitat diversity of central European fens in relation to environmental gradients and an effort to standardise fen terminology in ecological studies. Perspectives in Plant Ecology, Evolution and Systematics 8(2)(13), 97–114.

Heinselman, M.L., 1970. Landscape evolution, peatland types, and the environment in the Lake Agassiz peatlands natural area, Minnesota. Ecological Monographs 40, 235–261.

Hill, B.M., Siegel, D.I., 1991. Groundwater flow and the metal content of peat. Journal of Hydrology 123, 211–224.

Hilty, S.L., Brown, W.L., 1986. A guide to the birds of Colombia. Princeton University Press, Princeton, New Jersey, U.S.A.

Instituto de Investigaciones de la Amazonía Peruana, 2004. Diversidad de vegetación de la Amazonía Peruana expresada en un mosaico de imágenes de satélite. Documento técnico no. 12. (Online: http://www.iiap.org.pe/biodamaz/faseii/download/literatura_gris/12.pdf).

Jowsey, P.C., 1965. An improved peat sampler. New Phytologist 65, 245–248.

Junk, W.J., 1983. Ecology of swamps on the middle Amazon. In: Gore, A.J.P. (Ed.), Mires: swamp, bog, fen and moor, regional studies; Ecosystems of the World 4B. Elsevier, Amsterdam, the Netherlands, pp. 269–294.

Kahn, F., Granville, J., 1992. Palms in forest Ecosystems of Amazonia. Springer Verlag, Heidelberg.

Kahn, F., Mejia, K., 1990. Palm communities of wetland forest ecosystems of Peruvian Amazonia. Forest Ecology and Management 33–34, 169–179.

Lähteenoja, O., Ruokolainen, K., Schulman, L., Oinonen, M., 2009. Amazonian peatlands: an ignored C sink and potential source. Global Change Biology. doi:10.1111/j.1365-2486.2009.01920.x.

Laine, J., Komulainen, V.M., Laiho, R., Minkkinen, K., Rasinmäki, A., Sallantaus, T., Sarkkola, S., Silvan, N., Tolonen, K., Tuittila, E.S., Vasander, H., Päivänen, J., 2002. Lakkasuo – opas suon ekosysteemiin. Publications from the Department of Forest Ecology, University of Helsinki 26, Finland. 120 pp.

Ledru, M.P., 2001. Late Holocene rainforest disturbance in French Guiana. Review of Palaeobotany and Palynology 115, 161–170.

Mäki, S., Kalliola, R., 1998. Geoecological map of the region of Iquitos, Peru. Annexed in Kalliola, R., Flores Paitán, S. (eds.), Geoecología y desarrollo amazónico: estudio integrado en la zona de Iquitos, Perú. Annales Universitatis Turkuensis Ser A II 114, University of Turku, Finland.

Maltby, E., Immirzi, P., 1993. Carbon dynamics in peatlands and other wetland soils, regional and global perspectives. Chemosphere 27, 999–1023.

Maltby, E., Proctor, F., 1996. Peatlands: their nature and role in the biosphere. In: Lappalainen, E. (Ed.), Global peat resources. International Peat Society, Jyskä, Finland, pp. 11–19.

Marengo, J.A., 1998. Climatología de la zona de Iquitos, Perú. In: Kalliola, R., Flores Paitán, S. (Eds.), Geoecología y desarrollo amazónico: estudio integrado en la zona de Iquitos, Perú. Annales Universitatis Turkuensis Ser A II, vol. 114. University of Turku, Finland, pp. 35–57.

McNamara, J.P., Siegel, D.I., Glaser, P.H., Beck, R.M., 1992. Hydrogeologic controls on peatland development in the Malloryville Wetland, New York (USA). Journal of Hydrology 140, 279–296.

Morley, R.J., 1981. Development and vegetation dynamics of a lowland ombrogenous peat swamp in Kalimantan Tengah, Indonesia. Journal of Biogeography 8 (5), 383–404.

Muller, J., Wust, R.A.J., Weiss, D., Hu, Y., 2006. Geochemical and stratigraphic evidence of environmental change at Lynch's Crater, Queensland, Australia. Global and planetary change 53 (4), 269–277.

Page, S.E., Rieley, J.O., Shotyk, O.W., Weiss, D., 1999. Interdependence of peat and vegetation in a tropical peat swamp forest. Philosophical Transactions of the Royal Society of London. Series B 354, 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, 61–65.

Richards, P.W., 1952. The tropical rain forest. Cambridge University Press, Cambridge.

Rieley, J.O., Page, S.E., 2005. Wise use of tropical peatlands: focus on Southeast Asia. Alterra – Wageningen University and Research Center and the EU INCO-STRAPEAT and RESTORPEAT Partnerships.

Ruokolainen, K., Schulman, L., Tuomisto, H., 2001. On Amazonian peatlands. International Mire Conservation Group Newsletter 2001 (4), 8–10.

Schulman, L., Ruokolainen, K., Tuomisto, H., 1999. Parameters for global ecosystem models. Nature 399, 535–536.

Shier, C.W., 1985. Tropical peat resources — an overview. Tropical Peat Resources – Prospects and Potential, Proceedings of Symposium held in Kingston, Jamaica 1985. International Peat Society, Helsinki, Finland, pp. 29–46.

Stotz, D.F., Fitzpatrick, J.W., Parker, T.A.III, Moskovits, D.K., 1996. Neotropical Birds: Ecology and Conservation. The University of Chicago Press, Chicago, U.S.A.

Suszczynski, E.F., 1984. The peat resources of Brazil. Proceedings of the 7th International Peat Congress, Dublin, Ireland, volume 1. International Peat Society, Jyväskylä, Finland, pp. 468–492.

Troxler, T.G., 2007. Patterns of phosphorus, nitrogen and delta N-15 along a peat development gradient in a coastal mire, Panama. Journal of Tropical Ecology 23, 683–691.

Verhoeven, J.T.A., 1986. Nutrient dynamics in minerotrophic peat mires. Aquatic Botany 25, 117–137.

Waniek, E., Szatylowicz, J., Brandyk, T., 2000. Determination of soil–water contact angles in peat- moorsh soils by capillary rise experiments. Suo 51 (3), 149–154.

Weiss, D., Shotyk, W., Cheburkin, A.K., Gloor, M., Reese, S., 1997. Atmospheric lead deposition from 12,400 to Ca. 2000 yrs BP in a peat bog profile, Jura mountains, Switzerland. Water, Air and Soil Pollution 100 (3–4), 311–324.

Weiss, D., Shotyk, W., Rieley, J., Page, S., Gloor, M., Reese, S., Martinez-Cortizas, A., 2002. The geochemistry of major and selected trace elements in a forested peat bog, Kalimantan, SE Asia, and its implications for past atmospheric dust deposition. Geochimica et Cosmochimica Acta 66 (13), 2307–2323.

Wheeler, B.D., Proctor, M.C.F., 2000. Ecological gradients, subdivisions and terminology of North-West European Mires. The Journal of Ecology 88 (2), 187–203.