CONTROLS OF CARBON TURNOVER IN LOWLAND TROPICAL PEATLANDS

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Abstract

Lowland tropical peatlands can act as sinks and sources of carbon, interchanging greenhouse gases (GHG) with the atmosphere. Despite the importance of lowland tropical peatlands in the past, present and future global carbon cycle, uncertainties exists about the controls regulating the processes of carbon turnover. Therefore, this study examined different controls of carbon turnover, including abiotic, biotic and anthropogenic. For this purpose, six peatlands with different dominant vegetation were selected in the north western region of the Republic of Panama (9° 4' 16.06" N; 82° 6' 28.98" W). Two phasic communities were used as experimental models; *Raphia taedigera* palm swamps and mixed forest swamps with *Campnosperma panamensis*. A combination of *in situ* and *ex situ* experiments were performed between March 2010 and November 2012: i) *ex situ* respirometric assays were used to quantify differences in carbon turnover through the peat profile under different redox regimes, ii) litter bags experiments were used to investigate the effect of plant materials with distinct botanical origins on peat accumulation, iii) the effect of vegetation on greenhouse gases emissions was assessed with *in situ* and *ex situ* experiments and iv) land use change (LUC) was monitored to evaluate its consequences on the short term carbon turnover processes. *Ex situ* respirometric assays suggested that organic matter composition of peat plays a major role in controlling the potential CO_2 and CH_4 production. Under anaerobic conditions, the potential CO_2 and CH_4 production decreased with depth. The potential CO_2 and CH_4 productions in the surface peat layers of the anaerobic assays were 7 and 120 fold higher than those in deeper layers of the peat profile respectively. The change in redox regime affected the carbon turnover; the CO_2 potential production in the surface layers (< 50 cm depth) increased 20 fold when exposed to aerobic conditions, whilst the deeper layers (> 50 cm depth) increased 47 fold. In contrast, CH_4 production was reduced two orders of magnitude under aerobic conditions. Tissue types of *R. taedigera* and *C. panamensis* showed different *in situ* decomposition rates. Decomposition was significantly slower belowground than at the surface, reflecting the importance of the redox regime on

the litter decomposition. Roots presented the lowest *in situ* decomposition rates among tissues both at the surface (*R. taedigera*: 0.59 ± 0.04 y^{-1}; *C. panamensis*: 0.45 ± 0.01 y^{-1}) and belowground (*R. taedigera*: 0.13 ± 0.01 y^{-1}; *C. panamensis*: 0.17 ± 0.005 y^{-1}). Macromolecular analyses revealed that roots and stems have similar composition to the peat material accumulated in deeper layers. Vegetation exerted a direct control on GHG fluxes from lowland tropical peatlands. In both *ex situ* and *in situ* measurements, fluxes of CO_2 and CH_4 varied with vegetation activity. In terms of CO_{2eq} (Addition of mass flow of GHG, converted with the global warming potential of each gas), the agricultural LUC increased CO_{2eq} emissions from the *R. taedigera* swamp at Cricamola by *ca.* 20 tCO_{2eq} ha^{-1} y^{-1}. At the pristine site, CO_2, CH_4 and N_2O contributed with *ca.* 90, 9 and 1 % of the Total CO_{2eq} respectively. In contrast, in the anthropogenically impacted plot, CO_2, CH_4 and N_2O contributed with *ca.* 29, 69 and 2 % of the Total CO_{2eq} respectively. Water table strongly influenced the carbon turnover. Under flooded conditions (water table at or above the surface; 0 to 0.15 m), the CH_4 emissions were *ca.* 4 times higher in comparison with those where the water table was below the surface (−0.01 to −0.4 m). In contrast, CO_2 emissions were *ca.* 1.5 times higher when the water table was below the surface. It was concluded that the interdependence of hydrology, peat composition and vegetation activity are the main factors controlling carbon turnover in the lowland peatlands of the north western region of Panama. This thesis has shown that fine scale alterations of these three factors can have large scale consequences, demonstrating sensitivity to perturbations and ease shift of lowland tropical peatlands from carbon sinks to carbon sources.

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Contents

Chapter 1

Introduction

According to the Intergovernmental Panel on Climate Change (IPCC), "Warming of the climate system is unequivocal" and it is likely to be, at least in part, induced by anthropogenic activities (Pachauri *et al.* 2008). The main anthropogenic contributions to the global warming of the climatic system are the emission of greenhouse gases (GHG) to the atmosphere (Solomon *et al.* 2007). Carbon dioxide (CO_2) was early recognized as an important greenhouse gas (Arrhenius 1896; Tyndall 1861; Callendar 1938). However, besides CO_2 emissions which are related to fossil fuel burning, it was later proven that other trace gases in the atmosphere are actively involved in the greenhouse effect; methane (CH_4) and nitrous oxide (N_2O) being the most relevant for their radiative properties and volume of emissions (Wang *et al.* 1976; Migeotte 1948). It has been suggested that GHG emissions may have amplified the climatic consequences of the eccentricity orbital forcing phenomena, which is closely related to the glacial-interglacial climate change cycles (occurring each $\approx 100,000$ years) (Petit *et al.* 1999). Thus, the climatic warming phenomena forms part of a normal long-term climatic cycle involving the glacial-interglacial periods (Petit *et al.* 1999; Jouzel *et al.* 2007). However, the 420, 000 years atmospheric CO_2 record from the Vostok ice core indicated that the Earth´s climatic system has functioned within a constrained atmospheric CO_2 concentration range. The atmospheric CO_2 concentration range fluctuated periodically, increasing and decreasing from 180 to 280-300 ppmv at each interglacial period (Falkowski 2000; Barnola *et al.* 1987). Presently, atmospheric CO_2 concentrations have reached 397 ppmv (Tans *et al.* 2013); this CO_2 concentration is *ca.* 100 ppmv above the upper limit of the previously mentioned range and the increment occurred after the start of the industrial revolution (*ca.* 200 years ago) (Crowley 2000; Ward 1994; Crafts 1977).

The changes in the concentration of atmospheric constituents are not solely dependent on human activity, but also on biogeochemical and climatic processes and the way these factors interact with the global carbon cycle (Falkowski 2000). Peatlands have been suggested to actively participate in regulating atmospheric constituents in the long term by being among the dominant controlling factors of the global carbon cycle (Yu *et al.* 2013; Klinger *et al.* 1996). Carbon on Earth is ubiquitously distributed in several chemical species. The most important carbon reservoir on Earth is located in the lithosphere as sedimentary carbonates and kerogens ($\approx$ 75,000,000 Gt; 1 Gt = 1×10^{15} g) (Berner *et al.* 1983; Berner 1989). The rest of the carbon on Earth represents *ca.* 0.07 % of the total carbon and is distributed among: i) aquatic biosphere (*ca.* 1.5 Gt) (Holland 1978), ii) atmosphere (*ca.* 720 Gt) (Trabalka 1985), iii) terrestrial biosphere (*ca.* 2000 Gt) (Trabalka 1985), iv) fossil fuels ($\approx$ 4130 Gt) (Falkowski 2000) and v) oceans (38,400 to 42,000 Gt) (Berner 1989). Carbon does not remain static, it reallocates through time and moves among the atmosphere, terrestrial and aquatic ecosystems within the global carbon cycle (Kasting *et al.* 1988). Due to the role of the global carbon cycle influencing the atmospheric GHG concentration, the study of the global carbon cycle has gained importance during the last decades.

1.1 Peatlands

Peatlands are one of the most dynamic ecosystems on Earth exchanging carbon across the carbon cycle. In these wetlands, waterlogging conditions are almost permanent and the water table remains close to the peat surface (Schumann *et al.* 2007). Under waterlogged conditions, plant litter gradually losses its physical structure by losing organic matter as gas, solution or by removal by small invertebrates (Clymo 1984). The process of organic matter decomposition occurs mainly anaerobically, because the flux of oxygen from the air to the soil is lower than the rate at which it is consumed by the microorganisms (Clymo 1984). Consequently, autochthonous plant material does not fully decay and so is progressively accumulated as peat (Rieley *et al.* 2005). A peatland can be defined as an ecosystem which is covered with a naturally accumulated layer of peat (Joosten 2008; Jauhiainen *et al.* 2005). Peat has been defined differently regarding its organic matter content, depending of the author it should consist of at least 30 (Joosten *et al.* 2002), 45 (Wüst *et al.* 2003), 50 (Andriesse 1988) or 65 % (Rieley *et al.* 2005) of organic matter (dry weight). In addition, the depth of the deposit has to have a minimum thickness of 0.3 (Joosten *et al.* 2002), 0.5 (Rieley *et al.* 2005)

or 0.8 m (Andriesse 1988). The lack of consensus in the definition of peat has complicated the unification in the estimations of the extent and carbon content of global peatlands (Page *et al.* 2011). Throughout this study, peat is defined as an organic soil consisting of > 30 % of organic matter (dry weight) and a minimum thickness of 0.3 m.

1.1.1 Peatlands extent

The formation of peat is strongly influenced by climatic conditions and topography (Joosten *et al.* 2002). Peatlands are located in regions with high precipitation and large flat areas (Joosten *et al.* 2002). Global peatland extent is equivalent to *ca.* 2.67 % of the Earth's land surface area (Central Intelligence Agency 2013; Rieley *et al.* 2008a); approximately 89 % of the peatlands occur in continental boreal and temperate regions (Armentano *et al.* 1986), occupying an area of 314 to 385 Mha (Armentano *et al.* 1986; Gorham 1991; Immirzi *et al.* 1992; Page *et al.* 2011; Bord na Móna 1984). At least 10 % of the global peatland area occurs in the tropics, located in South East Asia (SEA), Africa, the Caribbean and Central and South America; occupying near to 44 Mha (Joosten *et al.* 2002; Immirzi *et al.* 1992; Page *et al.* 2011). However this estimate is dynamic, as degradation of tropical peatlands and forests is occurring rapidly throughout the tropics, particularly in SEA and the Neotropics (Miettinen et al. 2011; Miettinen *et al.* 2013; Langner *et al.* 2007; van der Werf *et al.* 2010; Gutiérrez-Vélez *et al.* 2013). Though smaller in area than boreal and temperate peatlands, it has been recognized that tropical peatlands are important for their carbon storage and emission capacity (Page *et al.* 2011). To date, most of the research in peatlands has been carried out in boreal and temperate ecosystems, followed by a recent increase in research at SEA tropical peatlands; however, Neotropical peatlands in Central and South America remain understudied limiting our possibilities to fully understand the role of tropical peatlands in the global carbon cycle (Lähteenoja *et al.* 2009; Clark 2004; Clark *et al.* 2001).

1.1.2 Lowland tropical peatlands

The processes underlying the formation and accumulation of peat in the tropics are very similar to those in boreal and temperate regions (Andriesse 1988). The most relevant features differentiating lowland tropical peatlands from boreal-temperate ones is climate. Lowland tropical peatlands are subjected to high precipitation rates (1500 – 3000 mm y^{-1}), high evapotranspiration and high mean annual tem-

peratures (22 – 35 °C) (Andriesse 1988; Zinck 2011; Wüst *et al.* 2007; Whitmore 1998). As a result, the extent and location of tropical peatlands is inherently linked to the definition of tropical-region climate (Page *et al.* 2007). The most obvious approach is to define tropics as the area between the Tropics of Cancer and Capricorn. However, in order to include most peatlands based on the climatic conditions mentioned above, some authors have expanded the inter-tropical zone from 35 °N to 35 °S as to include some peatlands in subtropical regions (Andriesse 1988); this is the definition that will be applied throughout this thesis.

1.1.3 Role of lowland tropical peatlands in the carbon cycle

Tropical peatlands have been accumulating carbon for longer than boreal-temperate ones (Yu *et al.* 2010). Boreal-temperate peatlands formation started in the late-Pleistocene *ca.* 16.5 thousand years ago (ka) and rapidly expanded in the early Holocene *ca.* 11.5 to 9 ka (Macdonald *et al.* 2006), during the termination of the last ice age (Schaefer *et al.* 2006). In contrast, tropical peatlands formation started around 38 to 20 ka in the Pleistocene (Anshari *et al.* 2004; Anshari *et al.* 2001; Page *et al.* 2004), followed by a rapid expansion of coastal peat deposits during mid to late-Holocene from 8 to 4 ka as sea level stabilized (Yu *et al.* 2010; Dommain *et al.* 2011). Globally, peatlands hold *ca.* 610 Gt of carbon below-ground (Page *et al.* 2011); this is equivalent to 84 % of the total carbon in the atmosphere (Falkowski 2000).

Through analysis of ice core records, it has been suggested that tropical wetlands (peatlands among them) contributed to alter the composition of the late-Pleistocene and Holocene atmosphere by releasing large amounts of CH_4 and by sequestering CO_2 (Schaefer *et al.* 2006). This variation in the atmospheric composition was a response to the severe climatic changes (precipitation and temperature) during the interglacial and interstadial transitions (Macdonald *et al.* 2006; Johnsen *et al.* 1992); suggesting a rapid response of wetlands to climatic changes. At millennial time scales, lowland tropical peatlands are spatially the most effective terrestrial ecosystem in sequestrating carbon from the atmosphere (Dommain *et al.* 2011).

It is estimated that tropical peatlands currently hold around 50 to 92 Gt of carbon globally (Page *et al.* 2011; Yu *et al.* 2010); representing up to 20 % of the global peat carbon pool (Page *et al.* 2011). These estimations have to be considered with caveats, as the lack of reliable information (depth, extent and

mean carbon concentration of peat) results in substantial uncertainty. Thus, it is generally recognized that there is a need for greater quantity and quality of data regarding tropical peatlands such as extent, depth, bulk density, carbon content and hydraulic conductivity; that can be compared to improve the current estimate of the tropical peatlands carbon pool (Page *et al.* 2007). Furthermore, estimates have to be dynamic as tropical peatlands have been subjected to increasingly fast degradation over the past three decades (Murdiyarso *et al.* 2006; Page *et al.* 2009). Deforestation in tropical wetland forests is the highest among any other type of forest (Warren *et al.* 2012); when deforestation occurs in tropical peatlands, it accelerates peat subsidence, significantly reducing the carbon stock (Hooijer *et al.* 2012; Hirano *et al.* 2007).

Peatlands that are currently accumulating peat are denominated mires (Joosten *et al.* 2002). The estimation of the potential global carbon accumulation by peatlands in the present ranges from 0.1 to 0.3 GtC y^{-1} (Armentano *et al.* 1986; Rieley *et al.* 2008b; Rieley *et al.* 2005). In the tropics, the potential current carbon accumulation is estimated to range from 0.06 to 0.093 GtC y^{-1} (Rieley & Page, 2005; citing Franzén, 1994; Immirzi *et al.*, 1992; Maltby & Immirzi, 1993). These estimates consider the potential capacity of peatlands that have not been disturbed by anthropogenic activities. Therefore, these values are currently being reduced as peatland degradation occurs and as peat accumulation is no longer possible due either to natural or to anthropogenic causes (Rieley *et al.* 2008b).

The above mentioned carbon accumulation rates are low considering the capacity of peatlands to emit carbon to the atmosphere. Currently, wetlands (peatlands among them) are estimated to be the most important natural source of CH_4 to the atmosphere (Solomon *et al.* 2007), emitting 0.1-0.23 Gt of CH_4 y^{-1} equivalent to 17 to 40 % of the total global CH_4 emissions (Laanbroek 2010; Solomon *et al.* 2007). Additionally, soil respiration in terrestrial ecosystems is estimated to emit *ca.* 68 GtC y^{-1} (Raich *et al.* 1992), which is high in comparison with the *ca.* 9.2 GtC estimated for the 2010 global fossil-fuel carbon emissions (Boden *et al.* 2013).

In summary, the role of tropical peatlands in the global carbon cycle is unclear. Although it is certain that over millennial scales tropical peatlands have accumulated carbon; it is not certain what role they will play under the increasingly dynamic scenario of climate change and anthropogenic degradation (Yu *et al.* 2011; Blodau 2002; Limpens *et al.* 2008; Belyea *et al.* 2004).

1.2 Factors controlling peat accumulation

Ultimately, the processes involved in peat formation (carbon accumulation) and degradation (carbon emissions) are strongly influenced by microbial activity. Thus, microbial activity in soils, such as peat, has played a major role in shaping the atmosphere's composition in the past and will do so in the future (Conrad 1996). In lowland tropical peatlands, microbial activity is regulated by abiotic, biotic and anthropogenic factors. The redox potential, water table, temperature, pH and nutrients availability are among the most important abiotic factors controlling microbial activity; whilst, vegetation is one of the main biotic factors. In addition, factors such as land use change and climate change can be classified as anthropogenic. All of these factors are closely interrelated; in the following section, each of them is addressed regarding their role in the carbon cycle of lowland tropical peatlands.

1.2.1 Abiotic factors

1.2.1.1 Redox regime

Most lowland tropical peatlands in SEA are raised bogs. In these ecosystems peat, water and vegetation interact to maintain a stable self-regulating system; these three components are closely connected and are mutually interdependent (Joosten *et al.* 2007). As the peat dome rises, two major layers with distinct structural and functional characteristics are defined in the peat profile (Brady 1997). The two layers have been recurrently referred to as the active layer (surface) and the inactive layer (subsurface). These concepts were developed by Ivanov (1981) and further renamed by Ingram (1978) as acrotelm and catotelm. In this model, the boundary between these two layers was located at the mean depth of the minimum water table in summer (Ivanov 1981). The definition of such diplotelmic system was developed for temperate peatlands, where peat is primarily formed by non-vascular plants, the concept can be modified to be applied to lowland tropical peatlands. In lowland tropical peatlands, the acrotelm extends above the peat surface, up to the highest annual water table and includes the area of chemical, biological, and physical influence generated by root growth and activity (rhizosphere) (Pinton *et al.* 2007). The lower limit of the acrotelm where the catotelm begins is situated as deep as the living rhizosphere reaches within the deep peat layers (Joosten *et al.* 2007). The living root systems functions as the interface between the peat forming vegetation and the peat deposit (Rieley 2007). Vascu-

lar plants in tropical peatlands have developed structural adaptations to aerate their roots which are under permanent waterlogging conditions (Armstrong 1979; Armstrong *et al.* 1991; Armstrong 1967). Thus, the microbial community in the waterlogged peat layer is influenced by the rhizosphere and is exposed to aerobic or microaerophilic conditions (relatively high redox potential), where aerobic and facultative anaerobic microorganisms can coexist. In contrast, the microbial community living beneath the rhizosphere-influenced peat layer is exposed to anaerobic conditions (low redox potential), where only facultative and strict anaerobes can live. Through this process, vegetation contributes to define microbial stratigraphic profiles, under which microbial activity and peat decomposition are significantly different. Microbial organic matter decomposition under anaerobic conditions is about a thousand times slower when compared to decomposition under aerobic conditions (Ingram 1978; Belyea *et al.* 2001).

It is necessary to develop a new conceptual framework that fully considers the structural and functional differences between lowland tropical and temperate-boreal peatlands. In addition, research is needed to explore the role of the vegetation in influencing organic matter decomposition processes in lowland tropical peatlands.

1.2.1.2 Water table

The water table contributes to the development of a diplotelmic system, under which the decomposition of plant material occurs at different rates. Thus water input is fundamental for peat formation and its subsequent stable accumulation; in lowland tropical peatlands this water input is mainly derived from precipitation (Andriesse 1988). It has been proposed that a peat dome, as those in SEA and Panama (Staub *et al.* 1994; Cohen *et al.* 1989), is composed of peat and active plant tissues, the absence of peat and water (Couwenberg *et al.* 1999). The absence of peat can be conceptualized as those pores or spaces where water is stored; allowing water saturation and high water tables. All peat and plant material represents an obstruction to water flow; in contrast, water freely flows through the empty pores. Thus, the relative proportion of empty pores in the peat is an indirect measurement of hydraulic conductivity. The amount of empty pores in the peat is a direct reflection of the degree of plant material decomposition. The more advanced the decomposition, the smaller the pores are and the less water holding capacity the peat has. However, in a peatland currently accumulating peat, the freshly produced plant material that is not heavily decomposed in

combination with buttress roots and hollows-hummocks patterns increases water storages at the peatland surface (Couwenberg 2005). Consequently, a downward hydraulic conductivity profile is defined; having high hydraulic conductivity in the rhizosphere and low hydraulic conductivity in the deeper peat layers (Couwenberg et al. 1999). The main lateral water flow occurs at the surface impeding large water level fluctuations (Clymo 1991). A constant water input is required for the whole system to be stable. In absolute terms, precipitation must exceed evaporation throughout the year (Clymo 1991). The system can resist moderate water fluctuations, but it can irreversibly collapse if either the water input or the plant material input stops, leading to subsidence (Wösten *et al.* 1997). In the above model, microbial activity is responsible for decomposing plant material and thus defining the pore sizes through the peat profile. The rate at which microbial decomposition occurs is directly affected and affects the water table.

1.2.1.3 Temperature

Temperature has a range of effects on peat formation. Plants photosynthetic capacity and respiration is affected by temperature (Yamori *et al.* 2013; Berry *et al.* 1980; Lewis *et al.* 2009). Some studies suggest that aboveground net primary productivity (ANPP) is increased by temperature in tropical forests (Raich *et al.* 1997; Cheesman *et al.* 2013a; Cheesman *et al.* 2013b). In contrast, other studies suggest that as leaf temperature rises, evaporative demands increase causing stomata closure (to reduce water loss), increasing leaf temperature and thus decreasing photosynthetic rates (Doughty *et al.* 2008). It has also been suggested that temperature will indeed decrease photosynthetic rates but the effect will be temporarily offset by the concomitant increase in atmospheric carbon dioxide (CO_2 fertilization) (Lloyd *et al.* 2008; Huntingford *et al.* 2013) and vegetation will eventually adapt to the increment in temperature (Berry *et al.* 1980). The effect of CO_2 fertilization could have short-term effect as NPP is limited by soil nutrients availability (*e.g.* nitrogen and phosphorus) (Norby *et al.* 2010; Mercado *et al.* 2011); this could be more noticeable in nutrient limited ecosystems such as lowland tropical peatlands. In addition, it has been observed that CO_2 fertilization modifies carbon allocation, increasing fine roots production and roots exudates (Cernusak *et al.* 2013), thus altering the nature of the peat input. In summary, an increase in the NPP may result in an increase of the substrate to form peat; whilst a decrease in the NPP would reduce the supply of fresh substrate for peat formation. Hence, understanding of the effect of temperature on NPP in tropical wetlands is needed in order to quantify the role of vegetation in tropical peatlands

for carbon sequestration.

Litter decomposition and microbial activity are also affected by temperature (Swift *et al.* 1979; Anderson *et al.* 1983; Singh *et al.* 1977). Litter decay rates are faster in the tropics than in boreal-temperate peatlands (Jenny *et al.* 1949) and increase with temperature (Vitousek *et al.* 1994; Jenny *et al.* 1949; Daubenmire *et al.* 1963; Shanks *et al.* 1961; Mork 1939). For instance, variations of 4 – 5 °C have been observed to significantly increase the soil respiration in tropical peatlands; with soil respiration increasing 3 to 12 fold for each 10 °C temperature increment (Hirano *et al.* 2008). However, an inverse correlation has been observed between decomposition rates and temperature in temperate forests as decomposers are better adapted to low temperatures in these environments (Daubenmire *et al.* 1963). Thus the overall effect of temperature over litter decomposition is dictated by the effect temperature has on the microbial community that is best adapted to decompose certain plant material.

1.2.1.4 pH

Lowland tropical peatlands usually have slightly acidic conditions (pH < 5). The acidic pH results from the release of hydrogen ions and organic acids during plant material decomposition (Waksman 1938). These acidic conditions inhibit microbial activity and select acidophilic consortiums of decomposers. Additionally, pH directly influences the adsorption-desorption and precipitation-dissolution of nutrients such as phosphorus and its interactions with metals (Turner *et al.* 2013a; Brümmer *et al.* 1983; Jenne 1968). Thus, pH influences plants nutrients uptake and NPP, affecting the amount of plant material input to form peat.

1.2.1.5 Nutrient availability

In lowland tropical peat domes, nutrient availability (*e.g.* nitrogen and phosphorus) play a major role in shaping the distribution of phasic communities (Sjögersten *et al.* 2011; Cheesman *et al.* 2012; Troxler 2007; Anderson 1961; Staub *et al.* 1994; Esterle *et al.* 1994). In these ecosystems, the margins of the domes are rich in nutrients whilst the centre of the peat dome, which is topographically higher, is nutrients poor (Wright 2011; Esterle *et al.* 1994; Troxler 2007). The dome margins can support high vegetation biomass constituted by large arborescent species (hardwood and palm) with buttressed roots and dense root mats (Wright *et al.* 2013b). In contrast, the highest dome region has a low tree density and is mainly

covered with sedges (Phillips *et al.* 1997). Consequently, nutrients influence the type, quality and chemistry of peat-forming plant material (Dent *et al.* 2006), the microbial communities (Troxler *et al.* 2012) and the microbial decomposers activity (Kaspari *et al.* 2008; Hobbie *et al.* 2000; Magill *et al.* 1998; Li *et al.* 2011).

1.2.2 Biotic factors

1.2.2.1 Peat forming vegetation

The role of the vegetation in influencing peat formation lies at the heart of the origin of lowland tropical peatlands. The most extensive lowland tropical peatlands in SEA were formed through the evolution of wetlands systems across thousands of years following the stabilization of the sea level *ca.* 5.4 ka (Staub *et al.* 1994). During this time, plant successional changes developed a complex stratigraphic peat profile (Wüst *et al.* 2004; Anderson 1961; Anderson 1964). Based on the analysis of fossil pollen (Anderson *et al.* 1975; Wüst *et al.* 2004) and plant macrofossils in peat profiles (Staub *et al.* 1994; Phillips *et al.* 1997), it has been proposed that lowland tropical peatlands developed on marine clay and mangrove deposits of river deltas and coastal plains (Dommain *et al.* 2011). This is consistent in both lowland tropical peatlands of SEA (Anderson 1961) and the Neotropics (Phillips *et al.* 1997); where mangroves were initial colonizers that were eventually replaced by fresh-swamp forests species (Wüst *et al.* 2007; Anderson 1961). Mangrove litter in combination with sand and clay form a relatively impermeable layer that isolates peat from the mineral subsoil (Dommain *et al.* 2010), contributing to the maintenance of water saturation in the system. Furthermore, differences in the resistance to decomposition of the distinct plant materials throughout the peat layers affect the microbial activity belowground. It has been even proposed that differences in the composition of plant litter between the peat-forming plants of SEA and those in the Neotropics may be the reason why large peat domes are rare in the Neotropics (Dommain *et al.* 2010). However, the limited amount of comparative data regarding litter composition from SEA and the Neotropics does not make it possible to test such hypothesis yet.

1.2.2.2 Peat forming material

One of the main differences between boreal-temperate and lowland tropical peatlands is the plant material that forms the peat. After the initial mangroves colonization, the freshwater forest that replaces it develops large trees and dense

understory (Staub *et al.* 1994). The peat produced by these trees is mainly made of wood, bark and roots (Anderson 1961; Esterle *et al.* 1994). The roots and wood of vascular plants contain highly recalcitrant compounds in their cell walls (Zeikus 1981; Chimner *et al.* 2005). For instance, lignin is highly recalcitrant under anoxic conditions as those present in water-saturated peat layers. The substantial reduction in lignin degradability is due to the fact that ligninolytic microorganisms require oxygen to efficiently depolymerize and solubilize lignin (Zeikus 1981). This way, the peat-forming vegetation exerts a selective control on peat composition by restricting microbial activity. Despite the fact that roots only represent *ca.* 10 % of the plants productivity, several studies have suggested that roots are the main component of peat in tropical peatlands (Chimner *et al.* 2005; Silver *et al.* 2001; Hedges *et al.* 1985; Esterle *et al.* 1994). Furthermore, it is still uncertain if tropical peatlands accumulate carbon due to the low decomposition of the plant material or to the high NPP inherent to these ecosystems (Chimner *et al.* 2005). Further research regarding the role of belowground biomass in peat formation is necessary, as roots and wood seem to be the main stable carbon input to tropical peatlands.

1.2.3 Anthropogenic factors

1.2.3.1 Peat extraction and land use change

In the past, the study of peatlands around the world was linked to its potential use as fuel (Andriesse 1988). In fact, the peat definitions used today are based on the quality of peat to be used as fuel; for this reason, the ash (< 25 %) and sulfur content are critical in the definition (Wüst *et al.* 2003). In Europe, 90 % of the peatlands have been cleared, drained or degraded, the peat was used mainly as fuel; therefore they are no longer accumulating peat (Faizal *et al.* 2007; Joosten *et al.* 2002). In Panama, the first studies on the Changuinola Peat Deposit (CPD) were focused on the feasibility of using the peat as energy source (Cohen *et al.* 1989; Cohen *et al.* 1996). As peatlands importance in the global carbon cycle has been recognized (Jauhiainen *et al.* 2005), it is necessary to develop new definitions focused on peatlands and mire protection rather than in their economic exploitation as a fuel resource.

Due to the availability of water, nutrients and organic soils, lowland tropical peatlands are attractive for agriculture and forestry (Joosten *et al.* 2002). The main effects over peat accumulation due to land use change are related to the alter-

ation of the factors mentioned above, *e.g.* water table, redox regime, litter input (Jauhiainen *et al.* 2008; Jauhiainen *et al.* 2005). Common agricultural practices in the tropics require lowered water tables; for this purpose, peatlands are drained through drainage canals (Dommain *et al.* 2010). In addition, the clearance of vegetation with the use of controlled fires, *i.e.* slash and burn, is a common practice (Giardina *et al.* 2000; Kotto-Same *et al.* 1997). Deforestation and fire destroy the plants producing the fresh litter required for peat formation; additionally, the microenvironment below the canopy is removed and the soil temperature increases (Ludang *et al.* 2007). Without the fresh litter input, the hydraulic properties of peat are altered and the water holding capacity of the upper peat layer disappears (Couwenberg *et al.* 1999). The drainage lowers the water table and the peat is exposed to aerobic conditions. Under aerobic conditions, the microbial decomposition of peat is at least two orders of magnitude faster than under anaerobic conditions (Ingram 1978; Belyea *et al.* 2001).

The fast decomposition process of peat leads to peat subsidence and to the consequent loss of carbon stock (Hooijer *et al.* 2012). Peat subsidence is the continuing lowering of the peat surface as a result of compaction and compression, consolidation, biological oxidation and shrinkage (Rieley *et al.* 2005) and shows a linear dependency with water table (Couwenberg *et al.* 2009). The biological oxidation is the main cause of peat subsidence, contributing with up to 92 % of the subsidence in tropical peatlands (Hooijer *et al.* 2012). The subsidence rates are high during the first five years after drainage reaching up to 1.5 m (Wösten *et al.* 1997); afterwards, the subsidence rate has been estimated to be lower and constant (*ca.* 0.05 m y^{-1}; 5 m in 100 y) (Hooijer *et al.* 2012; Couwenberg *et al.* 2009). Additionally, the use of fertilizers influences microbial activity contributing to subsidence (Kyuma *et al.* 1992). It has been estimated that due to degradation of peatlands in SEA *ca.* 0.17 GtC are released every year to the atmosphere (Couwenberg *et al.* 2009). Although LUC is widespread in the Neotropics (Wassenaar *et al.* 2007), information about its consequences on peatland degradation are still scarce (Keller *et al.* 2005).

1.2.3.2 Climate change

The consequences of climate change on peat accumulation in the tropics are uncertain. The projected reduction of precipitation in most of the Caribbean due to climate change could gradually affect the water table in the peatlands of the region (Campbell *et al.* 2011; Wright *et al.* 2011). In addition, warming is predicted in

the Caribbean by the end of the century (Meehl *et al.* 2012; Solomon *et al.* 2007). This warming could affect NPP and increase evaporation (Lloyd *et al.* 2008). The reduction of precipitation, the increase in temperature and the alteration of NPP could trigger subsidence in the peatlands of the Caribbean. The increase in NPP due to the current increase of atmospheric CO_2 will have to be taken into account as a positive feedback to peat accumulation; however CO_2 fertilization may only be temporal as other nutrients become limiting (Cernusak *et al.* 2013; Norby *et al.* 2010). In addition, as photosynthesis is enhanced by CO_2 fertilization, the chemistry of the leaf tissue changes, increasing the amount of non-structural carbohydrates and decreasing its nitrogen content (Ceulemans *et al.* 1994; Poorter *et al.* 1997). These structural alterations affect plant material resistance to decomposition and consequently the carbon turnover in the system (Gleadow *et al.* 1998). The response of lowland Neotropical peatlands to droughts and increased temperatures are still uncertain, however shifts in the phasic communities distribution in the tropics have been attributed to heat stress and droughts (Allen *et al.* 2010). Further research related to the carbon cycle and its possible alterations due to climate change in the region is required as to improve our understanding of the role of Neotropical peatlands in the global carbon cycle.

1.3 GHG emissions

As part of the microbial decomposition process, the plant material gradually losses its physical structure by losing organic matter as gases or in solution (Clymo 1984). Depending of the redox regime under which the decomposition occurs, the gases that are released as byproduct of the microbial metabolism are different. Under aerobic conditions, the CO_2 represents the main gas produced by heterotrophic respiration. However, under anaerobic conditions both CO_2 and CH_4 are emitted, as methane is produced by strictly anaerobic microorganisms (Le Mer *et al.* 2001; Ferry 2010). The anaerobic pathway of plant material decomposition is carried out by a consortium rather than an axenic culture; the process occurs in three steps (Conrad 1999). First, fermenting bacteria excrete enzymes that hydrolyze large polymers (*e.g.* cellulose, proteins). The resulting monomers are catabolized to alcohols, fatty acids, amino acids and H_2. Second, syntrophic bacteria degrade the alcohols and fatty acids to acetate, H_2 and CO_2. Third, acetate, H_2 and CO_2 serve as substrates for methanogenic bacteria. Methanogenesis is affected by the presence of alternative electron acceptors, such as O_2, Fe^{3+}, NO_3^- and SO_4^{2-} (Roy *et al.* 1999). For this reason, variations in the redox regime due to water table

fluctuations, plant oxygen input or nutrient addition will alter methane production.

Globally, GHG emissions are affected by all the abiotic factors previously described. However, uncertainties arise regarding the role of vegetation in the production and emission of GHG. The influence of tropical vegetation on the peat decomposition or in the transport of its by-products remains poorly understood. For instance, it has been demonstrated that plants can mediate the gas transport from the peat to the atmosphere (Grosse *et al.* 1996; Thomas *et al.* 1996; Pangala *et al.* 2013b; Seiler *et al.* 1983; Gauci *et al.* 2010) and that plants input labile substrate that enhances methanogenesis (Silvola *et al.* 1996). For this reason, vegetation has been suggested as an important interface between the soil and atmospheric GHG (Dacey *et al.* 1979; Bartlett *et al.* 1988). However, the processes mentioned above can be antagonist, functioning both as positive or negative feedbacks to GHG emissions, *e.g.* methanogenesis inhibition by plant-mediated oxygen input to the rhizosphere (King *et al.* 1978; Armstrong *et al.* 1991; De Bont *et al.* 1978) and methanogenesis enhancement by root exudates (Chanton *et al.* 1995; Holzapfel-Pschorn *et al.* 1986; Kuzyakov *et al.* 2000). If we want to be able to predict GHG emissions from large areas of tropical peatlands based on either their type of vegetation or the dominant environmental variables, we need to improve our knowledge of the processes previously mentioned within an ecological framework.

1.4 Knowledge gaps and study objectives

Throughout this review, different gaps in our knowledge of lowland tropical peatlands and particularly on the controls of carbon turnover within these ecosystems have been identified. In the following section, the main gaps are outilined and the specific objectives of this thesis are presented.

- **Gap:** There is uncertainty about the role of peat chemistry in controlling GHG emissions through the peat profile.

1. **Obj:** Quantify how carbon turnover varies through the peat profile with respect to peat chemistry.

2. **Obj:** Assess how redox regime affects the decomposition of organic matter through the peat profile.

3. **Obj:** Assess the role of belowground biomass (roots) in peat formation.

4. **Obj:** Evaluate the effect of the addition of nutrients over the turnover of above and belowground biomass.

5. **Obj:** Explore the influence of plant-mediated oxygen input on GHG emissions.

- **Gap:** There is a lack of information regarding the consequences of land use change for carbon turnover in the Neotropics.

1. **Obj:** Assess the effect of slash and burn cultivation on the emission of greenhouse gases.

- **Gap:** There is a need for new approaches to predict greenhouse gases emissions from large areas of tropical peatlands.

1. **Obj:** Characterize the role of distinct phasic communities as controls of GHG emissions.

1.5 Main hypotheses

Three main hypotheses were formulated to address the objectives previously mentioned:

1. Peat chemistry controls GHG emissions through the peat profile.

2. Roots are the main peat forming tissue.

3. Vegetation exerts a direct influence on GHG emissions.

These hypotheses are addressed in the three following chapters using the following experiments:

Hypothesis 1 is addressed in **Chapter 3**:
"*Ex situ* potential CO_2 and CH_4 emissions from tropical peat soil profiles under aerobic and anaerobic conditions"
The experiments used to test hypothesis 1 were:

1. *Ex situ* respirometric assays under aerobic and anaerobic conditions throughout the peat profile in six peatlands.

2. Physicochemical characterization of peat cores; including macromolecular characterization using Pyrolysis – Gas Chromatography – Mass Spectrometry (Py-GC/MS).

Hypothesis 2 is addressed in **Chapter 4**:
"Roots are the main component of peat in lowland tropical peatlands"
The experiments used to test hypothesis 2 were:

1. Monitoring of *in situ* organic matter decomposition using litterbags to quantify the difference in decomposition rates across tissue type (leaf, stem and root) from two distinct arborescent species (*R. taedigera* palm and *C. panamensis* hardwood tree).

2. Molecular characterization of peat cores and *R. taedigera* and *C. panamensis* litter using Py-GC/MS.

3. Addition of nitrogen and phosphorus fertilizers in conjunction with litter decomposition studies and GHG (CO_2, CH_4 and N_2O) measurements.

4. A litterbags translocation experiment to evaluate site specific properties as decomposition controls.

Hypothesis 3 is addressed in **Chapter 5**:
"Role of vegetation as control of greenhouse gases emissions in lowland tropical peatlands"
The experiments used to test hypothesis 3 were:

1. Monitoring of *ex situ* diurnal CO_2/CH_4 emissions from *R. taedigera* seedlings growing on peat monoliths relative to controls without seedlings. b) Monitoring of *in situ* $CO_2/CH_4/N_2O$ emissions from the soil surface of an anthropogenically impacted *R. taedigera* palm swamp site compared to an undisturbed site. c) Monitoring of *in situ* CO_2/CH_4 emissions from the soil surface of peatlands with two distinct phasic communities (*R. taedigera* palms swamp and *C. panamensis* dominated mixed forest).

Chapter 2

Study area

Research on the peatlands of the north-western region of Panama can be traced back to the late 1980's and early 1990's, when the potential use of peat as an energy source was assessed (Thayer *et al.* 1995; Cohen *et al.* 1989; Cohen *et al.* 1995). The north-western region of Panama's Caribbean coast consists of two contiguous water bodies that are bounded by several islands (*i.e.* the Bocas del Toro Archipelago), peninsulas and mainland (D'Croz *et al.* 2005) (Fig. 2.1). These water bodies are the Bahía de Almirante and the Laguna de Chiriquí; their shores are heterogeneously covered with wetlands. The most studied peatland in the region is the Changuinola Peat Deposit (CPD), which is located in the San San Pond Sak wetland. Seven phasic communities are present in the CPD, which are described in more detail below (Phillips *et al.* 1997; Phillips 1995). Two of those phasic communities were chosen as study models for this thesis. *Raphia taedigera* palm and the *Campnosperma panamensis* hardwood tree form large mono-specific stands in swamps with contrasting characteristics across Central and South America (Urquhart 1999; Phillips *et al.* 1997; Myers 1981) and are consistently present throughout the peatlands in the studied region.

The study sites selected in here included two sites at the CPD, as well as sites in Chiriquí Grande, Cricamola River and the Damani-Guariviara wetland (Fig. 2.1); three are *R. taedigera* palm swamps and three mixed forests with *C. panamensis* (Table 2.1). All the sites were fresh water.

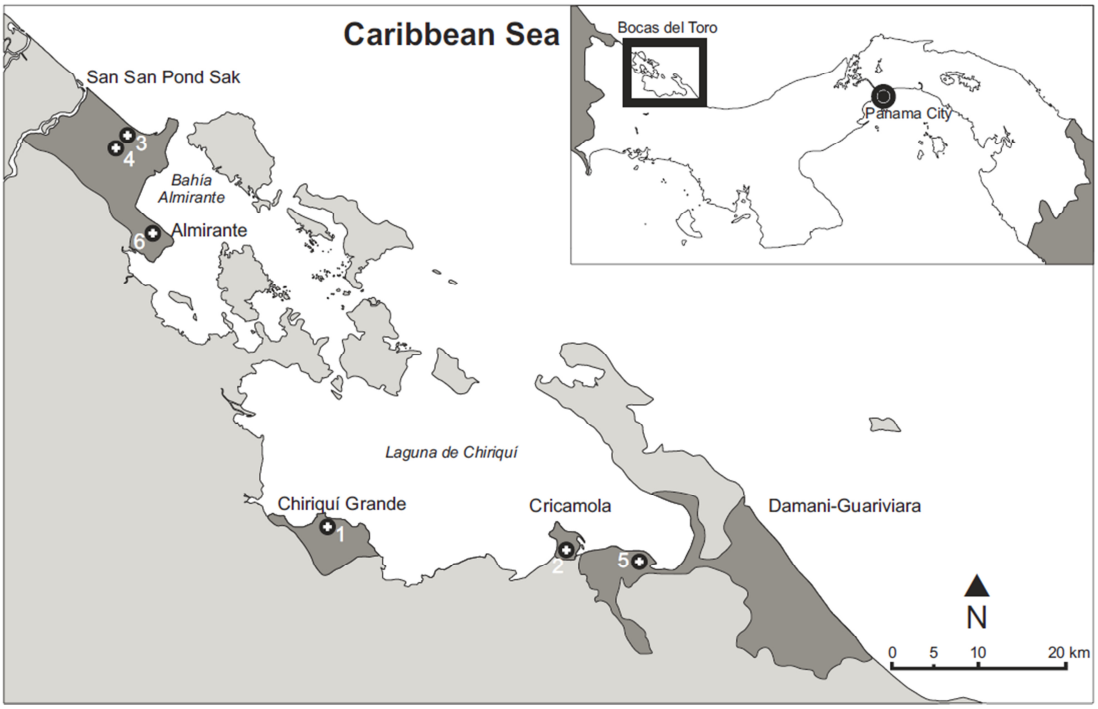

Fig. 2.1 Map of the north western region of the Caribbean coast of the Republic of Panama. Locations of the six study sites are shown and numbered according to Table 1; darker zones correspond to wetlands areas identified from aerial and satellite imagery.

Table 2.1: Location of study sites

Site		Coordinates	Distance to the coast (m)	Phasic community	Peat depth (cm)[c]
1	Chiriquí Grande	8°58'28.22"N, 82°07'52.85"W	140	Palm swamp	96 ± 7
2	Cricamola River	8°57'17.70"N, 81°54'41.35"W	1400	Palm swamp	316 ± 37
3	San San Pond Sak 1[a]	9°25'29.20"N, 82°24'05.60"W	500	Palm swamp	187 ± 5
4	San San Pond Sak 2[b]	9°25'15.00"N, 82°24'14.64"W	1000	Mixed forest	362 ± 19
5	Damani-Guariviara	8°57'02.34"N, 81°49'32.40"W	518	Mixed forest	483 ± 98
6	Bahia Almirante	9°18'17.46"N, 82°21'07.14"W	200	Mixed forest	165 ± 15

[a,b] San San Pond Sak sites 1 and 2 correspond to Sites 1 and 2 respectively from Sjögersten *et al*., 2010

[c] Peat definition: 30 % of dry weight organic matter(Joosten & Clarke, 2002). Depths correspond to the mean values recorded when peat cores were collected and do not reflect the overall depth in the sites (mean ± 1 SE, n = 3)

2.1 Bocas del Toro Climatic Conditions

The meteorological information available was obtained from the meteorological station installed at the Bocas del Toro Research Station (BDT) of the Smithsonian Tropical Research Institute (STRI). It is located *ca.* 18 km SE from the San San Pond Sak 1 site and *ca.* 12 km NE from the Bahia de Almirante site.

The Bocas del Toro Archipelago region is characterised by high precipitation averaging 3092 ± 181 mm y^{-1} (Fig. 2.2a) and a mean annual air temperature of 26.4 ± 0.1 °C (Fig. 2.2b), with no pronounced seasonality (Smithsonian Tropical Research Institute Physical Monitoring Program (2006 - 2011); Wright *et al.*, 2011).

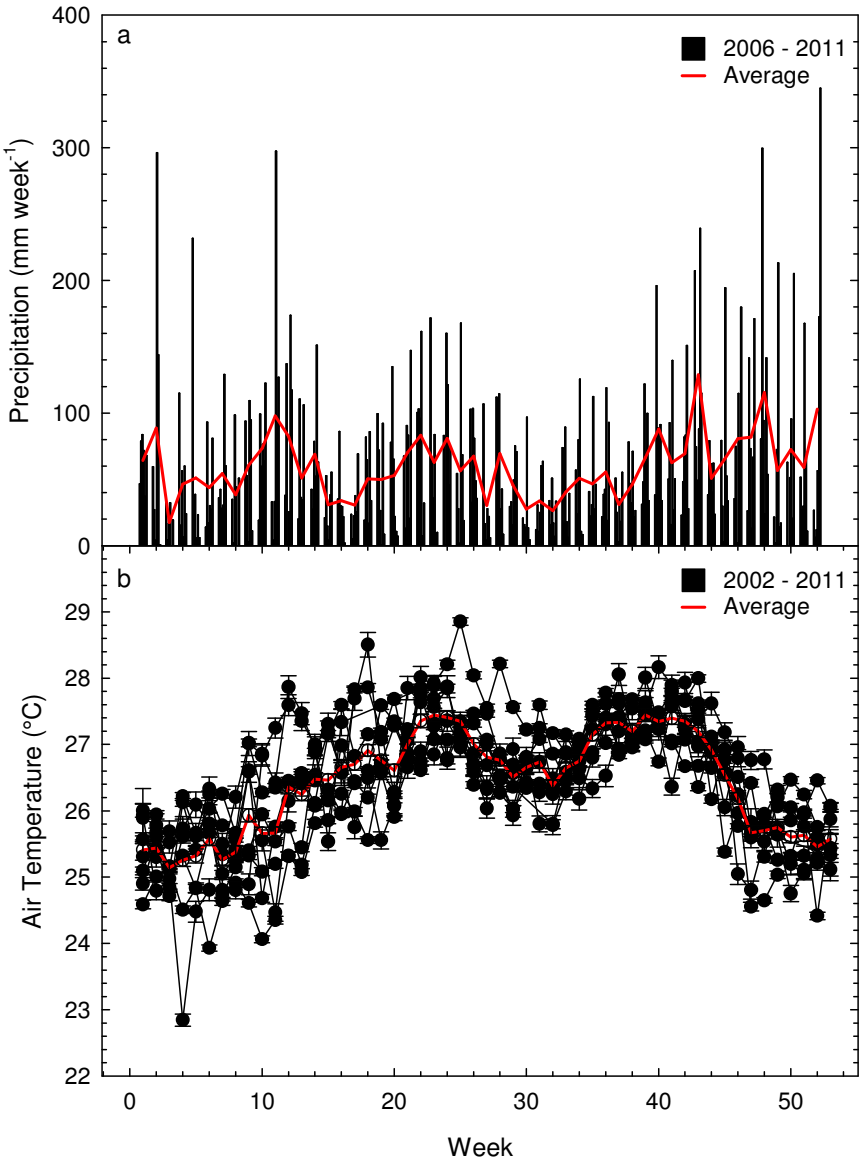

Fig. 2.2 (a) **Precipitation** (2006-2010) and (b) **Temperature** (2002-2011) at Isla Colon, Bocas del Toro. Information was obtained from the Smithsonian Tropical Research Institute Physical Monitoring Program (2006 - 2011) at the Bocas del Toro Research Station.

2.2 The Changuinola Peat Deposit

The San San Pond Sak wetland has a 164 km^2 extent; it was included in the Convention on Wetlands of International Importance (Ramsar Convention No. 611) in 1990. The CPD which can be found within the San San Pond Sak Wetland has an approximate extent of *ca.* 82 km^2 (Cohen *et al.* 1995). The peat deposit is rectangular in shape; its main axis runs 12.5 km from NW to SE parallel to the coast, from the alluvial plain of the Changuinola river towards the Bahia de Almirante. Its secondary axis goes from SW to NE, throughout the 8 km between the Talamanca hills and the coast (Phillips 1995). The maximum thickness of the peat deposit varies from 8.33 (Phillips 1995) to 9.45 m (Cohen *et al.* 1989) and the average peat thickness is estimated to be around 6.5 to 8 m (Phillips 1995; Cohen *et al.* 1995). The only 14C dating available (8.1 m depth = 3,040 ± 80 cal yr BP) reveals that the CPD started to accumulate peat *ca.* 4.5 ka. Thus it has been suggested that the peat accumulation in the CPD was triggered by a transgressive regime that lasted until 4.5 ka, when the sea level stabilized (Phillips 1995). This is consistent with the work developed in SEA (Anderson 1961; Dommain *et al.* 2011), suggesting that peat the large peat domes in SEA developed after the sea level stabilized in the mid-Holocene. The palynological records of both the CPD and the SEA suggest that the first phasic community colonizing the marine sand were mangroves (Anderson *et al.* 1975; Phillips *et al.* 1997). The CPD is analogous to the domed peatlands in SEA developing a concentric zonation of the phasic communities, also known as swamp catena (Anderson *et al.* 1975). The concentric zonation of the phasic communities from the edge to the centre is: i) *Rhizophora mangle* mangrove swamp; ii) mixed back-mangrove swamp; iii) *Raphia taedigera* palm swamp; iv) mixed forests swamp; v) *Campnosperma panamensis* forest swamp; vi) Sawgrass and vii) *Myrica-Cyriulla* bog-plain (Phillips *et al.* 1997). In this study, the *R. taedigera* palm swamp and the mixed forest swamp with *C. panamensis* were selected from a pre-existent transect (Sjögersten *et al.* 2011; Phillips *et al.* 1997; Troxler 2007); these sites correspond to sites 1 and 2 from Sjögersten *et al.* (2010).

2.2.1 San San Pond Sak 1 - *R. taedigera* palm swamp

The *R. taedigera* palm swamp located at the San San Pond Sak wetland was designated for the purposes of this thesis as San San Pond Sak 1 (SSPS1) (9° 25' 29.20" N, 82° 24' 05.60" W). It is located *ca.* 18 Km NW away from BDT (*ca.* 30 min boat trip) (Fig. 2.1). The access path is through the 30 m wide and 15 km

long canal built in 1903 by the Snyder Banana Co. (Fig. 2.3a) (Louis *et al.* 2004). The canal has been abandoned for commercial use and its entrance is partially blocked by a sand bank; for this reason it is recommended to use a shallow and relatively flat-bottom boat. The access to the site is located at the shores of the canal, approximately 5 km inside the canal (9° 25' 34.90" N, 82° 24' 1.80" W). A 30 minute walk is a good estimation to go across the more than 350 m from the shore of the canal to SSPS1 (Fig. 2.3b,c).

R. taedigera canopy at the site is dense, with leaves having a length $>$ 20 m; there is little to no understory vegetation (Myers 1981; Wright 2011). The surface at the site is covered by large amounts of leaf litter at the surface; its pneumatophores form a dense mat, which forms part of a dense but shallow (1.1 m) fibrous root system (Wright *et al.* 2013b). Shallow water ponds and raised areas (close to each *R. taedigera* stand-colony) are typical components of this sites microtopography. The water table at the site ranges from + 0.2 to – 0.2 m (Wright *et al.* 2013b). *R. taedigera* represents 98.9 % of the total basal area (m^2 ha^{-1}) of the arborescent species in the plot, being clearly dominant (Sjögersten *et al.* 2011).

Fig. 2.3 Entrance to **San San Pond Sak** sites through Changuinola canal (a). *R. taedigera* palm swamp; transect used by Sjogersten et al. (2011) (b,c).

2.2.2 San San Pond Sak 2 - Mixed forest swamp

The mixed forest swamp located at the San San Pond Sak wetland was named San San Pond Sak 2 (SSPS2) (9° 25' 15.00" N, 82° 24' 14.64" W). The site is a 60 to 90 minute walk from the canal shore (> 860 m). *C. panamensis* is the most abundant tree within the plot, accounting for 38.7 % of the total basal area (m^2 ha^{-1}) (Sjögersten *et al.* 2011). The surface of the plot is characterized by large amounts of leaf litter; in contrast with SSPS1, pneumatophores were no longer ubiquitous at the surface. *C. panamensis* develops buttress roots (1 m depth) with lenticels to aid oxygen transport to its roots (Fig. 2.4) (Wright *et al.* 2013b; Pangala *et al.* 2013b); similarly to SSPS1, the microtopography at the mixed forest sites was heterogeneous with an uneven surface characterized by shallow ponds and raised areas.

Fig. 2.4 San San Pond Sak 2 - mixed forests swamp. *C. panamensis* canopy (a) and buttress roots (b,c).

2.3 The Bahia Almirante - Mixed forest swamp

This site is located at the south-eastern region of the San San Pond Sak wetland (9° 18' 17.46" N, 82° 21' 07.14" W) (Fig. 2.1); approximately 12 km SW from BDT (30 minutes boat trip). The access is directly from the coast, which is covered with tall mangrove trees, *i.e. Rhizophora mangle*. Immediately adjacent to the mangrove margins a 30 m fringe of 25-30 m tall dead *C. panamensis* suggests a recent sea transgression (Fig. 2.5a,b). The *C. panamensis* trees showed the highest percentage of the total basal area *ca.* 45 % (m^2 ha^{-1}), followed by *Symphonia globulifera* accounting for 24 % of the total basal area (For further details see Chapter 5). This site showed the highest water table, reaching a maximum of 0.25 m above surface (Fig. 2.5c). The peat deposit in this area has a maximum depth of 2.1 m and an extent of *ca.* 31 km^2 (Cohen *et al.* 1989).

Fig. 2.5 Bahia Almirante - mixed forests swamp : Dead *C. panamensis* trees (a,b). Flooded conditions and *C. panamensis* raised hummock (c).

2.4 Chiriquí Grande - *R. taedigera* palm swamp

The site is located 46 km SE from BDT (8° 58' 28.19" N, 82° 7' 52.89" W) (1.2 h boat trip). The access is through a narrow beach (< 10 m). The ground was covered with undecayed *R. taedigera* leaf litter, seedlings and pneumatophores (Fig. 2.6a). The microtopography is typical of a *R. taedigera* palm swamp with shallow water ponds and raised areas; the water table fluctuated from – 0.2 to 0.08 m with respect to the surface (Fig. 2.6b,c). *R. taedigera* palms accounted for 84 % of the total basal area in the plot (m^2 ha^{-1}). The presence of peat has not yet been reported in this area and was confirmed by coring. The wetland area was estimated from the analysis of satellite imagery, with an extent of *ca.* 17 km^2.

Fig. 2.6 Chiriquí Grande – *R. taedigera* palm swamp. *R. taedigera* pneumatophres and seedlings (a). *R. tadigera* seedlings and water table at the surface (b). Water table *ca*. – 0.15 m (c).

2.5 Cricamola River - *R. taedigera* palm swamp

In 2004, this area was included within the Damani – Guariviara wetland as part of the Ramsar Convention Site no. 1907. The Cricamola River is located 66 km SE from BDT (2 h boat trip). This site presents the same characteristics as the *R. taedigera* swamps previously described, however pneumatophores density is greater (Fig. 2.7). This might be a stress response of *R. taedigera* to recurrent river flooding. The *R. taedigera* palms dominate the vegetation accounting for 71 % of the total basal area in the plot (m^2 ha^{-1}). Although the area is catalogued as a national protected area, the river has several human settlements. Consequently, the wetlands in the zone are subjected to anthropogenic impact, particularly to LUC for agriculture and rural housing (Fig. 2.8). Based on satellite imagery analysis, the extent of the wetland in the Cricamola river zone is 6.97 km^2. The presence of peat was confirmed by coring, this being the first time this area is recognized as a peatland.

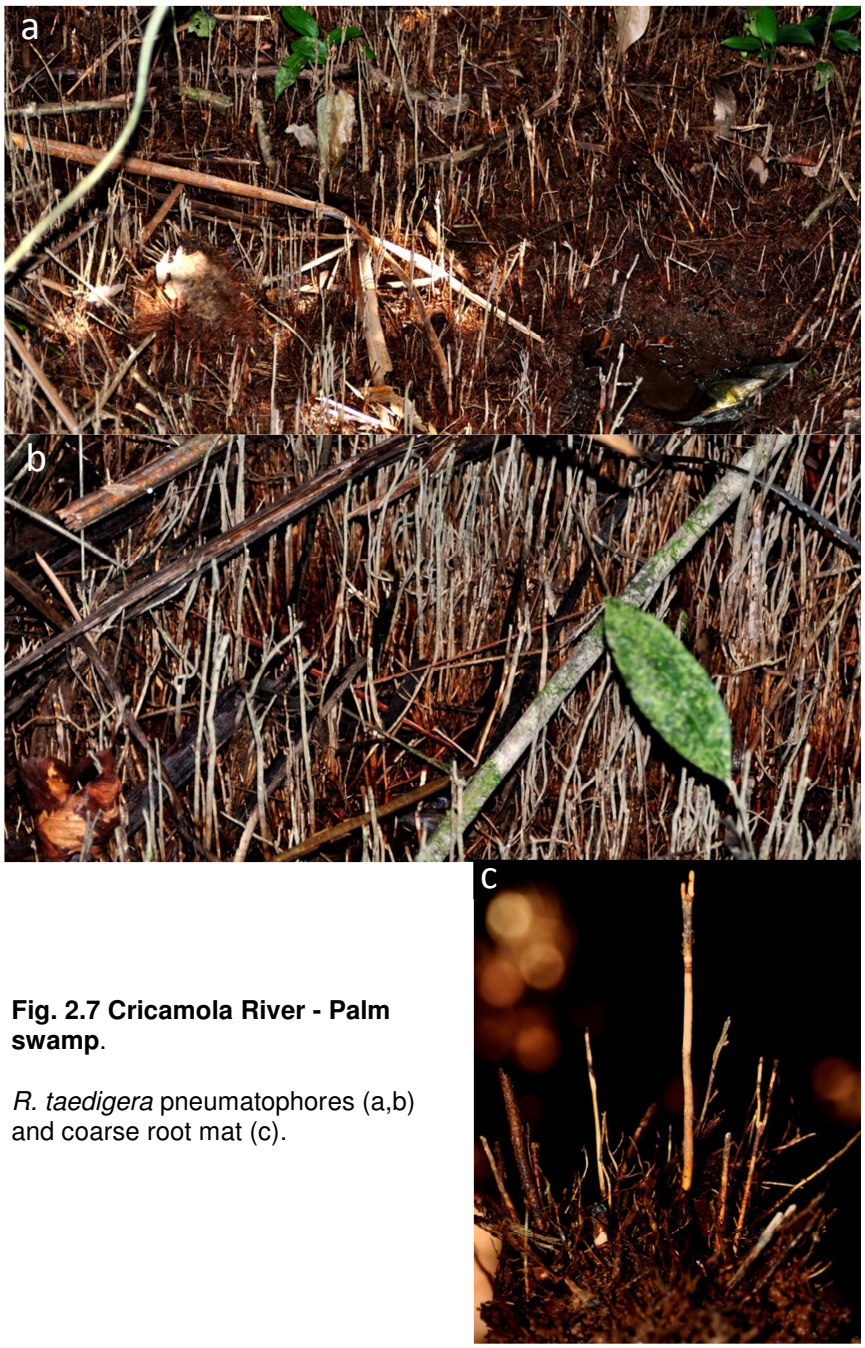

Fig. 2.7 Cricamola River - Palm swamp.

R. taedigera pneumatophores (a,b) and coarse root mat (c).

Fig. 2.8 Cricamola River-Palm swamp (a). Subsistence agriculture: Slash (b) and burn (c) agriculture practice to grow rice (d). The process occurred from April to September 2011.

2.6 Damani–Guariviara wetland - Mixed forest swamp

The Damani – Guariviara wetland is the largest wetland in the region (Ramasar site No. 1907), with an extent *ca.* 241 km^2. Extensive research has been carried out in the area regarding its biodiversity in flora and fauna (Meylan *et al.* 2013). Access to the site was achieved through a small creek surrounded by mangroves (*Rhizophora mangle* and *Pelliciera rhizophorae*) (Fig. 2.9a). The *C. panamensis* trees showed the highest percentage of the total basal area with *ca.* 45 % (m^2 ha^{-1}), accompanied by a dense understory (Fig. 2.9b). The area has not previously been explored for its potential importance as carbon pool. The presence of peat was confirmed by coring (Fig. 2.10). The mineral soils underlying the peat consisted of marine sediments with gastropod shells and fossil sponge spicules (Fig. 2.11a,b,c,d,e); the peat layer immediately above the marine sediments contained plant material such as mangrove and *R. taedigera* roots (Fig. 2.11f,g). The radio carbon dating of the plant material from the peat layers at a depth of 4.5 and 5.73 m were used to estimate the basal date of the peat deposit. The estimated dates ranged from 5330 ± 40 to 5920 ± 40 cal yr BP (Dr. Carlos Jaramillo, pers. comm. 2012); this is consistent with previous studies suggesting that lowland tropical peatlands rapidly expanded during the mid-Holocene (Phillips 1995; Anderson 1961; Dommain *et al.* 2011).

Fig. 2.9 Damani-Guariviara wetland. a) Mangroves in the entrance to the site; b) Understory.

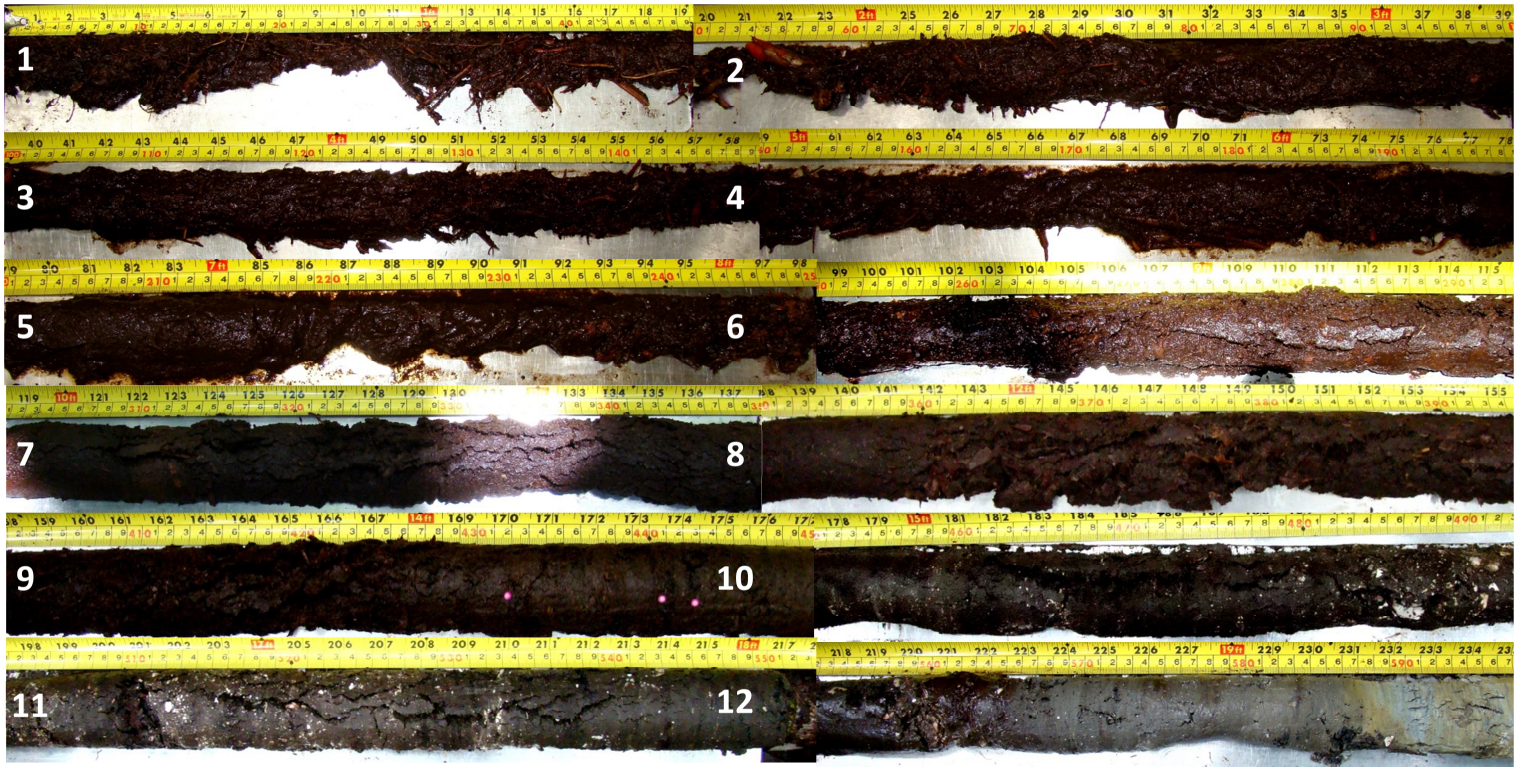

Fig. 2.10 Damani-Guariviara wetland. Peat core from the surface layers (1) and the mangrove swamp (11) to the mineral soil (12).

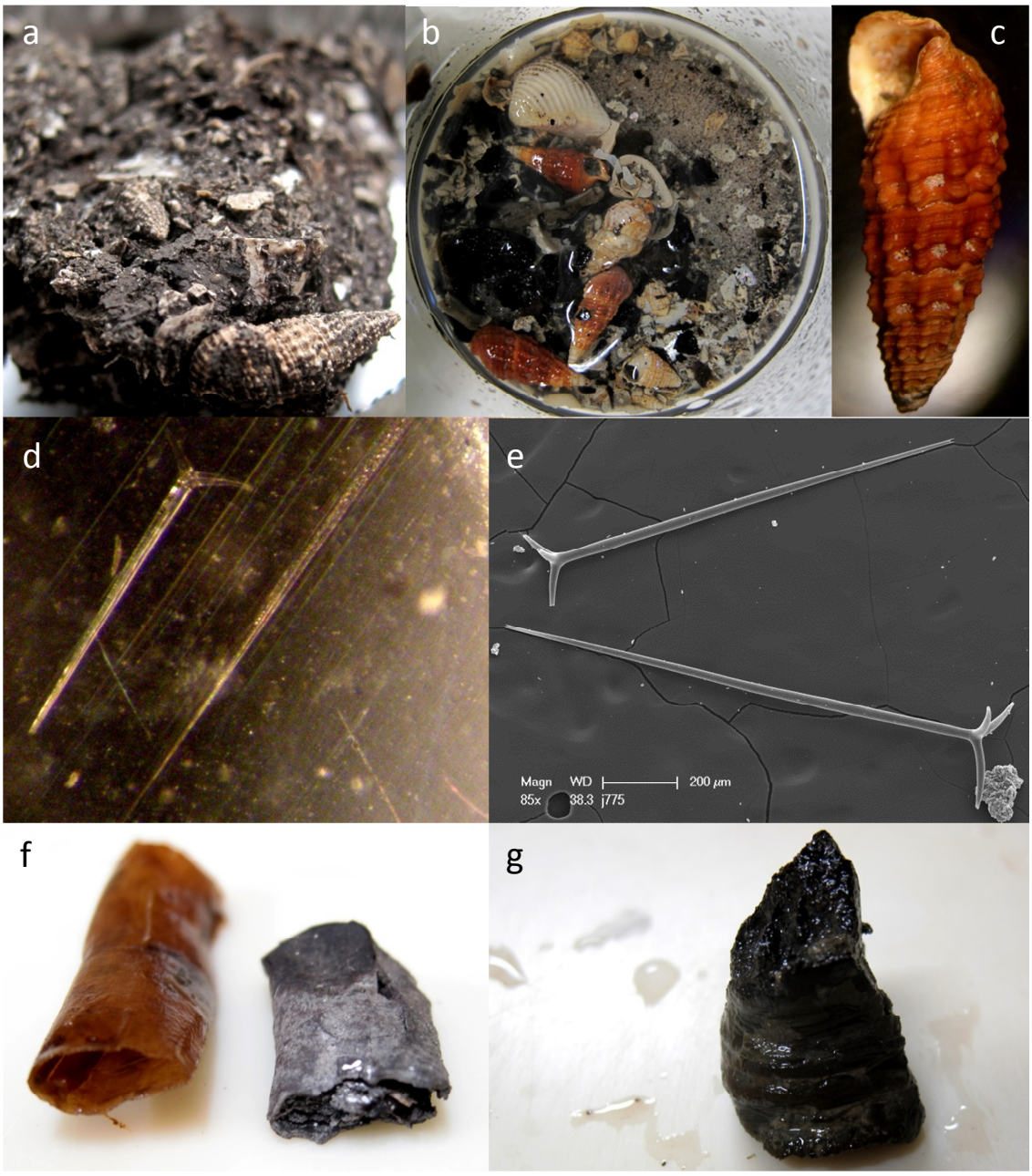

Fig. 2.11 Damani-Guariviara wetland.
a,b) Marine gastropod shells (6 m depth), c) *Cerithium vulgatum* (6 m depth)
d,e) Sponge spicules (6.2 m depth)
f) *R. taedigera* root: fresh root (left), carbonized root (5.9 m depth)
g) Mangrove root (6 m depth)

Chapter 3

Ex situ potential CO_2 and CH_4 emissions from tropical peat soil profiles under aerobic and anaerobic conditions

3.1 Introduction

Tropical peatlands act as both carbon (C) sinks and sources exchanging greenhouse gases (*e.g.* CO_2 and CH_4) with the atmosphere and are hence important in the context of climate change (Parish *et al.* 2008; Jaenicke *et al.* 2008; Rieley *et al.* 2008a). Paleoecological records suggest that carbon sequestration by peatlands, through thousands of years, has had an impact on the global climatic system (Dommain *et al.* 2011; Franzén *et al.* 2007). At present, tropical peatlands hold the approximate equivalent of *ca.* 12 % of the total C in the atmosphere (Falkowski 2000; Page *et al.* 2011). Despite their importance, tropical peat forests are currently endangered (Rieley 2007; Jackson *et al.* 2009). Drainage, land use change and climate change are among the most important threats to tropical peatlands C sequestration capacity, turning them into net carbon sources (*i.e.* CO_2 and CH_4 emitters) with subsidence rates ranging from 10-50 mm y^{-1} (Couwenberg *et al.* 2009; Moore *et al.* 1989; Page *et al.* 2011; Page *et al.* 2004; Belyea *et al.* 2004). Thus gaining knowledge about the mechanisms controlling the peat soils capacity to act as C sink or source under the aforementioned threats is increasingly relevant (Krull *et al.* 2003).

Water level and the associated aerobic-anaerobic zones within the peat matrix are important controls in gaseous carbon fluxes from peatlands to the atmosphere (Moore *et al.* 1989). This is because organic matter decomposition under anaerobic conditions (*i.e.* high water levels - flooded conditions) and in the absence of oxidizing agents is about a thousand times slower when compared to decomposition under aerobic conditions (*i.e.* low water level - drainage, draughts) (Ingram 1978; Belyea *et al.* 2001). Most studies on the effect of water level fluctuations, or aerobic-anaerobic conditions, on carbon turnover within the peat stratigraphic profile have been carried out in boreal, subarctic and temperate peatlands both *ex situ* (Turetsky 2004; Scanlon *et al.* 2000; Moore *et al.* 1997; Moore *et al.* 1989; Beckmann *et al.* 2001; Hogg *et al.* 1992; Daulat *et al.* 1998; Charman *et al.* 1994; Sheppard *et al.* 2007; Macdonald *et al.* 1998; Elberling *et al.* 2011; Laing *et al.* 2010) and *in situ* (Benstead *et al.* 1994; Thomas *et al.* 1996; Charman *et al.* 1994; Mäkiranta *et al.* 2009; Elberling *et al.* 2011; Glatzel *et al.* 2004; Francez *et al.* 2000), using shallow cores (up to 1.1 m depth). In contrast, few studies have been carried out in tropical peatlands and most of them address surface peat emissions (Inubushi *et al.* 1998; Sjögersten *et al.* 2011; Wright *et al.* 2011; Jauhiainen *et al.* 2008; Jauhiainen *et al.* 2005; Hirano *et al.* 2008; Hirano *et al.* 2007). Research relating peat organic matter composition, peat botanical origin or microbial activity to C turnover in peat profiles is also scarce, despite being of importance for greenhouse gases release (Nilsson *et al.* 1993; Buttler *et al.* 1994; Jackson et al. 2009; Reiche *et al.* 2009; Wright *et al.* 2011).

Tropical peatlands develop a vertical stratigraphic profile characterised by overlying peat layers for which the peat chemical composition is related to vegetation succession (Phillips *et al.* 1997). Organic matter accumulated in peat layers is chemically distinct, as it is from different botanical inputs, and has been subjected to different decomposition processes (Krull *et al.* 2003). For instance, water level fluctuations affect the rate of peat decomposition (Wright *et al.* 2013a). Neotropical peatlands are commonly dominated by palms or mono-specific hardwood stands as well as mixed communities representing distinct phasic communities. The palm *Raphia taedigera* forms large mono-specific stands in swamps, whilst mixed communities with the hardwood tree *Campnosperma panamensis* also cover large areas of peatlands in Central and South America (Urquhart 1999; Phillips *et al.* 1997). The rhizosphere system of these phasic communities is distinct in structure and functionality. For example, *R. taedigera* sites have a substantial amount of pneumatophores protruding from the surface and a dense

but shallow (1.1 m) fibrous root system, whilst the mixed forest sites dominated by *C. panamensis* are characterized by buttress roots (1 m depth) with lenticels but without pneumatophores (Wright *et al.* 2013b). Thus, it is plausible that potential C emissions vary through the peat stratigraphic profile. Indeed, a strong relationship between the organic matter composition of the peat in the top 2 m of the stratigraphic profile and CO_2 and CH_4 emissions has been demonstrated in tropical peatlands in Panama (Wright *et al.* 2011). However, the role of oxygenation (*i.e.* aerobic-anaerobic conditions) on the substrate control of gas emissions is currently not resolved. We have formulated the following hypotheses: i) greater CO_2 and CH_4 production occurs in the surface peat layers and in the palms swamp sites; ii) potential CO_2 and CH_4 production is negatively correlated with peat degradation, and iii) the increase of CO_2 production following aeration is greatest at depth. To address these hypotheses, we conducted *ex situ* laboratory incubations under aerobic and anaerobic conditions, in conjunction with physico-chemical characterization of peat cores from six different peatlands located along the Caribbean coast of the Bocas del Toro Province, Republic of Panama.

3.2 Materials and methods

3.2.1 Study area

For full site description refer to Chapter 2. Water table at the CPD has been observed to fluctuate around ± 0.2 m from the surface (Wright *et al.* 2013a). In 2010, different potential peatlands were selected for exploration with the aid of aerial and satellite images. Sites were selected based on the presence of one of two phasic communities: *R. taedigera* palm swamp and mixed forest with *C. panamensis*; and accessibility from the coast. Following a field campaign where peat presence was corroborated by manual coring, three palm swamp and three mixed forests peatlands were selected. For this study, single 0.1 ha (20 × 50 m) plots were set up in each of the six sites (Table 3.1; Fig. 2.1).

Table 3.1: Location of study sites

Site		Coordinates	Distance to the coast (m)	Phasic community	Peat depth (cm)[c]	Carbon pool (kgC m^{-2})[d]
1	Chiriquí Grande	8°58'28.22"N, 82°07'52.85"W	140	Palm swamp	96 ± 7	17 ± 2
2	Cricamola River	8°57'17.70"N, 81°54'41.35"W	1400	Palm swamp	316 ± 37	128 ± 11
3	San San Pond Sak 1[a]	9°25'29.20"N, 82°24'05.60"W	500	Palm swamp	187 ± 5	50 ± 5
4	San San Pond Sak 2[b]	9°25'15.00"N, 82°24'14.64"W	1000	Mixed forest	362 ± 19	99 ± 10
5	Damani-Guariviara	8°57'02.34"N, 81°49'32.40"W	518	Mixed forest	483 ± 98	165 ± 61
6	Bahia Almirante	9°18'17.46"N, 82°21'07.14"W	200	Mixed forest	165 ± 15	78 ± 27

[a,b] San San Pond Sak sites 1 and 2 correspond to Sites 1 and 2 respectively from Sjögersten *et al*., 2010

[c] Peat definition: 30 % of dry weight organic matter(Joosten & Clarke, 2002). Depths correspond to the mean values recorded when peat cores were collected and do not reflect the overall depth in the sites (mean ± 1 SE, n = 3)

[d] Carbon pool was estimated from the bulk density, carbon content and depth of the peat cores.

Table 3.2.- Peat cores samples depths for respirometric assays

Sites	Peat core max. depth (m)	Peat cores samples depths:respirometric assays (m)	Assays[c]
Damani-Guariviara	6	0, 0.50, 1.00, 2.00, 3.00, 4.00, 5.00, 6.00$_{ms}$	8
Cricamola River	4.5	0, 0.50, 1.00, 2.00, 3.00, 3.50, 4.00$_{ms}$	7
San san pond sak 2[a]	4	0, 0.50, 1.00, 2.00, 3.00, 4.00$_{ms}$	6
Bahia Almirante	2.29	0, 0.50, 1.00, 1.75, 2.00, 2.25$_{ms}$	6
San san pond sak 1[b]	2.5	0, 0.50, 1.00, 2.00, 2.25$_{ms}$	5
Chiriqui Grande	1.5	0, 0.50, 1.00, 1.50$_{ms}$	4

[a,b] San san pond sak sites 1 and 2 correspond to Sites 1 and 2 respectively from Sjögersten *et al*., 2010

[c] Amount of incubations performed for each core.

ms Mineral soil sections of the cores

3.2.2 Sampling

At each site, four peat cores were collected between April and June 2010 using a Russian peat corer (*i.e.* 24 cores in total). The corer collected semi cylindrical peat samples of 0.5 m length and 48 mm diameter. We sampled the entire peat profile in 0.5 m increments from the surface to the underlying mineral material. Peat was defined as soil containing $\geq$ 30 % dry weight organic matter (Joosten *et al.* 2002). Due to the presence of coarse root material it was difficult to collect intact peat samples from the surface layers using the Russian corer, so additional peat samples (0.1 $\times$ 0.1 $\times$ 0.1 m) were taken from the surface adjacent to the location where each peat core was collected. Both the 0.5 m core segments and the surface soil samples were wrapped in aluminium foil and placed in plastic boxes for later transportation ($<$ 3 h) to the laboratory at the Smithsonian Tropical Research Institute's, Bocas del Toro Research Station. All samples were refrigerated (2 °C) until either analysis on site or transport to the University of Nottingham.

3.2.3 Peat characterization

Three of the four collected cores at each plot were used for physicochemical characterization; the remaining core was used to measure bulk density. Bulk density was determined by sectioning the peat core into 50 mm length samples, each with an approximate volume of 45 cm^3, and recording each samples weight after being oven dried at 105 °C for 24 h; bulk density was expressed as the quotient of the sample dry weight (dw) over the estimated volume (g_{dw} cm^{-3}). Water holding capacity (WHC) was determined by gravimetric analysis of the water mass loss of 10 g fresh peat samples after oven drying peat samples at 70 °C for 70 h (Wright *et al.* 2011). Loss on ignition (LOI) was determined as mass loss following ignition for 7 h at 550 °C. Soil pH was determined in a 1:2.5 ratio suspension of fresh peat (fw) to deionized water, using a glass electrode. Conductivity was simultaneously determined from the same suspension used to determined pH, using a conductivity meter. Total carbon (C), nitrogen (N) and sulphur (S) were determined on 0.5 g_{dw} homogenised peat samples by combustion, using a total element analyser (Flash EA 1112,CE Instruments, Wigan, UK). Peat ash samples were dissolved in 6 M HNO_3 to estimate the peat phosphorus (P) content by the molybdate-ascorbic acid method (Andersen 1976).

3.2.4 Pyrolysis-gas chromatography mass spectrometry

To determine the role of organic matter composition in the production of CH_4 and CO_2, peat samples were characterised at a molecular level using Py-GC/MS. Each sample used for analysis (*i.e.* individual samples from the different sites at different depths) consisted of 0.5 mg_{dw} homogenised peat. The samples were individually placed in quartz tubes and secured in place using quartz wool plugs (Carr *et al.* 2010). Prior to the pyrolysis, 10 µL of a 0.25 µg μL^{-1} solution of 5-α-cholestane in hexane were added to each sample as internal standard to enable quantification. In addition, each sample was soaked with 10 µL tetramethylammonium hydroxide (TMAH) to prevent thermal degradation of monomeric structures during the pyrolysis process (Carr *et al.* 2010). Py-GC/MS analyses were carried out using a CDS 1000 pyroprobe coupled with a gas chromatographer and mass spectrometer (Perkin Elmer Clarus 500 GC/MS), equipped with a CP Sil 5CB-MS column (30 m × 0.25 mm (0.25 µm film thickness). Samples were introduced into a preheated interface (310 °C) and pyrolyzed at 610 °C for 15 seconds. The GC injector temperature was set to 280 °C and the GC oven temperature was held at 40 °C for 2 minutes and was heated at a rate of 4 °C min^{-1} until it reached 320 °C for 20 minutes. A total of 43 major pyrolysis compounds were identified based on retention time and MS spectra. Compound concentrations were estimated by integrating from the pyrogram and calculating its corresponding concentration using the 5-α-cholestane as internal standard; concentration were expressed in relation to the total carbon content in the peat sample as $\mu g_{compound}$ mgC^{-1}. Each compound was assigned a chemical class *e.g.* lignin, carbohydrate or fatty acid based on their molecular structure; prist-1-ene, which is has been reported to be derived from chlorophyll, was given its own category (Ishiwatari *et al.* 1991). Additionally, the Short:Long ratio for the methylated fatty acids (Short $<$ C20 and Long $>$ C20, Short:Long FAME) was calculated. In the case of free lipids, high weight molecular fatty acids are typical components of terrestrial plants tissues (*e.g.* epicuticular waxes) (Eglinton *et al.* 1967), whilst low molecular fatty acids are ubiquitous (Disnar *et al.* 2008). The FAME hereby presented represent pyrolysis products; however, by using TMAH the pyrolysis decomposition of the free lipids was partially prevented. Thus, the molecular weight of the pyrolysis derived FAME reflects to some extent the original molecular weight from the free lipids they were originated.

3.2.5 Respirometric assays

Ex situ respirometric assays were performed on peat core samples from different depths through the peat profile to estimate the potential rates of CO_2 and CH_4 productions under aerobic and anaerobic conditions. The respirometric analyses were carried out using one of the three cores that were characterised. The anaerobic-aerobic treatment was performed on the same samples in two consecutive stages to simulate the effect of water level fluctuation on the overall CO_2 and CH_4 production (Table 3.2).

The estimated CO_2 and CH_4 production must be considered as potential due to disturbance and the experimental set up (*e.g.* agitation and addition of deionized water) (Moore *et al.* 1997; Kelly *et al.* 1979; Williams *et al.* 1984). Therefore, the potential gas production should not be used to estimate *in situ* emissions nor be extrapolated to large peatland areas.

3.2.5.1 Anaerobic assays

Anaerobic assays simulated high water table conditions at all sites at different depths. Assays were carried out using fresh peat samples from the surface (0 m depth), 0.5 m depth and each subsequent meter down until the mineral soil (Table 3.2; App. A). Each sample (10 g_{fw}) was introduced into 120 mL glass serum bottles (Kinesis, St. Neots, UK), then anaerobic deionized water was added until 70 mL volume within the bottles was occupied by the soil-deionized water solution (leaving 50 mL headspace); six additional bottles with 70 mL deionized water each were used as controls. Each bottle was then flushed with nitrogen for 5 min to displace the dissolved oxygen thus creating anaerobic conditions. Bottles were sealed with custom made rubber septa (13 × 19 × H12 mm; Rubber B.V., Hilversum, NL) and aluminium crimp tops. Incubations were carried out in the dark within temperature controlled chambers at 25 °C reflecting the *in situ* soil temperature (24.61 ± 0.05 °C) from different monitoring events across one year (Dec 2010- Dec 2011) at the six study sites. After two months acclimatization, allowing the microbial community to establish, each bottle was flushed again with nitrogen and resealed. Two consecutive anaerobic incubations were carried out with different duration periods (77 and 392 days). All bottles were manually shaken, not stirred on a daily basis. Bottles were flushed with nitrogen between the assays. Constant volume manometry was applied to the headspace of the bottles, in order to estimate biogas volume production in a non-invasive way

(Müller *et al.* 2004) using a portable differential manometer (Heavy Duty Differential Pressure Manometer-407910, EXTECH Instruments, USA). Manometric pressure measurements were carried out on a daily basis the first two weeks of each assay and on a weekly basis afterwards. The headspace gas of each bottle was analyzed by gas chromatography (GC) at the end of the assays (GC-2014, Shimadzu UK LTD, Milton Keynes, UK). CO_2 and methane CH_4 concentrations were determined using a single injection system with a 1 mL sample loop that passed the gas sample using N_2 as carrier through a non-polar methyl silicone capillary column (CBP1-W12-100, 0.53mmI.D., 12m, 5mm; Shimadzu UK LTD, Milton Keynes, UK). Thermal conductivity (TCD) and H_2 flame ionization (FID) detectors were used to measure CO_2 and CH_4, respectively (Wright *et al.* 2011). Gas concentrations were adjusted for temperature (25 °C constant) and pressure within the serum bottles according to the ideal gas law. The potential rate of gas production expressed as $mgCO_2/CH_4\ gC^{-1}\ h^{-1}$ was calculated under the assumption of linear accumulation of gases in the headspace through time (Hogg *et al.* 1992), confirmed by manometric measurements.

3.2.5.2 Aerobic assays

Once the anaerobic assay was completed, water was filtered out from each bottle simulating peat drainage. Each bottle was then covered with Parafilm and agitated twice on a daily basis for two weeks as an acclimatization period. To start the aerobic incubations, the bottles with drained peat were sealed with custom made rubber septums ($13 \times 19 \times H12$ mm; Rubber B.V., Hilversum, NL) and aluminium crimp tops. Then 30 mL of laboratory air were injected into each bottle to allow for the subsequent collection of gas samples for GC analysis. Incubations were carried out at 25 °C in temperature controlled chambers for 4 days. During the incubation period bottles were agitated twice a day and 10 mL headspace gas samples were taken with plastic syringes at 0, 50 and 96 h for immediate analysis on the GC system (as previously described). Gas concentrations obtained from the gase chromatography analyses were adjusted for temperature (25 °C constant) and pressure within the serum bottles. CO_2 and CH_4 production rates were calculated as described above. Aerobic assays were repeated twice with a 2 days interval between repetitions.

3.2.6 Pore water characterization

Pore water samples were taken from each peat core sample used for respirometric analysis (Table 3.2). Water was analysed for total (TC), inorganic (IC) and organic carbon (TOC) and total nitrogen (TN) using a total organic carbon analyser (TOC-VCPH, Shimadzu UK Ltd, Milton Keynes, UK) coupled with a total nitrogen measuring unit (TNM-1, Shimadzu UK Ltd, Milton Keynes, UK). Spectrophotometric analyses were performed to estimate the fulvic-humic acids ratio and the related degree of humification and aromaticity in the peat cores samples (Grayson et al. 2012). For this purpose, pore water samples were passed through cellulose filters (Whatman Grade 1, 11 µm) and absorbance was measured at 465 and 665 nm (U-2010, Hitachi UV-VIS Spectrophotometer); the absorbance values where then used to estimate the E_{465}/E_{665} index (Uyguner *et al.* 2005).

3.2.7 Data analysis

The Carbon pool was estimated by multiplying the peat's bulk density (g_{dw} m^{-3}) by its carbon content (gC g_{dw} $^{-1}$), considering 0.1 m depth layers. Then the amount of carbon in each layer was summed according to each core length; the estimations for the three cores from each plot were then averaged (Table 3.1). Care must be taken when estimating carbon pools over large areas, as the assumption of inadequate mean values for the peat depth can dramatically over/underestimate such figures.

3.2.8 Statistical analysis

Due to the differences of depths between sites, consequently data was unbalanced and analysis of variance was performed using the Residual Maximum Likelihood method (REML) in GenStat (VSN International 2011). Gas production rates were transformed logarithmically to comply with the normality condition of the REML and linear mixed models were used to compare CO_2 and CH_4 production rates. Relative depth from the surface and the two phasic communities (palm swamp and mixed forests) were added as fixed effects, whilst the specific site where the cores were taken was added as random effect. Independent linear models were used to analyse the anaerobic-aerobic treatments. The level of significance of the differences between the fixed effects was estimated by Wald tests using an F distribution. The effect of covariates (*e.g.* pH, conductivity, TC, TN, Total FAME) on the potential CO_2 and CH_4 productions was estimated by applying backward elimination using multiple linear regression models. Covariates used for statistical

analyses were expressed per g of carbon in peat. Significance was attributed at $P < 0.05$. Results are presented as mean ± SE.

3.3 Results

3.3.1 Peat physicochemical properties

Peat cores from both phasic communities contained a high amount of fresh vascular plants roots within the top 2 m. However, roots were considerably more fibrous and compact in the case of the palm swamp cores. In the layers below 2 m, peat ranged from fibrous with identifiable plant tissues to heavily decomposed in the deeper layers. Bulk density increased with depth from the surface layers of the peat profile to the deeper layers where the mineral soil was located (Fig. 3.1a). The mean values of bulk density were 0.08 ± 0.004 and 0.14 ± 0.014 g_{dw} cm^{-3} for the mixed forest and palm swamp peat cores respectively; reaching maximum levels of 1.17 g_{dw} cm^{-3} in the mineral soil section of the core. Showing an opposite trend to bulk density, water holding capacity (WHC) clearly decreased with depth (Fig. 3.1b). However WHC was consistently high reaching mean values of 90 % in the top 0.5 m layer of the peat cores. Similarly, LOI decreased with depth (Fig. 3.1c). Although no significant difference was found between phasic communities ($F_{1,4} = 5.37$, $P = 0.082$), clay deposition by the Cricamola river in one palm swamp decreased the mean LOI values in the palm swamp cores (54 ± 3.3 %) in comparison with the mixed forest ones (81 ± 1.8 %). pH throughout the peat section of the cores decreased with depth, with mean values of 5 ± 0.03 and 4.87 ± 0.07 for the mixed forest and palm swamp respectively (Fig. 3.1d). However, in the mineral section at the Damani-Guariviara site, higher pH values up to 6.5 were recorded. Conductivity was consistently higher in the deeper sections of the peat cores suggesting marine influences (Fig. 3.1e). For both phasic communities, the carbon and nitrogen content showed a strong decline over the first meter, below 1 m depth C and N continued to decline but less rapidly (Fig. 3.2a,b). The C:N mass ratios were constant throughout the peat profile in the palm swamp with a mean value of 22.5 ± 1.2, whilst in the mixed forest cores the C:N ratios increased with depth with a maximum of 63 (Fig. 3.2c). Both sulfur and phosphorus concentrations through the peat profile were greater in the surface peat layers and the mineral soil layers, with the lowest values recorded in the intermediate layers (Fig. 3.2d,e). Pore water TC, TOC, TIC and TN varied significantly with depth but did not present a particular trend (Fig. 3.3a,b,c,d). The E_{465}/E_{665} ratio

measured from pore water was higher in the surface (0 - 0.1 m) and declined with depth, the maximum observed value was 6.41 and the minimum was 0.66 (Fig. 3.3d). Potential carbon pools varied among sites, deeper peatlands presented the highest carbon pool estimations. Damani-Guariviara peatland showed the highest potential carbon pool per square meter (*ca.* 165 kgC m^{-2}) whilst Chiriquí Grande showed the lowest (*ca.* 17 kgC m^{-2}).

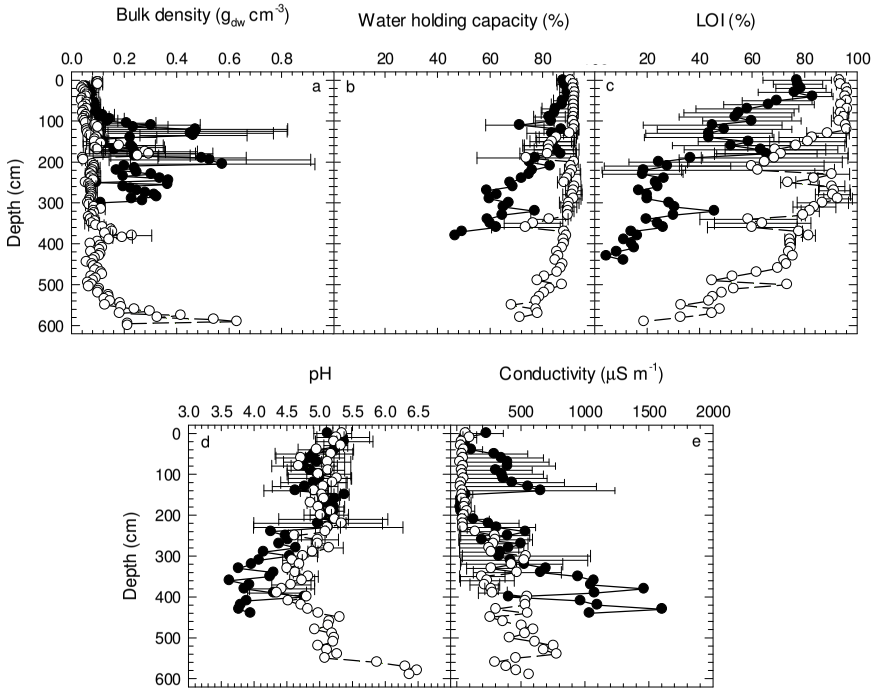

Fig. 3.1 Physicochemical characteristics of peat profiles from Palm swamp (●) and Mixed forest (○) phasic communities.
n varies from 1 to 3 depending if cores overlapped through depth. Symbols represent mean ± SE. REML outputs throughout the peat cores are
a) Bulk density, Depth: $F_{59,102} = 29.75$, $P < 0.001$, Phasic community: $F_{1,102} = 3.14$, $P = 0.155$, Depth.Phasic Community: $F_{38,102} = 13.4$, $P < 0.001$;
b) Water content (%), Depth: $F_{59,102} = 80.02$, $P < 0.001$, Phasic community: $F_{1,102} = 2.76$, $P = 0.17$, Depth.Phasic Community: $F_{38,102} = 31.15$, $P < 0.001$;
c) LOI (mg mg_{dw}^{-1}), Depth: $F_{59,102} = 148.89$, $P < 0.001$, Phasic community: $F_{1,102} = 5.37$, $P = 0.08$, Depth.Phasic Community: $F_{38,102} = 3.92$, $P < 0.05$;
d) pH, Depth: $F_{59,102} = 19.57$, $P < 0.001$, Phasic community: $F_{1,102} = 0.72$, $P = 0.44$, Depth.Phasic Community: $F_{38,102} = 67.88$, $P < 0.001$;
e) Conductivity (µS m^{-1}), Depth: $F_{59,102} = 125.45$, $P < 0.001$, Phasic community: $F_{1,102} = 1.48$, $P = 0.29$, Depth.Phasic Community: $F_{38,102} = 43.74$, $P < 0.001$

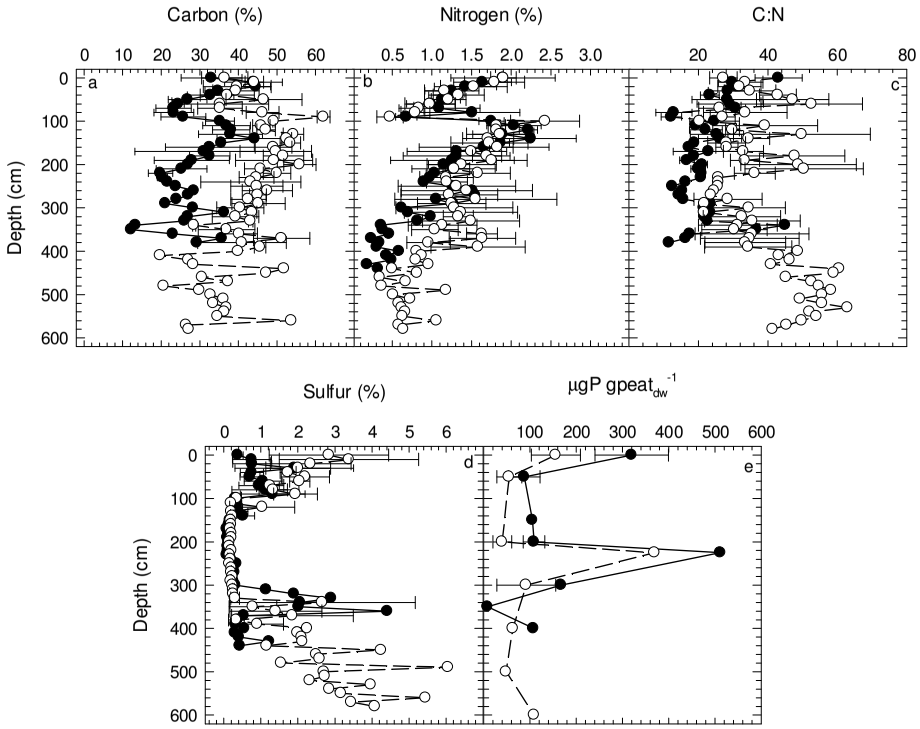

Fig. 3.2 Physicochemical characteristics of peat profiles from Palm swamp (●) and Mixed forest (○) phasic communities.
n varies from 1 to 3 depending if cores overlapped through depth. Symbols represent mean ± SE. REML outputs throughout the peat cores are
a) Carbon (%), Depth: $F_{59,102} = 5.19$, $P < 0.05$, Phasic community: $F_{1,102} = 15.87$, $P < 0.05$, Depth.Phasic Community: $F_{38,102} = 0.14$, $P > 0.05$;
b) Nitrogen(%), Depth: $F_{59,102} = 19.34$, $P < 0.001$, Phasic community: $F_{1,102} = 0.45$, $P = 0.536$, Depth.Phasic Community: $F_{38,102} = 9.25$, $P < 0.01$;
c) C:N, Depth: $F_{59,102} = 11.2$, $P < 0.001$, Phasic community: $F_{1,102} = 2.53$, $P > 0.05$, Depth.Phasic Community: $F_{38,102} = 0.01$, $P > 0.05$;
d) Sulfur (%), Depth: $F_{59,102} = 3.07$, $P < 0.001$, Phasic community: $F_{1,102} = 0.91$, $P > 0.05$, Depth.Phasic Community: $F_{38,102} = 0.98$, $P > 0.05$;
e) Phosphorus(µg g_{dw}^{-1}), Depth: $F_{12,17} = 6.01$, $P < 0.001$, Phasic community: $F_{1,17} = 7.02$, $P < 0.05$, Depth.PhasicCommunity: $F_{5,17} = 0.69$, $P > 0.05$

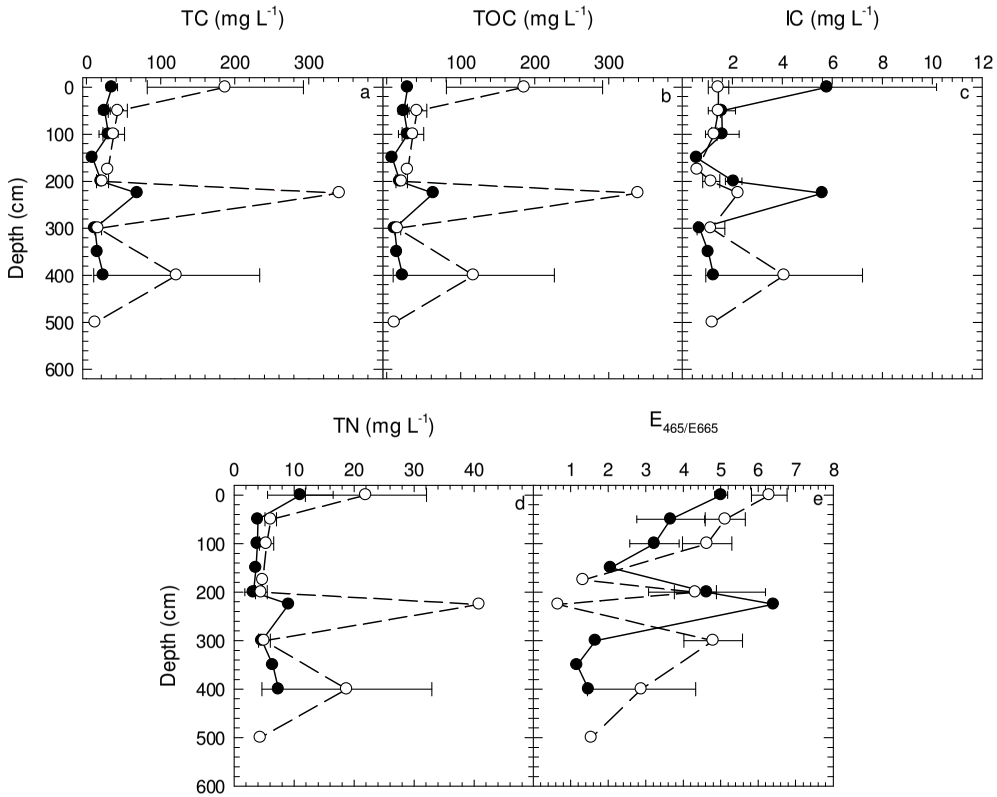

Fig. 3.3 Pore water analyses of peat profiles from Palm swamp (●) and Mixed forest (○) phasic communities.
n varies from 1 to 3 depending if cores overlapped through depth. Points represent mean ± SE. REML outputs throughout the peat cores:
a) TC (mg L^{-1}), Depth: $F_{11,13} = 0.93$, $P = 0.49$, Phasic community: $F_{1,3} = 0.52$, $P = 0.51$, Depth.Phasic Community: $F_{6,13} = 1.17$, $P < 0.38$;
b) TOC (mg L^{-1}),Depth: $F_{11,13} = 1.21$, $P = 0.36$, Phasic community: $F_{1,3} = 0.51$, $P = 0.49$, Depth.Phasic Community: $F_{6,13} = 1.24$, $P = 0.35$;
c) TIC (mg L^{-1}),Depth: $F_{11,13} = 21.68$, $P < 0.001$, Phasic community: $F_{1,2} = 0.49$, $P = 0.53$, Depth.Phasic Community: $F_{6,13} = 1.20$, $P = 0.36$;
d) TN (mg L^{-1}),Depth: $F_{11,13} = 1.58$, $P = 0.21$, Phasic community: $F_{1,2} = 0.50$, $P = 0.52$, Depth.Phasic Community: $F_{6,13} = 0.82$, $P = 0.57$;
e) E_{465}/E_{665},Depth: $F_{11,13} = 4.19$, $P = 0.008$, Phasic community: $F_{1,3} = 1.37$, $P = 0.31$, Depth.Phasic Community: $F_{6,13} = 3.16$, $P = 0.039$

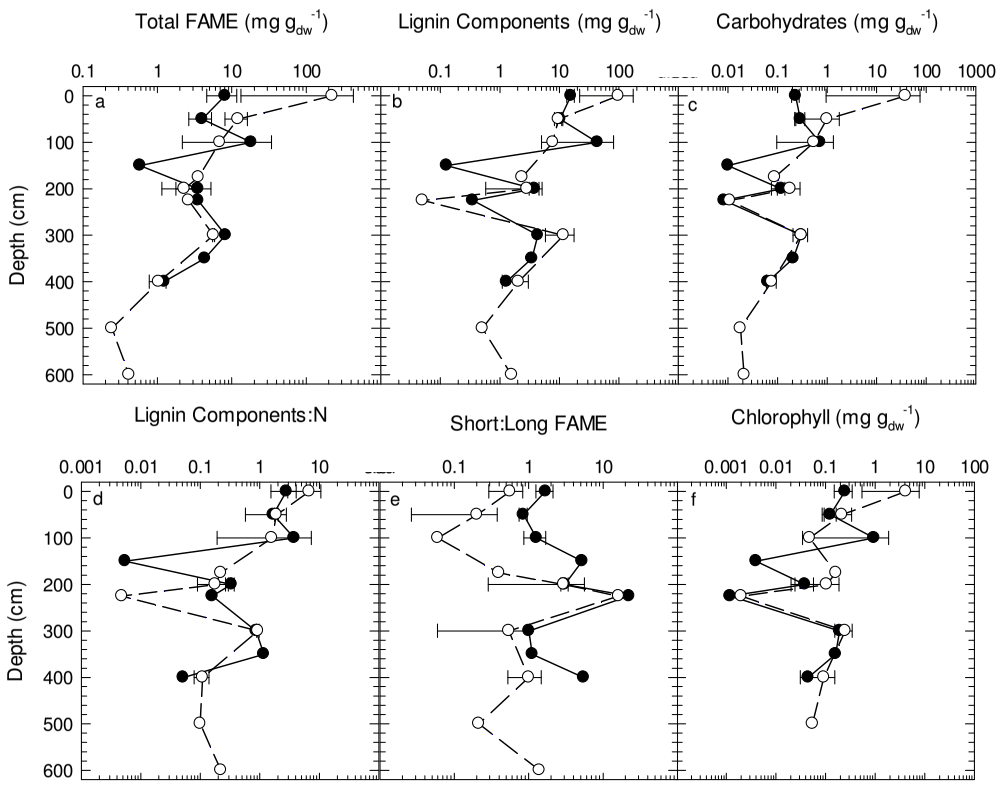

Fig. 3.4 Pyrolyzates concentration from Palm swamp (●) and Mixed forest (○) phasic communities.
n varies from 1 to 2 depending if cores overlapped through depth. Points represent mean ± SE. REML outputs throughout the peat cores are
a) Total FAME (mg g_{dw}^{-1}), Depth: $F_{11,10} = 0.29$, $P > 0.05$, Phasic community: $F_{1,2} = 0.81$, $P > 0.05$;
b) Total Lignin (mg g_{dw}^{-1}), Depth: $F_{11,10} = 0.41$, $P > 0.05$, Phasic community: $F_{1,2} = 0.57$, $P > 0.05$;
c) Total Carbohydrates (mg g_{dw}^{-1}), Depth: $F_{11,10} = 0.30$, $P > 0.05$, Phasic community: $F_{1,2} = 0.9$, $P > 0.05$;
d) Lignin:N, Depth: $F_{11,10} = 0.81$, $P > 0.05$, Phasic community: $F_{1,2} = 0.17$, $P > 0.05$;
e) Short:Long FAME, Depth: $F_{11,9} = 22.53$, $P < 0.001$, Phasic community: $F_{1,3} = 1.04$, $P > 0.05$;
f) Pristene (Chlorophyll) (mg g_{dw}^{-1}), Depth: $F_{11,10} = 0.31$, $P > 0.05$, Phasic community: $F_{1,2} = 0.87$, $P > 0$.

3.3.2 Macromolecular characterization of peat cores

Lignin, carbohydrates, fatty acids and chlorophyll related pyrolysis products decreased with depth in both phasic communities whilst the Short:Long FAME ratio increased with depth (Fig. 3.4).

3.3.3 Potential CO_2 and CH_4 emissions

Potential CO_2 production through the peat profile were not significantly different between the two phasic communities ($\log_{10}CO_2$, Phasic communities: $F_{1,4} = 0.18$, $P = 0.69$) (Fig. 3.5). Potential CO_2 productions were significantly higher in aerobic conditions ($\log_{10}CO_2$, Aerobic-Anaerobic: $F_{1,30} = 848.81$, $P < 0.001$). Potential CO_2 production were distributed through four orders of magnitude with the lowest production registered under anaerobic conditions (0.012 $mgCO_2$ gC^{-1} h^{-1}) whilst the highest (38.62 $mgCO_2$ gC^{-1} h^{-1}) occurred under aerobic conditions. Potential anaerobic CO_2 production decreased with depth (Fig. 3.5e), whereas potential aerobic production did not present a clear trend (Fig. 3.5b). Aerobic and anaerobic potential CO_2 productions were strongly related ($r(36) = 0.84$, $P < 0.001$). The aerobic:anaerobic ratio of the potential CO_2 productions ranged from 12 to 146 increasing from the surface to the deeper peat layers (CO_2 Aerobic:Anaerobic, Depth: $F_{11,13} = 9.55$, $P < 0.001$).

Potential CH_4 production decreased with depth ($\log_{10}CH_4$, Depth: $F_{11,31} = 17.66$, $P < 0.001$ (Fig. 3.5a,d). No significant differences were observed in the potential CH_4 production with respect to the phasic community that was present in the surface ($\log_{10}CH_4$, Phasic Communities: $F_{1,4} = 0.43$, $P = 0.55$). The aerobic and anaerobic treatment did have a significant effect on the potential CH_4 production, being two orders of magnitude greater under anaerobic conditions in the surface peat layers (Fig. 3.5a,d) ($\log_{10}CH_4$, Aerobic-Anaerobic: $F_{1,30} = 37.65$, $P < 0.001$). The aerobic:anaerobic ratio of the potential CH_4 production increased with depth from 0.005 in the surface layers to 22 in the deeper ones (CH_4 Aerobic:Anaerobic, Depth: $F_{11,14} = 41.1$, $P < 0.001$).

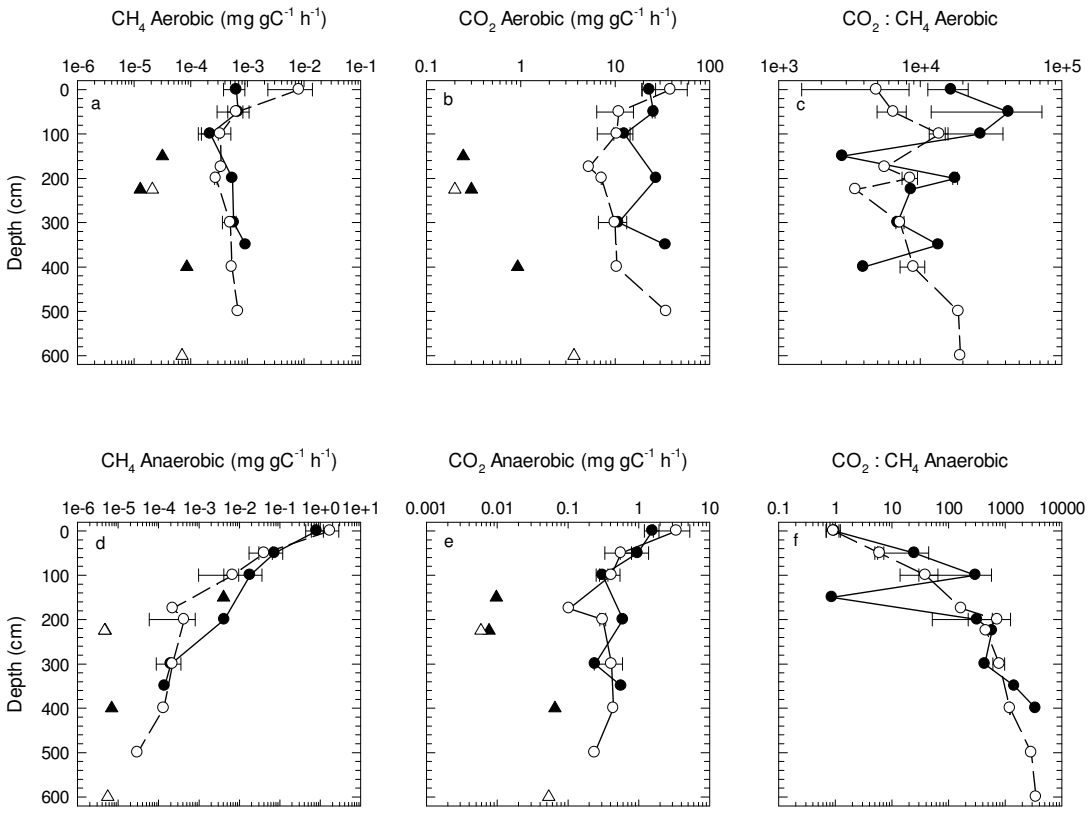

Fig. 3.5 Potential CO_2 and CH_4 emissions ($mgCH_4/CO_2$ gC^{-1} h^{-1}) through peat profiles of Palm swamp (●) and Mixed forest(○) phasic communities. ▲ and △ correspond to the mineral soil sections of the cores of Palm swamp and Mixed forest respectively. Symbols represent mean ± standard error. REML outputs throughout the peat cores are:

a) $\log_{10}$ $CH_{4\ aerobic}$, Depth: $F_{11,13} = 4.14$, $P < 0.01$, Phasic Community: $F_{1,3} = 0.45$, $P = 0.54$, Depth.Phasic Community: $F_{6,13} = 1.94$, $P = 0.147$;
b) $\log_{10}$ $CO_{2\ aerobic}$, Depth: $F_{11,13} = 15.01$, $P < 0.001$, Phasic Community: $F_{1,3} = 1.03$, $P = 0.37$, Depth.Phasic Community: $F_{6,13} = 4.28$, $P = 0.013$;
c) $\log_{10}$ CO_2:$CH_{4\ aerobic}$, Depth: $F_{11,13} = 2.18$, $P > 0.05$, Phasic Community: $F_{1,3} = 3.28$, $P > 0.05$, Depth.Phasic Community: $F_{6,13} = 2.79$, $P > 0.05$;
d) $\log_{10}$ $CH_{4\ anaerobic}$, Depth: $F_{11,13} = 33.4$, $P < 0.001$, Phasic Community: $F_{1,3} = 0.19$, $P = 0.69$, Depth.Phasic Community: $F_{6,13} = 1.12$, $P = 0.402$;
e) $\log_{10}$ $CO_{2\ anaerobic}$, Depth: $F_{11,13} = 11.06$, $P < 0.001$, Phasic Community: $F_{1,3} = 0$ $P = 0.98$, Depth.Phasic Community: $F_{6,13} = 0.85$, $P = 0.55$
f) $\log_{10}$ CO_2:$CH_{4\ anaerobic}$, Depth: $F_{11,13} = 28.84$, $P < 0.001$, Phasic Community: $F_{1,3} = 28.84$, $P = 0.63$, Depth.Phasic Community: $F_{6,13} = 0.93$, $P = 0.50$

3.3.4 Influence of physicochemical parameters on potential CO_2 and CH_4 productions

The variance of the potential aerobic CO_2 production was accounted by the Short:Long FAME ratio and peat phosphorus content ($\log_{10}CO_2$ Aerobic = - 0.11× Short:Long FAME + 5.66 × Soil Phosphorus + 1.051), each of them contributing with 57 and 15 % of the variance respectively. Potential CO_2 anaerobic productions variance was also accounted by the Short:Long FAME ratio (50 %) and the peat phosphorus content (19 %), but also in a lesser extent by Total Lignin (8 %) ($\log_{10}CO_2$ Anaerobic = 6.84 × Soil Phosphorus – 0.12 × Short:Long FAME + 0.003 × Total Lignin – 0.563).

Potential CH_4 productions also seemed to be driven by the composition of the organic matter in the different peat layers. The variance of the aerobic and anaerobic potential CH_4 production was accounted by those parameters related to the availability and quality of the carbon sources in peat, such as the Short:Long fatty acids ratio and the E_{465}/E_{665} ratio and to a lesser extent by the phosphorus content and pH. Thus, under aerobic conditions the potential CH_4 productions variance was accounted by the Short:Long FAME ratio, the E_{465}/E_{665} ratio and the pH in a 20, 13 and 9 % respectively ($\log_{10}CH_4$ Aerobic = 0.12 × E_{465}/E_{665} – 0.05 × Short:Long FAME - 0.22 × pH – 2.64); whilst under anaerobic conditions the Short:Long FAME ratio, the E_{465}/E_{665} and the phosphorus concentration accounted for 27, 13 and 14 % of the variance respectively ($\log_{10}CH_4$ Anaerobic = 17.83 × Soil Phosphorus + 0.36 × E_{465}/E_{665} – 0.25 × Short:Long FAME – 4.16).

3.4 Discussion

The data provided in this study suggest that organic matter composition of peat plays a major role in controlling the potential CO_2 and CH_4 production. Previous studies suggest that peat botanical origin is a main driver of subsurface carbon mineralization (Coulson *et al.* 1978; Williams *et al.* 1984; Yavitt *et al.* 1987; Conrad 1996; Moore *et al.* 1997). For instance, Nilsson and Bohlin (1993) observed a difference in the CO_2 production between peat originating from bryophytes (rich in cellulose and hemicellulose) and peat with herbaceous origins (rich in lignin). They attributed this difference to the contrasting chemical composition of the peat produce by those organisms. However, in our data, the potential CO_2 and CH_4 production as well as the CO_2:CH_4 molar ratios were not significantly different

between the two phasic communities (palm swamp and mixed forest) (Fig. 3.5). Coupled with the peat chemical characterization, this suggests that the peat originated from palm and hardwood trees is chemically similar. Consequently, carbon mineralization rates, in the surface layers, did not vary with respect to the phasic community that generated the peat forming material. To fully test this, palynological studies are required.

Despite the lack of significant difference between phasic communities, the aerobic-anaerobic treatment indicated that carbon mineralization rates are driven by the peat chemical composition. Under anaerobic conditions, the greatest potential gas productions occurred in the surface layers, but this was no longer the case under aerobic conditions (Fig. 3.5a,b,d,e). The CO_2:CH_4 molar ratios indicated that CO_2 production is dominant at all depths, indicating that CO_2 production occurs through several biogeochemical processes, including those involved in methanogenic pathways (Fig. 3.5c,f) (Gujer *et al.* 1983). The shift from anaerobic conditions to aerobic conditions significantly reduced the potential CH_4 production and increased the potential CO_2 production at all depths. It is plausible that the low potential CO_2 production under anaerobic conditions is due to the substantial reduction of lignin degradability by ligninolytic microorganisms in the absence of oxygen, as the latter is required for efficient lignin depolymerization and solubilization (Zeikus 1981). Moreover, the potential CO_2 production in the deeper layers of the peat profile is more affected than the surface layers by the aerobic treatment. The reduction on potential CH_4 production is related to the toxic effect that oxygen exerts on methanogenic bacteria (Whitman *et al.* 2006). Thus, under anaerobic conditions the potential CO_2 and CH_4 production were controlled by organic matter composition, specifically the recalcitrance of the organic matter (Valentine *et al.* 1994; Nilsson *et al.* 1993; Yavitt *et al.* 1990). In contrast, under aerobic conditions, potential CH_4 production was strongly inhibited (without being absent) and potential CO_2 production was no longer limited by the substrate recalcitrance.

Additional evidence to support the role of peat chemical composition in driving carbon mineralization was obtained from the macromolecular characterization of the peat profiles. The Short:Long FAME ratio was negatively correlated with the potential production of CO_2 and CH_4 under both aerobic and anaerobic conditions. Low Short:Long FAME ratio (*i.e.* abundance of high weight FAME) might be related to higher terrestrial plants components, leaf epicticular waxes (Harji *et*

al. 2008; Eglinton *et al.* 1967). In the peat profile, the low Short:Long FAME ratio would result from the microbial decomposition of recently fallen plant litter and thus less degraded organic matter (Chanton *et al.* 1997; Ström *et al.* 2005; Rinnan *et al.* 2006). The less degraded organic matter in the surface is also related to a higher availability of labile substrates, such as fatty acids, amino acids and carbohydrates, that can be used by fermenters to produce the substrates required by methanogens (Conrad 1999; Nilsson *et al.* 1993). The correlation between the potential CH_4 production and the E_{465}/E_{665} ratio, but not the C:N ratio suggests that it is not the amount of available carbon in the peat, but its recalcitrance that controls methanogenesis (Valentine *et al.* 1994; Yavitt *et al.* 1990; Nilsson *et al.* 1993). Besides the Short:Long FAME ratio and the E_{465}/E_{665} ratio, which are related to peat composition, phosphorus was the only nutrient that accounted for a significant amount of the variance in the potential productions. This correlation has been previously observed for CO_2 by Sjögersten *et al.* (2010) along a nutrient gradient in the San San Pond Sak wetland; the highest potential CO_2 production declined as phosphorus declined along the nutrient gradient. Therefore, phosphorus is likely to be a limiting factor for carbon mineralization in tropical peatlands (Cheesman *et al.* 2012; Sjögersten *et al.* 2010).

3.4.1 Implications to regional carbon balance

Due to climate change, it has been estimated that the mean precipitation in the Caribbean region will be reduced by 20 % during the current century (Bates *et al.* 2008). This reduction in regional rainfall, added to the projected increase in mean air temperature, could lead to an eventual long term lowering of peatlands water table (Moore *et al.* 1989; Couwenberg *et al.* 2011). Consequently, the deeper peat layers (otherwise recalcitrant) would become accessible to microbial degradation under aerobic conditions. This will dramatically affect the subsurface carbon mineralization rates, enhancing CO_2 release by orders of magnitude. Drainage of peatlands for agriculture would have a similar effect (Hirano *et al.* 2008; Jauhiainen *et al.* 2005; Hooijer *et al.* 2012), but will also stop the regular organic matter input that forms peat. Therefore, climate change in conjunction with local agricultural practices has the potential to transform the peatlands in the region into net carbon emitters, annulling their function as long term carbon stores. By using Cohen *et al.* (1989) and Phillips *et al.* (1997) figures for peat depth in San san pond sak ($\approx$ 9,230 ha, max peat depth = 8.1 m), we estimated a 0.02 Gt belowground carbon deposit. For the Damani-Guariviara wetland ($\approx$ 24,089 ha, max peat depth = 6 m), using a conservative mean peat depth of 3 m,

we estimated a 0.021 Gt belowground carbon deposit. Thus, long term alterations in the peatlands water table could trigger the gradual release of *ca.* 0.041 Gt of carbon from the region.

Additional research is needed in order to develop a better understanding of the processes governing the carbon mineralization in tropical peatlands. This will require improving our estimates of the total above and belowground carbon deposits tropical forests; estimations of organic matter degradation rates *in situ* (discussed in Chapter 4); as well as monitoring temporal and spatial variations of carbon emissions and peat subsidence in the region.

Chapter 4

Roots as main component of peat in lowland tropical peatlands

4.1 Introduction

Global warming has become a central topic on the international agenda over the past decades. According to the IPCC, warming of the climate system is unequivocal and is "extremely likely" to be related to anthropogenically induced emissions of greenhouse gases (GHG) to the atmosphere (Solomon *et al.* 2007). Carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) are the main trace GHG altering the Earth's energy budget. From 1750 to 2011, the concentration of CO_2, CH_4 and N_2O has increased by 40, 150 and 20 % respectively in the atmosphere (Solomon *et al.* 2007). Hence, research related to quantifying GHG sinks and sources has gained importance. Peatlands can act as sink and source of GHG, interchanging CO_2, CH_4 and N_2O with the atmosphere (Rieley *et al.* 2008a; Jaenicke *et al.* 2008; Conrad 1996; Ueda *et al.* 2000). Over the long-term (millennia), peatlands act as carbon sinks due to an imbalance between the above and belowground production of plant material (net primary productivity; NPP) and its decay (organic matter decay; OMD) (Laiho 2006; Clymo 1984; Frolking *et al.* 2011; Turunen *et al.* 2002). Peatlands hold globally *ca.* 610 Gt of carbon belowground (Page *et al.* 2011); this is equivalent to 84 % of the total carbon in the atmosphere (Falkowski 2000). In contrast, wetlands (peatlands among them) represent, in the short-term (decades), the single most important source of biogenic CH_4 to the atmosphere, emitting *ca.* 32 % of the annual global CH_4 emissions (Kirschke *et al.* 2013). CH_4 and CO_2 are produced as plant material decays under anaerobic conditions and occurs throughout the peat profile (Wright *et al.* 2011; Belyea *et al.* 2006; Ingram 1978). In addition, significant amounts of CO_2 are produced as peat decays under

aerobic conditions.

On a millennial time scale, lowland tropical peatlands have the highest peat accumulation rates in the world, accumulating peat up to 10 times faster than temperate, subarctic and boreal peatlands (Dommain *et al.* 2011; Chimner *et al.* 2005; Gorham *et al.* 2003). Lowland tropical peatlands are located in regions where mean annual temperatures, precipitation rates, and organic matter decomposition rates are high. This conditions have been associated with high NPP (Jenny *et al.* 1949; Olson 1963) and OMD (Jenny *et al.* 1949; Ewel 1976). As the role of lowland tropical peatlands as net sinks (continuing accumulating peat) or sources (no longer accumulate peat) of carbon to the atmosphere is dependent of NPP and OMD, understanding the factors controlling OMD is important. OMD in lowland tropical peatlands is controlled by different factors. i) The environmental conditions under which decay takes place (Daubenmire *et al.* 1963); for example, higher temperatures increase organic matter decay (Jenny *et al.* 1949; Daubenmire *et al.* 1963; Shanks *et al.* 1961; Mork 1939). ii) The chemical composition of the plant material (Bernhard-Reversat 1972; Day 1982); decomposition of plant material vary among plant species in relationship to their nutrient content (Ewel 1976; Bartholomew *et al.* 1953; Odum *et al.* 1970) and structural traits (Edwards 1977; Meentemeyer 1978; Melillo *et al.* 1982). In contrast with boreal, subarctic and temperate peatlands, the peat in tropical peatlands is believed to be mostly constituted of vascular plants roots and wood as these contain highly recalcitrant compounds in their cell walls, *e.g.* lignin (Zeikus 1981; Chimner et al. 2005). iii) The nature, abundance and successions of decomposing organisms also affect OMD (Hayes 1965; Coûteaux *et al.* 1995; Schneider *et al.* 2012); furthermore, microbial metabolism is affected by environmental conditions (temperature, nutrients availability and chemical composition of plant material) (Singh *et al.* 1977; Fierer *et al.* 2005). For instance, an inverse correlation has been observed between decomposition rates and temperature in temperate forests as decomposers are better adapted to low temperatures in these environments (Daubenmire *et al.* 1963).

Land use change (drainage) and the effects of climate change in Central America (droughts) might trigger subsidence of the subsurface peat (Couwenberg *et al.* 2009; Solomon *et al.* 2007). The rate of subsidence is controlled by the factors controlling plant material decay. Despite this, OMD studies in the tropics are mainly focused on aboveground fine litter *i.e.* leaves (Chambers *et al.* 2000). As

previously mentioned, the peat forming material will define to some extent the rate of peat subsidence, thus improving our knowledge about peat composition. Its susceptibility to decay in the Neotropics is important within the climate change framework. Peat composition has been studied through different approaches: direct observation of macro and microfossils (Phillips *et al.* 1997) and study of biomarkers records (Kuder *et al.* 2001). Pyrolysis-gas chromatography-mass spectrometry (Py-GC/MS) represents an alternative for fingerprint peat composition and establishing the dominant plant input through time (McClymont *et al.* 2011; Parsi et al. 2007; Carr *et al.* 2010). Understanding how plant material decay is controlled in the tropics represents one of the main challenges that has to be overcome in order to be able to define the role of tropical peatlands in the global carbon cycle (Brown *et al.* 1982).

In this study, two peat-forming arborescent species (*Raphia taedigera* palm and *Campnosperma panamensis* hardwood tree) with distinct litter composition were used as models to explore different aspects of the carbon turnover in four neotropical peatlands. We hypothesized that: i) Rates of decomposition vary among tissue types (leaf, stem and root) and between two arborescent species belonging to different functional groups (*R. taedigera* palm and *C. panamensis* hardwood tree), with roots contributing most to peat formation; ii) Decomposition rates are slower belowground (0.5 m depth) than at the peat surface; iii) Site specific properties control decomposition and iv) Nutrient addition accelerates decomposition. In order to test these hypotheses, the following approaches were carried out: *in situ* litter decomposition experiments, characterization of plant tissues and peat at a molecular level using Py-GC/MS and *in situ* measurement of GHG emissions.

4.2 Materials and methods

4.2.1 Study sites

The full description of the study area is presented in Chapter 2. Four sites were selected for this study, with respect to the presence of two specific phasic communities (palm swamp and mixed forest). A vegetation survey was undertaken in order to classify the phasic communities in the peatlands; the monodominance was defined using the % of basal area (m^2 ha^{-1}). Two sites were dominated by *R. taedigera* (an evergreen canopy forming palm) and two were mixed forests

dominated by *C. panamensis* (an evergreen canopy forming hardwood tree) (for further details see Chapter 2). Two of the sites are located in the CPD where several studies have been previously carried out (Sjögersten *et al.* 2011; Wright *et al.* 2011; Troxler 2007; Cheesman *et al.* 2012). The additional two sites were selected following satellite imagery analysis, aerial reconnaissance of the area and field campaigns conducted in April 2010 (Table 4.1).

All sites are freshwater with water table fluctuating from + 0.15 to − 0.4 m relative to the peat surface. *R. taedigera* sites had large amounts of leaf litter at the surface, a substantial amount of pneumatophores protruding from the surface and a dense but shallow (1.1 m) fibrous root system (Wright *et al.* 2011). Shallow water ponds and raised areas (close to each *R. taedigera* colony) are typical components of this sites microtopography. Mixed forest sites are also characterized by large amounts of leaf litter, however pneumatophores were no longer ubiquitous at the surface. *C. panamensis* was characterized by large buttress roots (1 m depth) with lenticels (Wright *et al.* 2011); similar to *R. taedigera* sites the microtopography at the mixed forest sites was heterogeneous characterized by shallow ponds and raised areas. At each site, permanent plots of 0.1 ha were established (20 m × 50 m) for the census of vegetation, the collection of peat cores and the installation of litterbags.

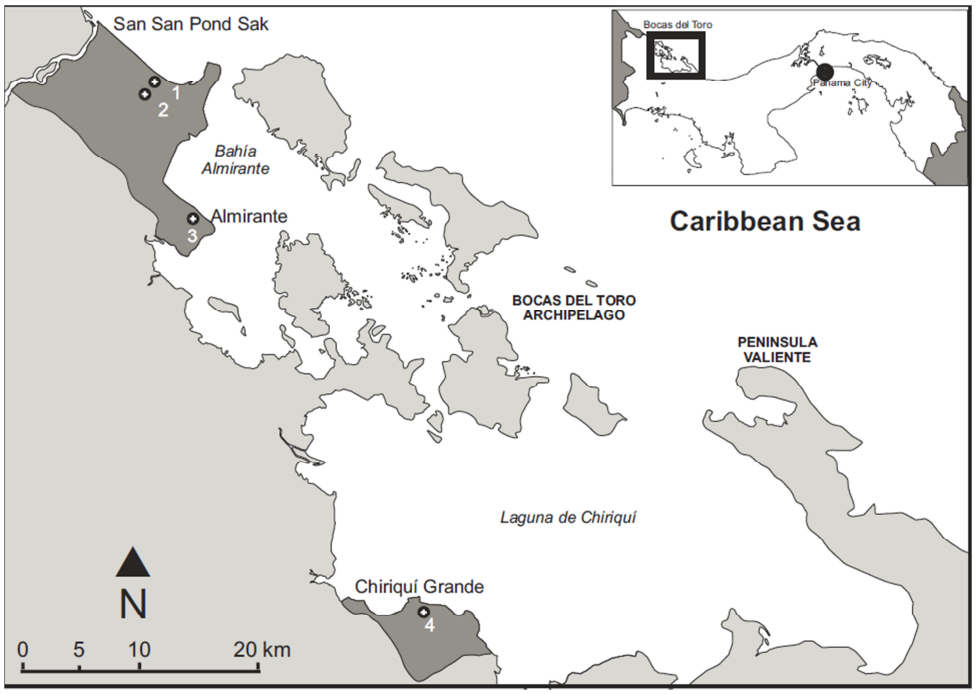

Fig. 4.1 Map of the north western region of the Caribbean coast of the Republic of Panama. Locations of the four study sites are shown and numbered according to Table 4.1; darker zones correspond to wetlands areas identified from aerial and satellite imagery.

Table 4.1: Location of study sites

Site		Coordinates	Distance to the coast (m)	Dominant vegetation	Peat depth (m)[c]
1	San San Pond Sak 1[a]	9°25'29.20"N, 82°24'05.60"W	500	*R. taedigera*	1.87 ± 0.05
2	San San Pond Sak 2[b]	9°25'15.00"N, 82°24'14.64"W	1000	*C. Panamensis*	3.62 ± 0.19
3	Almirante Bay	9°18'17.46"N, 82°21'07.14"W	200	*C. panamensis*	1.65 ± 0.15
4	Chiriqui Grande	8°58'28.22"N, 82°07'52.85"W	140	*R. taedigera*	0.96 ± 0.07

[a,b] San San Pond Sak sites 1 and 2 correspond to Sites 1 and 2 respectively from Sjögersten *et al*., 2010

[c] Peat definition: 30 % of dry weight organic matter(Joosten & Clarke, 2002). Depths correspond to the mean values recorded when peat cores were collected and do not reflect the overall depth in the sites (mean ± 1 SE)

4.2.2 Work programme

The following approaches were used to determine the controls of organic matter decomposition: i) Monitoring *in situ* organic matter decomposition using litterbags to quantify the difference in decomposition rates across tissue type (leaf, stem and root) from two distinct tree species (*R. taedigera* palm and *C. panamensis* hardwood tree); ii) Molecular characterization of peat cores and *R. taedigera* and *C. panamensis* litter by Py-GC/MS; iii) Addition of nitrogen and phosphorus fertilizers in conjunction with litter decomposition studies and GHG (CO_2, CH_4 and N_2O) measurements and iv) Litter translocation experiment to evaluate site specific properties as decomposition control.

4.2.3 Experimental design

In order to compare the *in situ* decomposition rates of *R. taedigera* and *C. panamensis* litter, a total of 216 litterbags were prepared: 72 of each tissue (leaf, root stem). The experimental unit consisted in groups of three litterbags (one of each tissue) tied together. Each unit was installed *in situ* to be incubated at the surface (0 m depth) and belowground (0.5 m depth) in three locations within each of the four plots (Table 4.1). Litterbags containing *R. taedigera* and *C. panamensis* litter were installed at the palm swamp and mixed forest sites respectively. Within each location sufficient units were installed to be sampled sequentially at 9, 14 and 24 months (litterbags were installed in March 2010 and subsequently sampled during December 2010, May 2011 and April 2012). In addition, fresh litter from the two arborescent species (*R. taedigera* and *C. panamensis*) and peat samples throughout the peat profile from the four sites (SSPS1, SSPS2, Almirante and Chiriquí) were characterized to a molecular level in order to define the main constituents of peat (leaf, stem and root).

The effect of nutrient addition on the decomposition was explored by performing an additional five months (from October 2011 to March 2012) litterbag experiment. The nutrient treatments were: control (C), nitrogen (N), phosphorus (P) and nitrogen + phosphorus (NP). The experimental design consisted of ten blocks distributed along 150 m transects running from SE to NW at SSPS1 (9°25'29.20" N; 82°24'5.60" W) and SSPS2 (9°25'14.00" N; 82°24'15.49" W). Transects were perpendicular to the direction of the water flow running from centre to the outer regions of the peat dome (perpendicular to the transect used by Cheesman *et al.*, 2012; Sjögersten *et al.*, 2010 and Wright *et al.*, 2011). Each block had a square

shape (10 × 10 m) with the nutrient enrichment treatments applied at each vertex. Blocks were distributed with a separation of 5 m between each other. Adjacent vertices had the same nutrient treatment to avoid cross-contamination. At each vertex, experimental units (*i.e.* one litterbag with each tissue) were incubated at both the peat surface and the belowground (0.5 m depth). Litterbags at SSPS1 and SSPS2 contained *R. taedigera* and *C. panamensis* litter respectively. After five months litterbags were collected and prepared for gravimetric and chemical analysis. Simultaneously with the litterbags collection, gas samples were collected (March 2012) to measure the CO_2, CH_4 and N_2O fluxes at every vertex of each block.

In addition to the nutrient enrichment experiment, a litter translocation experiment was performed. The translocation allowed exploring the difference of the decomposition of *R. taedigera* and *C. panamensis* leaves in a mixed forest and palm swamp site respectively where they were allochthonous and with respect to the decomposition of *R. taedigera* and *C. panamensis* leaves in a palm swamp and a mixed forest site where they were autochthonous. The translocation of leaves was performed at the peat surface of five of the ten blocks at SSPS1 and SSPS2; litterbags with leaves were installed at the Control vertex of the odd blocks (Block number: 1,3,5,7,9).

4.2.4 Methodology

4.2.4.1 Litterbags preparation and recollection

R. taedigera and *C. panamensis* litter was collected at San San Pond Sak 1 (SSPS 1; Palm swamp) and San San Pond Sak 2 (SSPS 2; Mixed forest). Litter consisting of senescent leaves and freshly cut stems and roots was cleaned with deionized water, dried at 70 °C for five days and cut into small even sized pieces. Litter was weighed (Leaves: *ca.* 2 g; Stems and Roots: *ca.* 1 g) and placed separately into pre-weighed polyester mesh litterbags (0.1 × 0.1 m; 560 µm); litterbags were tied with polyamide thread (ø = 0.8 mm).

During each sampling event, one unit was collected from the surface and belowground at each location within each plot. Litterbags were then carefully rinsed with deionized water, opened and its content was put in aluminium trays for gravimetric and chemical analysis.

4.2.4.2 Nutrient addition

Nutrient enrichment was applied by filling 0.25 m sections of dialysis tubing (Spectra/Por® membrane: 40 mm diameter, 6000 to 8000 molecular weight cut off) with 0.86 mol of either nitrogen (Urea: $CO(NH_2)_2$, 46%) or phosphorus (Monocalcium phosphate: $Ca(H_2PO_4)_2 \bullet H_2O$, 45%) fertilizer. This allowed a slow release of nutrients through the membrane (Feller 1995). At each block fertilizer was applied at both the surface (0 m) and belowground (0.5 m) according to the experimental design.

4.2.4.3 Peat sampling

Peat cores were collected from each plot (Table 4.1) between April and June 2010 using a Russian peat corer. The corer collected semi cylindrical peat samples of 0.5 m length with 48 mm diameters. We sampled the entire peat horizon in 0.5 m increments from the top (surface, 0 m) to the bottom (mineral soil underlying the peat deposit) (App. A). Due to the presence of coarse root material it was difficult to collect intact peat samples from the surface layers using the Russian corer. Thus additional surface peat samples (0.1 × 0.1 × 0.1 m) were taken adjacent to the location where each peat core was collected. Additionally, surface peat samples (0.1 × 0.1 × 0.1 m) from the nutrient addition plots at the palm swamp and the mixed forest were collected at the vertex of each block (80 surface peat samples). Both the 0.5 m core segments and the top surface peat samples were wrapped in aluminium foil and placed in plastic boxes for transportation ($<$ 3 h) to the laboratory at the Smithsonian Tropical Research Institute, Bocas del Toro Research Station. All samples were refrigerated (4 °C) until either being analysed in the research station laboratory or sent to the University of Nottingham.

4.2.4.4 Peat and litter characterization

Samples from different depths of the peat cores including the mineral soil and litter samples were subjected to the same processes of chemical characterization. Dry weight was determined by gravimetric analysis of the water mass loss after oven drying 10 g fresh weight (fw) of peat and litter samples at 70 °C for 120 h (Wright et al. 2011). Total organic carbon (TOC), total nitrogen (TN) and total sulfur (TS) were determined from 0.5 g_{dw} homogenised peat and litter samples (homogenization was carried out in a Planetary Ball Mill, Retsch-PM400, Castleford, UK) using a total element analyser (Flash EA 1112,CE Instruments, Wigan, UK).

4.2.4.5 Peat extractable nutrients

To corroborate the effect of the nutrient addition treatment, total dissolved organic carbon (DOC) and nitrogen (TDN) were extracted from surface peat samples by shaking 40 g_{fw} of peat in 75 mL of 0.5M K_2SO_4 for 1 h (Sjögersten *et al.* 2011). Extracts were centrifuged (8000g, 15 min) and the dissolved organic carbon in the supernatant was determined after a five-fold dilution by automated combustion and gas chromatography on a TOC-VCSH anlyzer (Shimatzu, Columbia, MD). Ammonium and nitrate were determined by automated colorimetry using a Lachat Quickchem 8500 flow injection analyser (Hatch Ltd, Loveland, CO). Ammonium was determined by automated colorimetry at 660 nm following reaction with phenolate while nitrate was determined at 520 nm following cadmium-catalyzed reduction of nitrate and reaction with sulfanilamide at pH 8.5. Total nitrogen was determined in the extracts by alkaline persulfate oxidation (Cabrera *et al.* 1993) overnight at 80 °C in sealed gas tubes, with detection as nitrate by automated colorimetry as described above. Dissolved organic nitrogen was calculated as the difference between total nitrogen and the sum of ammonium and nitrate.

Readily-exchangeable phosphate was determined by extraction with anion exchange membranes (AEM) using a method based on Myers, Thien, & Pierzynski (1999). Surface peat (20 g_{fw}) was shaken for 24 h with 80 mL deionized water and five anion-exchange resin strips (1 × 40 mm; manufactured by BDH Prolabo and distributed by VWR International, Lutterworth, Leicestershire, UK). The strips were rinsed in deionized water and the phosphate recovered by shaking for 1 h in 50 mL of 0.25M H_2SO_4. Phosphate was determined in the acid solution at 880 nm following online neutralization and automated molybdate colorimetry using a flow injection analyser (Lachat Quickchem 8500, Hach Ltd, Loveland, CO).

4.2.4.6 Peat microbial biomass nutrients

Microbial biomass nutrients were determined by fumigation (Sjögersten *et al.* 2011). Carbon and nitrogen contained within soil microbial biomass was estimated by $CHCl_3$ fumigation and 0.5 M K_2SO_4 extraction using a correction factor of 2.64 to account for the unrecovered biomass carbon (Vance *et al.* 1987) and 1.85 to account for unrecovered biomass nitrogen (Brookes *et al.* 1985). Microbial phosphorus was determined by extraction with anion-exchange membranes; soils were extracted as previously described for available phosphate, but with the addition of hexanol (0.5 mL) (Myers *et al.* 1999). Fumigation-released phosphorus

was calculated as the difference between phosphate determined in fumigated and unfumigated samples.

4.2.4.7 Hydrolytic enzyme assays

The activity of five different hydrolytic enzymes was measured in the surface peat of three of the nutrient addition experimental blocks at the palm swamp and the mixed forest. These enzymes are involved in the release of carbon, phosphorus and sulfur from organic compounds. Assays were conducted using methylumbelliferone-linked fluorogenic substrates (Marx *et al.* 2001). Enzymes and substrates were: i) Phosphomonoesterase: 4-methylumbelliferyl phosphate (MUP); ii) Phosphodiesterase: bis-(4-methylumbelliferyl) phosphate (BisMUP); iii) Aryl sulfatase: 4-methylumbelliferyl sulfate (MUS); iv) β-Glucosidase: 4-methylumbelliferyl β-D-glucopyranoside (MUBG); v) N-acetyl-β-glucosaminidase: 4-methylumbelliferyl N-acetyl-β-D-glucosaminide (MUNA). Each surface peat sample used for the analysis consisted in the equivalent in fresh weight of 2 g_{dw}; peat samples were added to 200 mL of 1mM NaN_3 and stirred for 10 min. Aliquots (50 µL) of peat suspension were dispenses into a 96-well microplate containing 100 µL of 200 µM substrate (100 µM final concentration in the assay mixture) and 50 µL of sodium acetate-acetic acid buffer adjusted to pH 4 (the approximate mean peat pH). Microplates were incubated at 30 °C for 30 min. Following incubation, 50 µL of 0.5 M NaOH was added to terminate the reaction and fluorescence was determined immediately on a FLUOstar Optima spectrofluometer (BMG Labtech, Offenburg, Germany).

4.2.4.8 Pyrolysis-gas chromatography- mass spectrometry (Py-GC/MS)

To determine the origin of the organic matter forming peat, peat and litter samples were characterised at a molecular level using Py-GC/MS. Each sample used for analysis (*i.e.* individual samples from the different sites and depths) consisted of 0.5 mg_{dw} homogenised peat. The samples were individually placed in quartz tubes and secured in place using quartz wool plugs (Carr *et al.* 2010). Prior to the pyrolysis, 10 µL of a 0.25 µg $µL^{-1}$ solution of 5-α-cholestane in hexane were added to each sample as internal standard to enable quantification. In addition, each sample was soaked with 10 µL tetramethylammonium hydroxide (TMAH) to prevent thermal degradation of monomeric structures during the pyrolysis process (Carr *et al.* 2010). Py-GC/MS analyses were carried out using a CDS 1000 pyroprobe coupled with a gas chromatographer and mass spectrometer (Perkin

Elmer Clarus 500 GC/MS) equipped with a CP Sil 5CB-MS column (30 m × 0.25 mm (0.25μm film thickness)). Samples were introduced into a preheated interface (310 °C) and rapidly pyrolized at 610 °C for 15 seconds. The GH injector temperature was set to 280 °C and the GC oven temperature was held at 40 °C for 2 minutes and was heated at a rate of 4 °C min^{-1} and was held at 320 °C for 20 minutes. A total of 43 major pyrolysis compounds were identified based on retention time and MS spectra. Compound concentrations were estimated by integrating the areas obtained in the pyrogram and calculating its corresponding concentration using the 5-α-cholestane as internal standard; concentration were expressed in relation to the total carbon content in the peat sample as $\mu g_{compound}$ mgC^{-1}. Each compound was assigned a chemical class *e.g.* lignin, carbohydrate or fatty acid based on their molecular structure. Prist-1-ene, which is thought to be derived from chlorophyll, was given its own category (Ishiwatari *et al.* 1991). In order to interpret the characterization data, short and long methylated fatty acids (Short < C20 and Long > C20) were grouped. In the case of free lipids, high molecular fatty acids are typical components of terrestrial plants tissues (*e.g.* epicuticular waxes) (Eglinton *et al.* 1967), whilst low molecular fatty acids are ubiquitous (Disnar *et al.* 2008). Though the components we present in here are pyrolysis products, this classification aids to the discussion of the results.

4.2.4.9 *In situ* gas flux measurements

In situ gas fluxes were determined from the surface of peat at each treatment (Control, Nitrogen, Phosphorus and Nitrogen + Phosphorus). Gas samples were collected between 10:00 and 16:00 h. Gas collection for flux estimation was performed using the closed chamber technique (Sjögersten *et al.* 2011). Plastic chambers had an area of 0.075 m^2 and were *ca.* 0.1 m high, with a total volume of 7 L. Each chamber had a sampling port equipped with a Suba-Seal® rubber septa (Fisherbrand, Loughborough, UK). Small vegetation and fallen branches were removed before the installation of the chamber. Peat disturbance was avoided as much as possible during the installation of the chambers but slight pressure was applied in order to ensure a tight seal. Once installed and prior to the collection of gas samples, the chamber headspace was homogenised by repeatedly pumping the air within the chamber with a 20 mL syringe equipped with a hypodermic needle. Afterwards, gas samples were collected from each chamber after 0, 2, 10 and 20 min using a 20 mL syringe equipped with a thin needle (25 Gx1'', TERUMO, UK). Gas samples were injected into pre-vacuumed 12 mL borosilicate glass vials sealed with an screw cap-septum (Exetainer; LABCO, UK), leaving each vial

with overpressure. All samples were shipped to the University of Nottingham for gas chromatography analysis. Vials were discarded if overpressure was no longer present. CO_2, CH_4, and N_2O concentrations were determined using a single injection system with a 1 mL sample loop that passed the gas sample using N_2 as carrier through a non-polar methyl silicone capillary column (CBP1-W12-100, 0.53 mm I.D., 12 m, 5 mm; Shimadzu UK LTD, Milton Keynes, UK) and porous polymer packed column (HayeSep Q 80/100). Thermal conductivity (TCD) and flame ionization (FID) detectors were used to measure CO_2 and CH_4, respectively; whilst N_2O was measured with an electron capture detector (ECD). Flux calculations were based on the linear accumulation of gases within the closed chamber; therefore gas concentrations that did not follow a linear trend were discarded for the calculation of gas fluxes.

4.2.4.10 Statistical analyses

The remaining mass of litter and the decomposition rates were calculated as a proportion of the initial mass remaining at the end of the experiment (Wider *et al.* 1982). Analysis of variance on the remaining mass of litter, decomposition rates and GHG fluxes were performed using the Residual Maximum Likelihood method (REML). Linear mixed models were used to compare the amounts of remaining mass of different tissues of different plants at different incubation depths and under different nutrient enrichment treatments; as well as to define the differences in GHG fluxes under different nutrient enrichment treatments. Level of significance for the differences between the fixed effects was estimated by Wald tests using an F distribution. Significance was attributed at $P < 0.05$. For the *in situ* organic matter decomposition experiment (% of remaining massdw), the two types of arborescent species from different phasic communities (*R. taedigera*-palms swamp and *C. panamensis*-mixed forest), the three different tissues (leaf, stem and root) and the incubation depth (surface and belowground) were used as fixed factors. To analyse the rates of organic matter decomposition (k: y^{-1}), the above mentioned fixed factors were used and the four different sites (Table 4.1) were used as random factors. For the analysis of the litter translocation experiment (% of remaining massdw), the sites (SSPS1 and SSPS2) and the translocation treatment were used as fixed factors whilst the blocks were used as random factor. To analyse the effect of nutrients addition on the nutrients concentration in surface peat, the phasic community and the nutrient treatment (C, N, P and NP) were used as fixed factors whilst the block was used as random factor. The same model was used to analyse the effect of nutrient addition on the hydrolytic enzyme activity

in peat. To analyse the effect of the nutrient addition on decomposition (% of remaining massdw), the nutrient treatment (C,N,P and NP), the different tissues and the incubation depth were used as fixed factors using block as the random factor. Finally, the effect of nutrient enrichment on GHG fluxes (mg m^{-2} h^{-1}) was analysed by using the sites (SSPS1 and SSPS2) and the nutrient treatment as fixed factors with block as the random factor. The decomposition trends of the different tissues from the two different plants were adjusted to single negative exponential decay models ($X_n = X_0 \times e^{-kt}$) (Olson 1963).

Similarities in the molecular composition of the litter and the peat samples from different depths were explored by Principal Component Analysis (PCA) based on correlation matrices. Results throughout the text and figures are presented as mean ± SE. All statistical analysis were performed in GenStat (VSN International 2011).

4.3 Results

4.3.1 Litter characterization

The total organic carbon (TOC), nitrogen (TN) and C:N ratio varied significantly between the *R. taedigera* palm and the *C. panamensis* hardwood tree (TOC; Species: $F_{1,6} = 5.37$, $P < 0.05$; TN, Species: $F_{1,6} = 485$, $P < 0.001$; C:N, Species: $F_{1,6} = 9.55$, $P < 0.05$) (Table 4.2). The different tissues (leaves, stems and roots) showed significantly different TN (TN, Tissue: $F_{2,6} = 594$, $P < 0.001$) and C:N (C:N, Tissue: $F_{2,6} = 74.42$, $P < 0.001$) but not TOC (TOC, Tissue: $F_{2,6} = 2.25$, $P > 0.05$) (Table 4.2). The tissues of each species presented significantly different TOC (TOC, Specie × Tissue: $F_{2,6} = 6.81$, $P < 0.05$) TN (TN, Specie × Tissue: $F_{2,6} = 291$, $P < 0.001$) and C:N (C:N, Specie × Tissue: $F_{2,6} = 40.36$, $P < 0.001$). The highest TOC (30 ± 0.2 %), TN (1.01 ± 0.003 %) and C:N (30 ± 0.59) in *R. taedigera* was observed in the stems, leaves and stems respectively; whilst in *C. panamensis* the highest TOC (35 ± 3.9 %), TN (0.6 ± 0.03 %) and C:N (80 ± 9) was observed in leaves, roots and leaves respectively. By using the lignin related compounds obtained from the Py-GC/MS analyses it was possible to calculate an LigningPy:TN ratio. The highest LigninPy:N ratio was showed by the root tissue of both species (0.17 ± 0.01), with the exception of *R. taedigera* stems (0.26); in contrast, the lowest LigninPy:N ratio was consistently observed in leaves of both species (0.03 ± 0.005).

Table 4.2 *R. taedigera* and *C. panamensis* senescent litter* : Total carbon, nitrogen and sulfur (g g_{dw}^{-1} × 100) and Py-GC/MS characterization (µg mgC^{-1})

		Tissue		
	Tree Species	Leaf	Stem	Root
Nutrient				
Total Carbon	*R. taedigera*	25.1 ± 0.03	30.1 ± 0.19	27.7 ± 0.47
	C. panamensis	34.9 ± 3.89	30.4 ± 0.03	26.6 ± 0.12
Total Nitrogen	*R. taedigera*	1.01 ± 0.00	0.27 ± 0.01	0.93 ± 0.00
	C. panamensis	0.43 ± 0.00	0.39 ± 0.04	0.60 ± 0.03
Total Sulfur	*R. taedigera*	0.13 ± 0.03	0.30 ± 0.12	0.24 ± 0.05
	C. panamensis	0.04 ± 0.00	0.13 ± 0.01	0
Molecular precursor				
Lignin	*R. taedigera*	38.92	72.04	146.78
	C. panamensis	12.20	15.69	117.48
Short FAME**	*R. taedigera*	26.47	4.30	3.20
	C. panamensis	15.39	5.84	1.28
Long FAME	*R. taedigera*	8.70	2.28	3.36
	C. panamensis	3.88	2.10	3.76
Carbohydrates	*R. taedigera*	7.67	1.17	1.34
	C. panamensis	1.99	2.20	1.49
Chlorophyll	*R. taedigera*	1.63	0.24	0.09
	C. panamensis	0.78	0.03	0.94

* Plant material used for decay experiments

**FAME, Methylated fatty acids

4.3.2 *In situ* decomposition of organic matter

Litter decomposition was significantly different between the phasic communities, tissues and the incubation depth (Fig. 4.2). Decomposition at the surface was consistently higher than belowground. Decomposition of *R. taedigera* tissues was higher in comparison with *C. panamensis* tissues when litter was incubated at the surface; in contrast, *R. taedigera* litter decomposed less than that of *C. panamensis* when litter was incubated belowground. Stems were the most labile tissue of *R. taedigera* whilst leafs were the most labile tissue of *C. panamensis*. Roots were the most recalcitrant tissue when decomposed belowground in both phasic communities. However, when decomposed at the surface, roots were the most recalcitrant tissue of *R. taedigera* but stems were the most recalcitrant tissue of *C. panamensis*.

Roots showed the lowest decomposition rates across all tissues both at the surface and belowground. The lowest decomposition rates were observed belowground Fig. 4.3; Table 4.3). For example, roots of *R. taedigera* and *C. panamensis* decomposed 5 and 3 times faster at the surface than belowground respectively (Fig. 4.3c,f). Leaves of *R. taedigera* decomposed slower than *C. panamensis* leaves at the surface and belowground (Fig. 4.3a,d). Leaves showed the highest decomposition rates among *C. panamensis* tissues whilst stems showed the highest decomposition rates in *R. taedigera*. With respect to the nutrient composition of the litter decomposed at the surface, the TOC in all tissues rapidly increased 19.52 ± 1.2 % during the first 9 months and remained constant afterwards (TOC, Time: $F_{3,22} = 731$, $P < 0.001$). In contrast, TN showed a steep decrease of 0.32 ± 0.08 % during the first 9 months followed by a moderate increase (0.07 ± 0.02 %) (TN, Time: $F_{3,22} = 59.5$, $P < 0.001$).

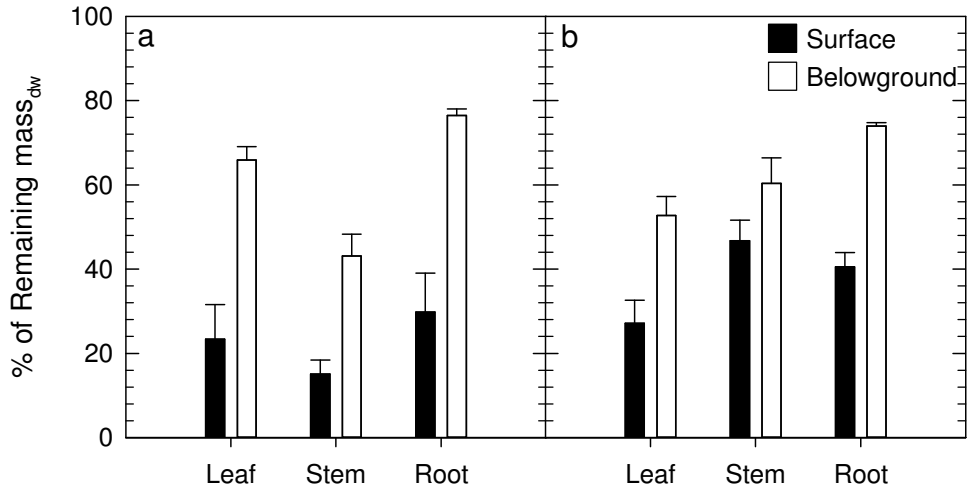

Fig. 4.2 Percentage of remaining mass$_{dw}$ of *R. taedigera* (a) and *C. panamensis* (b) litter (leaves, stems, roots) after 24 months. REML outputs are:

Phasic community: $F_{1,51} = 6.04$, $P < 0.05$;
Surface/Belowground: $F_{1,51} = 108.59$, $P < 0.001$;
Tissues: $F_{2,51} = 9.52$, $P < 0.001$;
Phasic community × Surface/Belowground : $F_{1,51} = 4.8$, $P < 0.05$;
Phasic community × Tissues: $F_{2,51} = 7.38$, $P < 0.01$;
Surface/Belowground × Tissue: $F_{2,51} = 3.4$, $P < 0.05$;
Phasic community × Surface/Belowground × Tissues: $F_{2,51} = 0.03$, $P > 0.05$

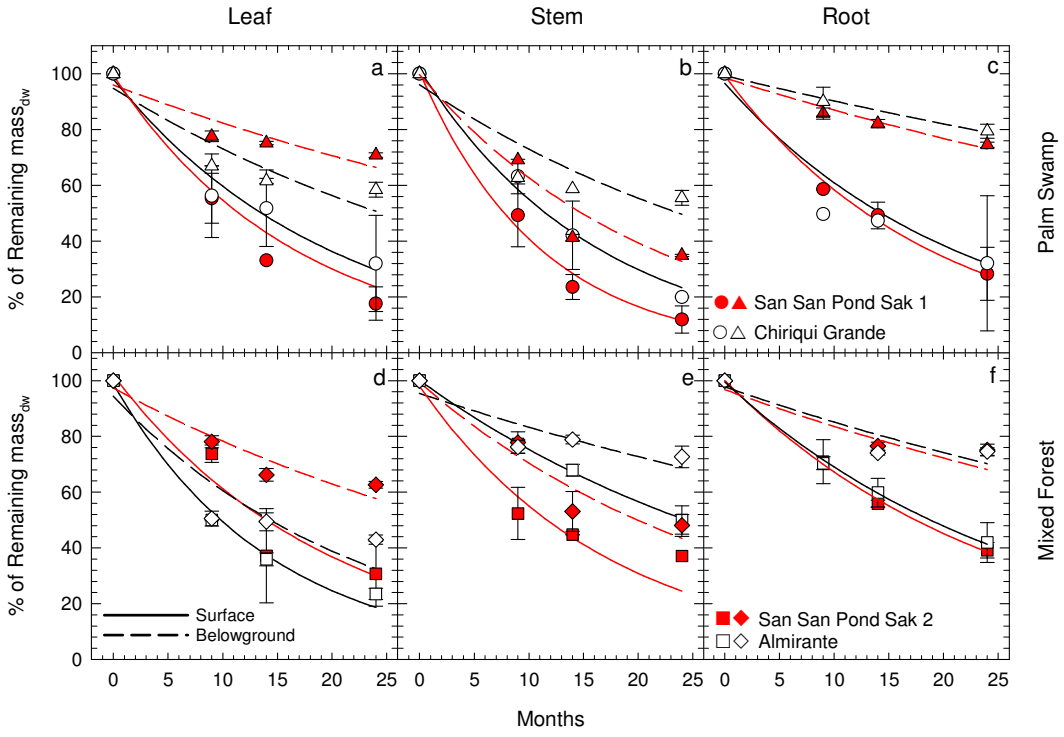

Fig. 4.3 *In situ* organic matter decomposition. Figures a-d, b-e and c-f correspond to leaf, stem and root tissue respectively. Closed symbols ●▲ and ■◆ correspond to San San Pond Sak 1 (Palm swamp) and San San Pond Sak 2 (Mixed forest) respectively; whilst open symbols ○△ and □◇ correspond to Chiriquí Grande (Palm swamp) and Almirante (Mixed forest) respectively. Solid lines and dashed lines describe the degradation in the surface (0 m depth) and belowground (0.5 m depth) respectively. Statistical analyses were perform on the decomposition constant (*k*) estimated when fitting data to a single negative exponential model (Table 1). REML outputs for k values are as follows:

Phasic community: $F_{1,2} = 1.49$, $P > 0.05$;
Surface/Belowground : $F_{1,10} = 36$, $P < 0.001$;
Tissue: $F_{2,10} = 4.22$, $P < 0.05$;
Phasic community × Surface/Belowground : $F_{1,10} = 1.87$, $P > 0.05$;
Phasic community × Tissue: $F_{2,10} = 3.33$, $P > 0.05$;
Surface/Belowground × Tissue: $F_{2,10} = 0.02$, $P > 0.05$;
Phasic community × Surface/Belowground × Tissue: $F_{2,10} = 0.13$, $P > 0.05$

Table 4.3. Exponential decay parameters of *in situ* organic matter decomposition of leaves (L), stems (S) and roots (R) of *R. taedigera* and *C. panamensis* at the surface (0 m depth) and belowground (0.5 m depth)

Phasic Comty	Site	Depth	Tissue	% of Remaining mass t_{24}[b] ± SE	Exponential decay model[a]		
					k (y^{-1})	P	% σ^2
Palm swamp	SSPS1	Surface	L	17.6 ± 5.9	0.718	< 0.001	81
			S	11.9 ± 4.9	1.083	< 0.001	91
			R	28.2 ± 9.4	0.636	< 0.001	91
		Belowground	L	70.8 ± 0.8	0.183	< 0.001	82
			S	34.8 ± 0.4	0.557	< 0.001	94
			R	74.5 ± 0.9	0.149	< 0.001	92
	Chiriquí Grande	Surface	L	31.9 ± 21.1	0.596	< 0.001	68
			S	19.9 ± .3	0.734	< 0.001	93
			R	32.0 ± 24.2	0.552	< 0.01	55
		Belowground	L	58.4 ± 2.6	0.312	< 0.001	82
			S	55.5 ± 2.6	0.330	< 0.001	85
			R	79.4 ± 2.5	0.114	< 0.001	82
Mixed forest	SSPS2	Surface	L	30.7 ± 11.6	0.611	< 0.001	78
			S	37.1 ± 0.1	0.692	< 0.001	86
			R	39.1 ± 2.7	0.477	< 0.001	93
		Belowground	L	62.6 ± 1.1	0.262	< 0.001	89
			S	48.1 ± 3.9	0.414	< 0.001	85
			R	73.1 ± 0.8	0.176	< 0.001	80
	Almirante	Surface	L	23.5 ± 2.1	0.832	< 0.001	98
			S	50.1 ± 5.1	0.342	< 0.001	95
			R	41.9 ± 7.1	0.439	< 0.001	91
		Belowground	L	42.9 ± 1.6	0.533	< 0.001	82
			S	72.6 ± 3.8	0.163	< 0.001	67
			R	74.5 ± 1.3	0.165	< 0.001	82

[a] Organic matter decomposition data was fitter to a single negative exponential decay model (Olson, 1963): $X_n = X_0 \times e^{-kt}$

[b] t_{24}: remaining mass after 24 months

4.3.3 Molecular characterization of peat cores and litter

The 43 major pyrolysis compounds were used as a fingerprint to compare the molecular composition of the peat profiles of the four plots and the three distinct tissues of the arborescent species. The PCA analyses showed a distribution pattern where the peat core samples were arranged in a descendent order with respect to the peat profile depth (Fig. 4.4a,b,c,d). In all cases the surface peat layers were related to the leaf tissues, whilst the peat samples from the deeper sections of the peat cores clustered with the roots and stems. The molecular components driving the distribution of PCA scores were mostly but not exclusively related to lignin, carbohydrates and lipids (App. B).

4.3.4 Translocation experiment

Decomposition of *R. taedigera* leaves was higher at the palm swamp site where it was autochthonous in comparison with the decomposition observed at the mixed forest site where it was allochthonous (Fig. 4.5). The same relationship was observed for *C. panamensis* leaves showing higher decomposition at the mixed forest site in comparison with their decomposition at the palm swamp site.

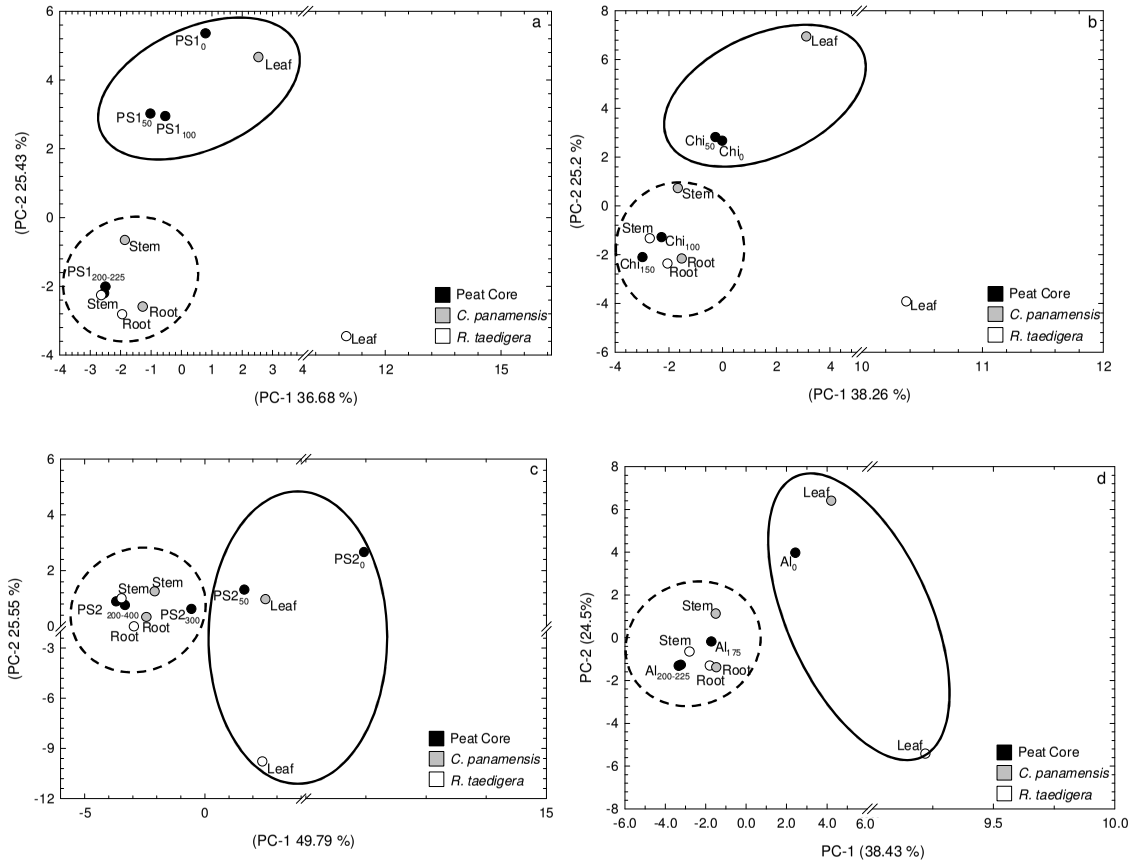

Fig. 4.4 Principal component scores from PCA analyses on the Py-GC-MS chemical characterization of peat cores and *R. taedigera* and *C. panamensis* tissues. Figures a and c correspond to San San Pond Sak 1 (Palm forest) and San San Pond Sak 2 (Mixed forest) respectively; whilst figures b and d correspond to Almirante (Mixed forest) and Chiriqui Grande (Palm swamp) respectively. Subindices indicate the relative depth from the surface of peat core samples (cm). Solid line and dashed line circles have been included as visual aid to indicate surface from deeper peat layers respectively.

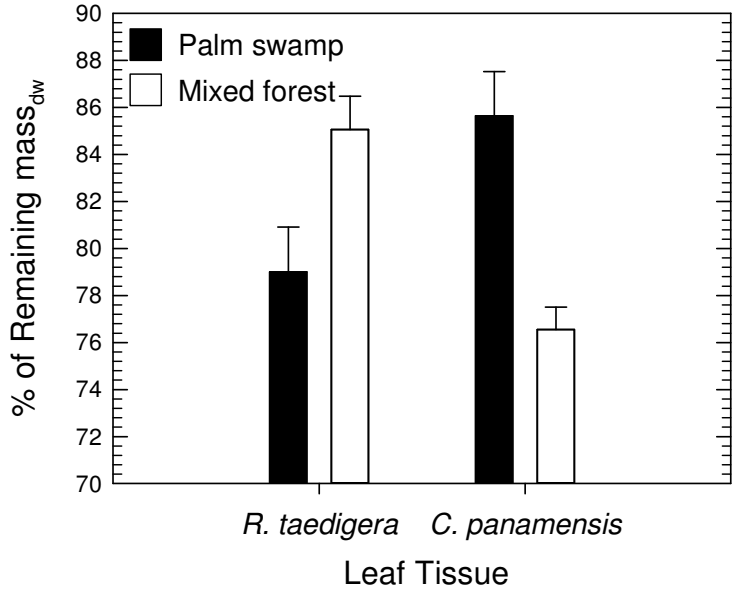

Fig. 4.5 Translocation experiment: % of remaining mass (dry weight) of *C. panamensis* and *R. taedigera* leaves litter after 5 months. Litterbags were placed at the peat surface (0 m depth). REML outputs are as follows:

Site: $F_{1,17} = 1.49$, $P > 0.05$
Translocation treatment: $F_{2,55} = 101.48$, $P < 0.001$
Site × Translocation treatment: $F_{2,56} = 1.28$, $P > 0.05$

4.3.5 Effect of nutrient addition on the *in situ* decomposition and GHG fluxes

4.3.5.1 Nutrient addition

The extractable TDOC was lower in comparison with the microbial TDOC at both sites (Site: $F_{1,32} = 24.4$, $P < 0.001$). Neither extractable nor microbial dissolved organic carbon (TDOC) varied significantly with respect to the addition of nutrients ($Nitrogen_{add}$: $F_{1,29} = 0.2$; $P > 0.05$; $Phosphorus_{add}$: $F_{1,29} = 0.9$; $P > 0.05$). The TDOC did vary significantly between the palm swamp and the mixed forest site (Site: $F_{1,21} = 25.8$, $P < 0.001$) (Fig. 4.6a,b). Five months after the nutrient addition, nitrogen and phosphorus were found to be significantly higher in those locations within the block where the nutrients were applied ($Nitrogen_{add}$: $F_{1,28} = 8.71$, $P < 0.01$; $Phosphorus_{add}$: $F_{1,56} = 7.67$, $P < 0.01$) (Fig. 4.6c,d,e,f). The increment in extractable phosphorus was clearly observed at the sites where it was added in both the palm swamp and the mixed forest sites (Site $\times$ $Phosphorus_{add}$: $F_{1,56} = 1.8$, $P > 0.05$); however, the increment in N was only observed at the mixed forest site (Site $\times$ $Nitrogen_{add}$: $F_{1,28} = 12.23$, $P < 0.01$). Without the addition of phosphorus, microbial phosphorus was equivalent to 90 to 94 % of the total readily-extractable phosphorus (extractable + microbial); in contrast, microbial phosphorus accounted for only *ca.* 41 % of the total readily-extractable phosphorus in the locations were phosphorus was applied (Ext/Mic $\times$ $Phosphorus_{add}$: $F_{1,56} = 24.6$, $P < 0.001$) (Fig. 4.6c,d). Without the addition of nitrogen, the microbial nitrogen represented 50 to 70 % of the total dissolved nitrogen. After nitrogen was added, microbial nitrogen represented 14 to 65 % of the total dissolved nitrogen whilst the extractable nitrogen represented 34 to 85 % (Ext/Mic $\times$ $Nitrogen_{add}$: $F_{1,28} = 7.3$, $P < 0.05$) (Fig. 4.6e,f). The alteration of the extratable/microbial nitrogen ratios was only observable at the mixed forest (Site $\times$ Ext/Mic $\times$ $Nitrogen_{add}$: $F_{1,28} = 5.04$, $P < 0.05$). Nitrate concentrations in peat did not vary significantly with the treatment nor between the sites ($Nitrogen_{add}$: $F_{1,24} = 4$, $P > 0.05$; Site: $F_{1,8} = 0.03$, $P > 0.05$) (Fig. 4.7a,b). Ammonium increased across the sites where nitrogen was added ($Nitrogen_{add}$: $F_{1,24} = 5.14$, $P < 0.05$) and no difference was observed between the sites (Site: $F_{1,8} = 4.16$, $P > 0.05$) (Fig. 4.7c,d).

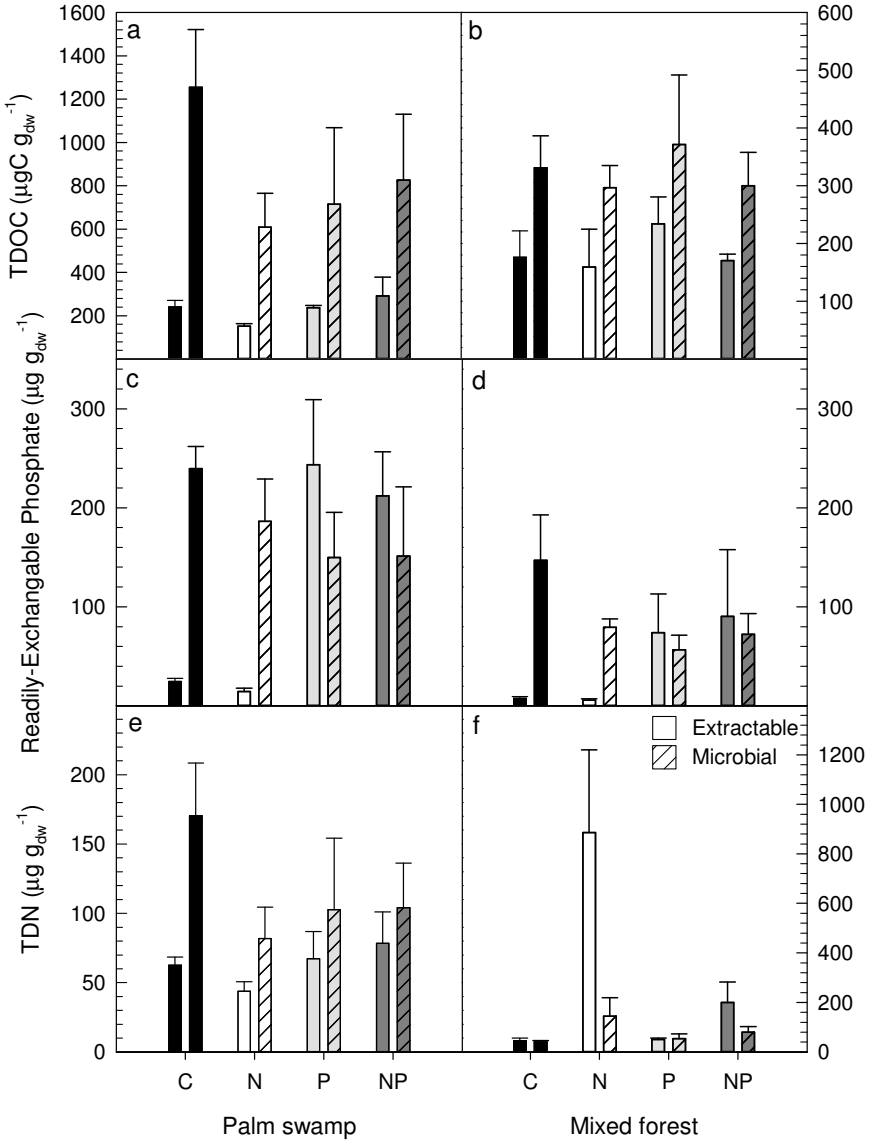

Fig. 4.6 Nutrients addition; Control (C), Nitrogen (N), Phosphorus (P) and Nitrogen + Phosphorus (NP): Extractable and microbial a,b) Total dissolved organic carbon (TDOC), c,d) readily-exchangeable phosphate and e,f) total dissolved nitrogen. Peat samples were collected at the surface, five months after nutrients addition. Statistical analyses are presented in text.

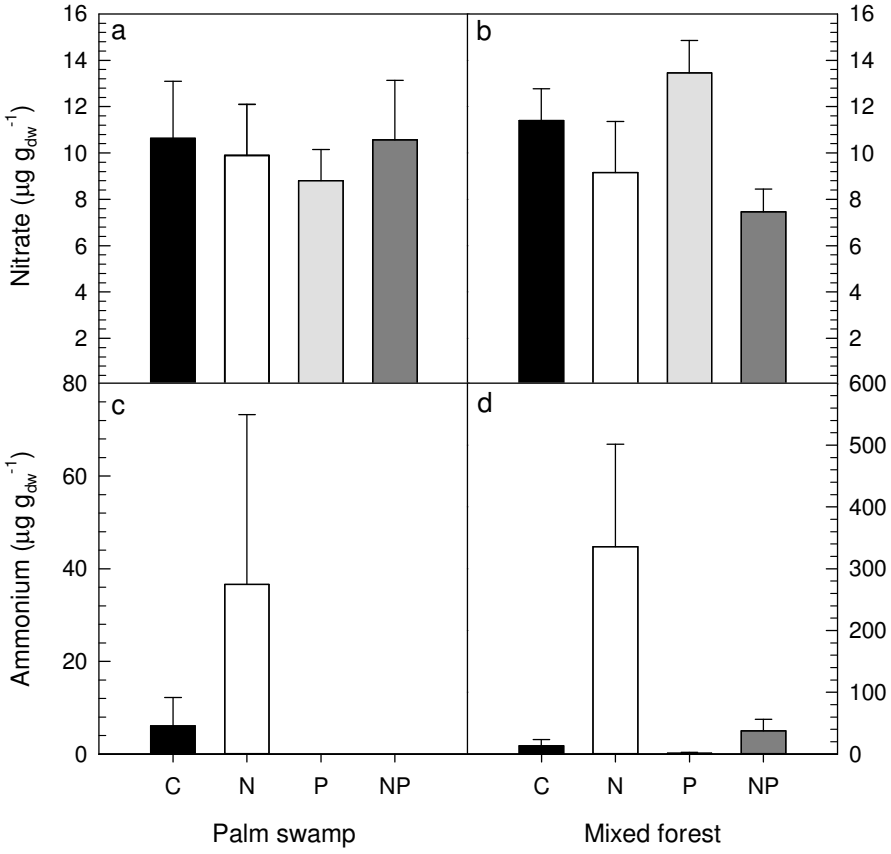

Fig. 4.7 Nutrients addition; Control (C), Nitrogen (N), Phosphorus (P) and Nitrogen + Phosphorus (NP): a,b) nitrate and c,d) ammonium. Peat samples were collected at the surface, five months after nutrients addition. Statistical analyses are presented in text.

4.3.5.2 Enzymatic activity

The addition of phosphorus to the peat increased the activity of phosphomonoesterase ($\text{Phosphorus}_{\text{add}}$: $F_{1,9} = 4.93$, $P < 0.05$) (Fig. 4.8 a,b); in contrast, the addition of nitrogen decreased its activity ($\text{Nitrogen}_{\text{add}}$: $F_{1,9} = 6.97$, $P < 0.05$) (Fig. 4.8a,b). When phosphorus was added together with nitrogen, the activity of phosphomonoesterase was no longer enhanced. Phosphomonoesterase was more active in the mixed forest site than at the palm forest site (Site: $F_{1,4} = 58.28$, $P < 0.01$) (Fig. 4.8a). The activity of phosphodiesterase did not vary significantly with the addition of nutrients, nor across the sites (Fig. 8 b). Arylsulfatase activity decreased with the addition of phosphorus ($\text{Phosphorus}_{\text{add}}$: $F_{1,12} = 5.72$, $P < 0.05$). The addition of nitrogen increased arylsulfatase activity at the palm swamp site, but this increment was not observed at the mixed forest site (Site $\times$ $\text{Nitrogen}_{\text{add}}$: $F_{1,12} = 5.5$, $P < 0.05$) (Fig. 4.8 c). The activity of β-glucosidase did not vary across sites (Fig. 4.8d).The addition of nitrogen increased the activity of β-glucosidase at the palm swamp but not at the mixed forest (Site $\times$ $\text{Nitrogen}_{\text{add}}$: $F_{1,12} = 4.03$, $P < 0.05$). In contrast, the addition of phosphorus increased the activity of β-glucosidase at the mixed forest but not at the palm swamp (Site $\times$ $\text{Phosphorus}_{\text{add}}$: $F_{1,12} = 14.19$, $P < 0.01$). The activity of N-acetyl-β-glucosaminidase was not affected by either the nutrient addition or different across sites (Fig. 4.8e).

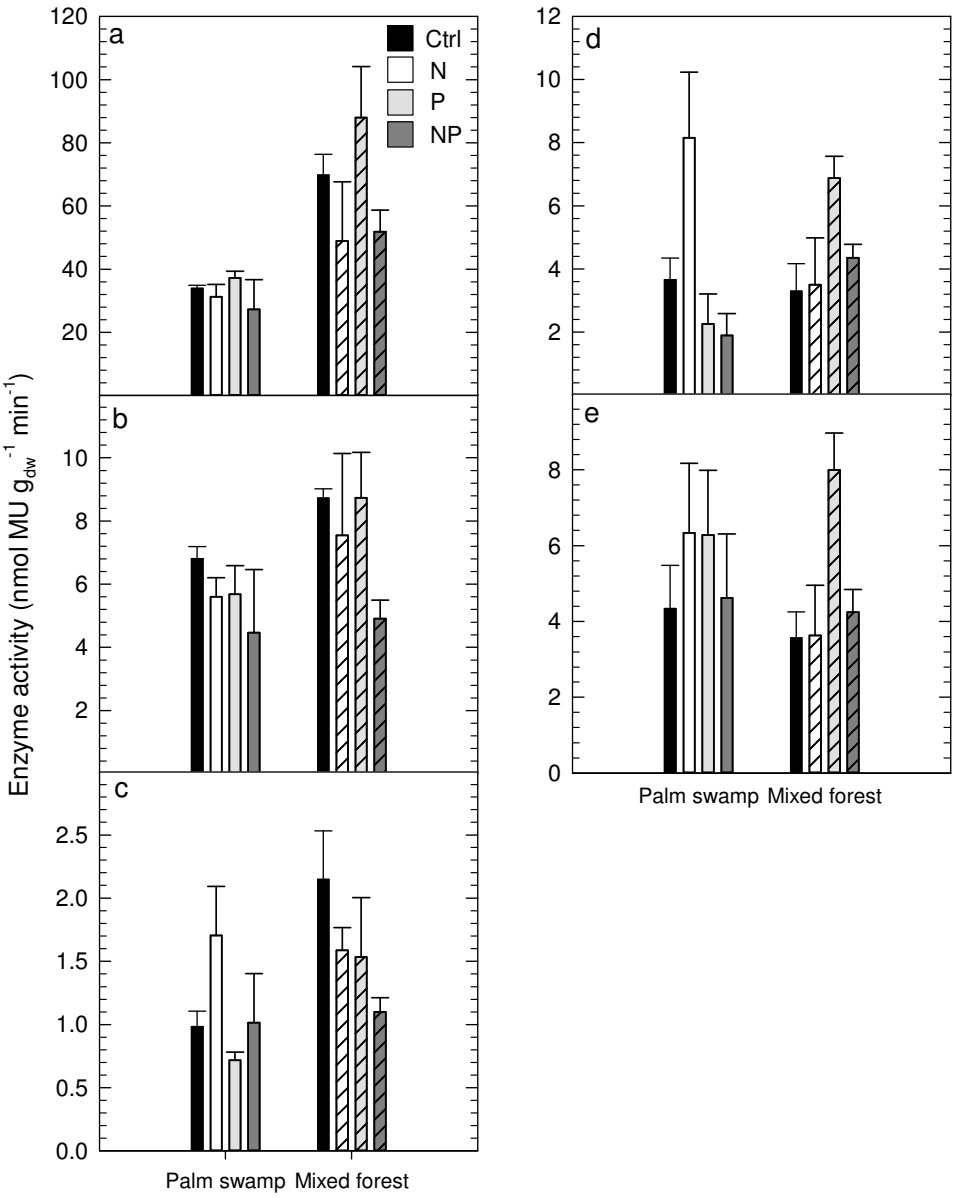

Fig. 4.8 Hydrolytic enzymes activity (nmol MU g_{dw}^{-1} min^{-1}): a) Phosphomonoesterase (MUP), b) Phosphodiesterase (BisMUP), c) Arylsulfatase (MUS), d) β-glucosidase (MUBG) and e) N-acetyl-β-glucosaminidase (MUNA). Samples were taken 5 months after nutrient addition. Nutrient treatment are: Control (Ctrl), Nitrogen (N), Phosphorus (P) and Nitrogen + Phosphorus (NP).

4.3.5.3 Nutrient addition: Litter decomposition and GHG fluxes

The magnitude of decomposition varied significantly among tissues and with the incubation depth (surface and belowground). Mass loss across *R. taedigera* and *C. panamensis* tissues was consistent with those previously reported in this chapter (Fig. 4.9; Fig. 4.10). Nitrogen increased the decomposition of both *R. taedigera* and *C. panamensis* leaves belowground (Fig. 4.9d; Fig. 4.10d). However, this effect was no longer observed when nitrogen was applied together with phosphorus. Though not significant, phosphorus decreased the mas loss of *R. taedigera* and *C. panamensis* leaves belowground (Fig. 4.9d; Fig. 4.10d). CO_2, CH_4 and N_2O fluxes did not vary significantly with the nutrient addition (Fig. 4.11). In contrast, a significant difference was observed between the sites with different phasic communities (palms swamp and mixed forest). CO_2 and N_2O fluxes were highest at the palm swamp site where the water table was below the surface (Fig. 4.11a,c). In contrast, CH_4 fluxes were highest at the mixed forest site where the water table was above the surface (Fig. 4.11b).

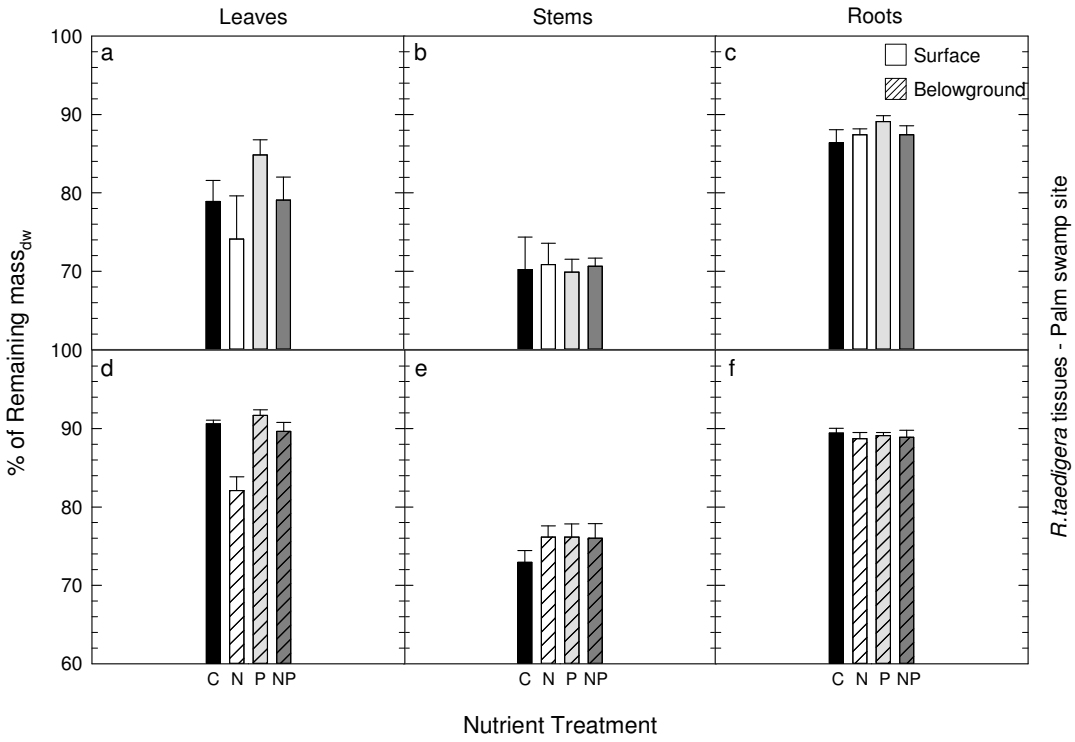

Fig. 4.9 Effect of nutrient addition (Control (C), Nitrogen (N), Phosphorus (P) and Nitrogen + Phosphorus (NP)) on the *in situ* % of remaining mass of *R. taedigera* litter after 5 months. Figures a,b and c correspond to litter decomposed in the surface (0 m depth), whilst d, e and f to litter decomposed belowground (0.5 m depth). REML output are:

Tissue: $F_{2,215} = 121.12$, $P < 0.001$;
Surface/Belowground : $F_{1,215} = 38.88$, $P < 0.001$;
Treatment: $F_{3,215} = 3.14$, $P < 0.05$;
Tissue × Surface/Belowground : $F_{2,215} = 7.33$, $P < 0.001$;
Tissue × Treatment: $F_{6,215} = 2.97$, $P < 0.01$;
Surface/Belowground × Treatment: $F_{3,215} = 0.19$, $P > 0.05$;
Tissue × Surface/Belowground × Treatment: $F_{6,215} = 0.44$, $P > 0.05$

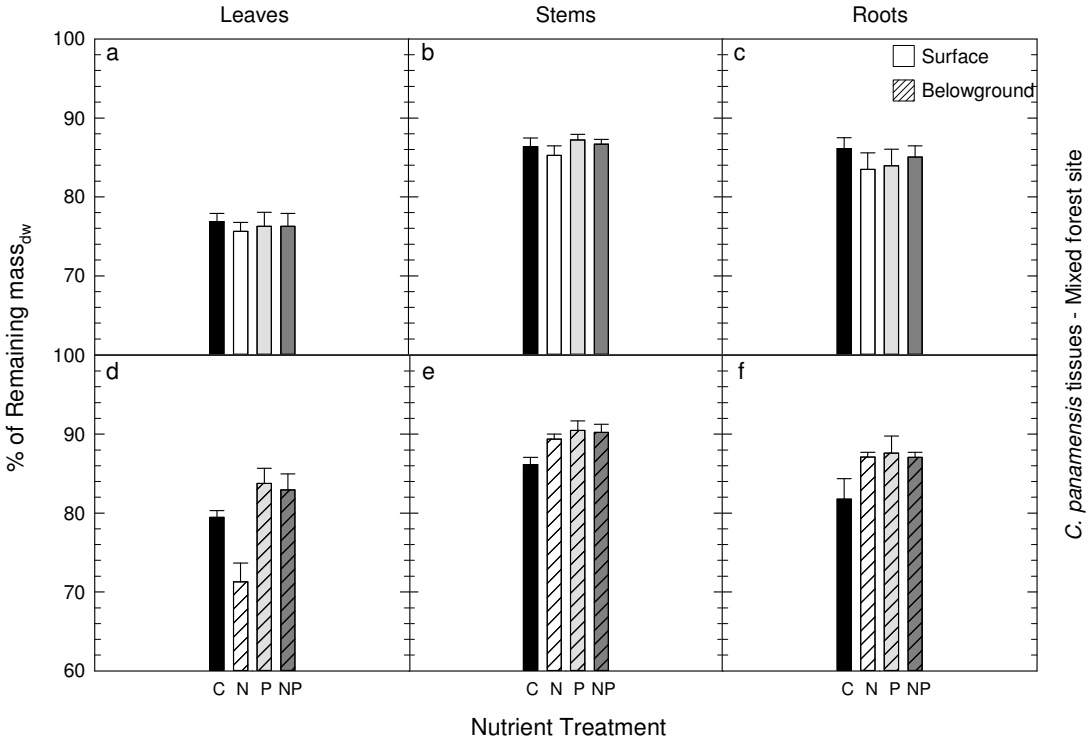

Fig. 4.10 Effect of nutrient addition (Control (C), Nitrogen (N), Phosphorus (P) and Nitrogen + Phosphorus (NP)) on the *in situ* % of remaining mass of *C. panamensis* litter after 5 months. Figures a,b and c correspond to litter decomposed in the surface (0 m depth), whilst d, e and f to litter decomposed belowground (0.5 m depth). REML output are:

Tissue: $F_{2,209} = 95.21$, $P < 0.001$;
Surface/Belowground : $F_{1,209} = 15.33$, $P < 0.001$;
Treatment: $F_{3,209} = 5.48$, $P < 0.001$;
Tissue × Surface/Belowground: $F_{2,209} = 0.75$, $P > 0.05$;
Tissue × Treatment: $F_{6,209} = 2.38$, $P < 0.05$;
Surface/Belowground × Treatment: $F_{3,209} = 4.23$, $P < 0.01$;
Tissue × Surface/Belowground × Treatment: $F_{6,215} = 3.14$, $P < 0.01$

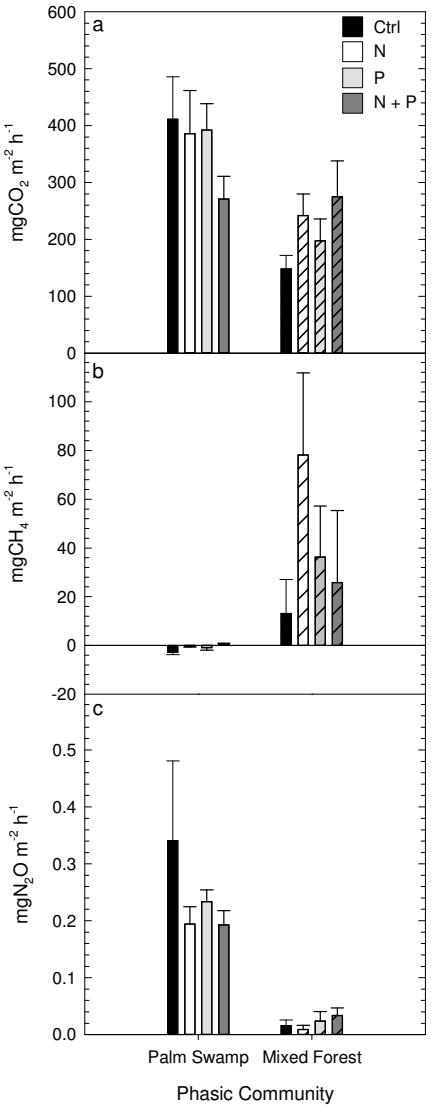

Fig. 4.11 CO_2, CH_4 and N_2O emissions from fertilized plots at Palm swamp and Mixed forest sites; emissions were measured 5 months after peat was fertilized. Nutrient treatment are: Control (Ctrl), Nitrogen (N), Phosphorus (P) and Nitrogen + Phosphorus (NP). Water table was below the surface at the palm swamp whilst it was above the surface at the mixed forest. REML outputs are:

a) CO_2 (mg m^{-2} h^{-1})
Phasic community: $F_{1,18} = 8.36$, $P < 0.01$
Treatment: $F_{3,51} = 0.34$, $P > 0.05$
Phasic community × Treatment: $F_{3,51} = 2.66$, $P = 0.05$
b) CH_4 (mg m^{-2} h^{-1})
Phasic community: $F_{1,16} = 9.22$, $P < 0.01$
Treatment: $F_{3,50} = 1.23$, $P > 0.05$
Phasic community × Treatment: $F_{3,50} = 1.23$, $P > 0.05$
c) N_2O (mg m^{-2} h^{-1})
Phasic community: $F_{1,18} = 26.81$, $P < 0.001$
Treatment: $F_{3,52} = 0.98$, $P > 0.05$
Phasic community × Treatment: $F_{3,52} = 0.89$, $P > 0.05$

4.4 Discussion

In support of our hypotheses i and ii, we demonstrated that the distinct tissues of the two arborescent plant species studied here have different decomposition rates (Fig. 4.3; Table 4.3). This is consistent with previous studies in both temperate (Daubenmire *et al.* 1963) and tropical (Ewel 1976) ecosystems, showing that decomposition rates vary significantly among plant species. The difference has been proposed to be related to the original litter chemical composition, for instance to the amount of carbon, nitrogen and lignin in the litter (Hobbie 2005; Melillo *et al.* 1982; Berg 2000; Meier *et al.* 2008). Litter with high nitrogen but low lignin content has been found to decompose faster than litter with low nitrogen and high lignin content (Melillo *et al.* 1984; Valiela *et al.* 1984; Singh *et al.* 1977). We found that *R. taedigera* litter, which have higher nitrogen content than *C. panamensis* (Table 4.2), decayed faster than *C. panamensis* litter when decomposition occurred at the surface (Fig. 4.3). In contrast, *R. taedigera* litter which have higher lignin content than *C. panamensis* litter, decomposed slower than *C. panamensis* litter when decomposition occurred belowground (Fig. 4.3). This suggests that at the surface, decomposition is faster in litter with higher nitrogen content (*i.e. R. taedigera* litter), irrespectively of the lignin content. In contrast, decomposition belowground is slower in litter with high lignin content (*i.e. R. taedigera*), as lignin is highly recalcitrant under anaerobic conditions. The substantial reduction in lignin degradability is due to the fact that ligninolytic microorganisms require oxygen to efficiently depolymerize and solubilize lignin (Zeikus 1981).

Different tissue type (leaves, stems and roots) presented contrasting decomposition rates as well (Fig. 4.3; Table 4.3). In addition, decomposition was significantly slower belowground than at the surface, reflecting the importance of the redox regime on the litter decomposition (aerobic-surface and anaerobic-belowground conditions) (Valiela *et al.* 1984). In our study, roots presented the lowest decomposition rates among tissues both at the surface (*R. taedigera*: 0.59 $\pm$ 0.04 y^{-1}; *C. panamensis*: 0.45 $\pm$ 0.01 y^{-1}) and belowground (*R. taedigera*: 0.13 $\pm$ 0.01 y^{-1}; *C. panamensis*: 0.17 $\pm$ 0.005 y^{-1}). This is consistent with studies reporting roots decomposing slower than leaves (Taylor *et al.* 1991; Aber et al. 1990; Bloomfield *et al.* 1993), but contrasting with studies reporting roots decomposing faster than leaves (Seastedt 1988; Seastedt *et al.* 1992; Ostertag *et al.* 1999). This discrepancy about roots having either faster or slower decomposition rates that leaves may play a crucial role in peat formation; where plants

producing highly recalcitrant roots contribute the most to peat formation in tropical ecosystems (Chimner *et al.* 2005; Silver *et al.* 2001; Dommain *et al.* 2010; Hedges *et al.* 1985). The decomposition rates of roots at the surface shown here are consistent with those previously reported for wood and roots in other tropical ecosystems ranging from 0.33 to 1.49 y^{-1} (Silver *et al.* 2001; Chimner *et al.* 2005; Scowcroft 2009; Cusack *et al.* 2009). In contrast, the decomposition rates of roots belowground are so low that are comparable to those reported for wood and roots in temperate ecosystems (Trofymow *et al.* 2002; Tripathi *et al.* 2006). The low decomposition rates of roots at the surface and belowground can be attributed to their relative high lignin content in comparison with the leaves and stems (Table 4.2).

Through the comparison of the molecular composition of peat and the different litter tissues (leaves, stems and roots), we demonstrated that roots and stems have a similar composition to the peat material accumulated in deeper layers (Fig. 4.4). Thus, if peat is made of undecayed plant material that accumulates through time in layers, the evidence presented here indicates that roots and stems are the main components of tropical peatlands; this is consistent with previous studies (Chimner *et al.* 2005; Esterle *et al.* 1994).

Our third hypothesis was supported by the evidence obtained from the translocation experiment (Fig. 4.5). Autochthonous litter decomposed faster than allochthonous litter, suggesting an specifically adapted microbial community to decompose the predominant type of litter at certain site (Gholz *et al.* 2000; Hunt *et al.* 1988; Zhou *et al.* 2008; Mayor *et al.* 2006; Freschet *et al.* 2012). It has been suggested that plants might have a symbiotic relationship with the microbial communities in the soil to keep nutrient mineralization low to avoid competition from fast-growing deciduous species (Cornelissen *et al.* 1999). This could be even more important in tropical forests, where highly competitive evergreen species are dominant and a dynamic vegetation succession has been recorded in the peat profile (Phillips *et al.* 1997). However, Makkonen *et al.* (2012) did not find evidence to support the hypothesis of strong adaptation of the decomposers community to a particular type of litter, instead they found a highly adaptable community of decomposers to different litter sources. Previous studies in the CPD have shown shifts in soil microbial communities along the nutrient gradient of the peat dome (Troxler *et al.* 2012); it is plausible that these differences in the microbial communities are related to the autochthonous-allochthonous litter

effect described above. The higher amounts of phosphorus at the palm swamp in comparison with the mixed forest is consistent with the nutrient gradient previously described at the CPD; with phosphorus limitation increasing towards the centre of the peat dome (Sjögersten *et al.* 2011; Cheesman *et al.* 2012; Troxler 2007). The addition of nutrients significantly increased the availability of nitrogen and phosphorus in the treated plots. Under pristine conditions, above 90 % of the readily extractable phosphorus was retained within the microbial biomass; suggesting that microorganisms might exert a strong influence in the phosphorus dynamics of the ecosystem (Turner *et al.* 2013b), and consequently in the ecosystem primary productivity (Rejmánková 2001). The amount of phosphorus that remained after 5 months was higher at the palm swamp than at the mixed forest, but the amount of nitrogen was significantly lower at the palm swamp in comparison with the mixed forest (Fig. 4.6 c,d,e,f). This may be related to a high consumption of nitrogen through the extensive root mat developed by *R. taedigera* (Hoyos-Santillan, personal observation). Indeed, *R. taedigera* has higher amounts of root biomass at the upper meter of the peat profile than the mixed forests with *C. panamensis* (Wright *et al.* 2011).

The activity of hydrolytic enzymes shown here are within the ranges reported in previous studies at the CPD (Sjögersten *et al.* 2011) (Fig. 4.8). The phosphomonoesterase and phosphodiesterase activity was higher at the mixed forest, suggesting a higher phosphorus limitation at the mixed forest (Sjögersten *et al.* 2011). However, phosphomonoesterase activity was increased by the addition of phosphorus (Fig. 4.8a), this contrast with previous studies reporting that phosphorus addition in soil supresses the enzyme activity (Rejmánková *et al.* 2008; Olander *et al.* 2000; Sjögersten *et al.* 2011; Nannipieri *et al.* 2011). This suggests up-regulation of the phosphomonoesterase, triggered by the addition of phosphate. The activity of the enzymes involved in the decomposition of large plant-derived polymers, *i.e.* β-Glucosidase and N-acetyl-β-glucosaminidase, was enhanced by the addition of nitrogen and phosphorus at the palm swamp and the mixed forest respectively (Fig. 4.8d,e); indicating a possible limitation of the organic matter decomposition by nitrogen at the palm swamp and by phosphorus at the mixed forest. The lower activity of arylsulfatase at the palm swamp site is related to a gradient of sulfate content in the surface peat, decreasing from the coast to the peat dome. The GHG emissions did not vary neither with the nutrients addition nor in relation to the enzymatic activity but by the water table position at the sites. The water table located below the surface at the palm swamp increased the

in situ surface CO_2 and N_2O emissions but reduced the CH_4 emissions. At the mixed forest, the water table above the peat surface increased the CH_4 emissions but reduced the CO_2 and N_2O emissions. This is consistent with previous studies assessing the effect of the water table on GHG emissions *in situ* (Moore *et al.* 1989; Chimner *et al.* 2003; Blodau *et al.* 2004; Couwenberg *et al.* 2009; Hirano *et al.* 2008).

Our data did not fully support our fourth hypothesis. Nitrogen only significantly increased mass loss of leaf litter belowground (Fig. 4.9d and Fig. 4.10d). Our results are contrasting with those reporting an increase in the decomposition of litter when nitrogen and phosphorus were added (Liu *et al.* 2006); in most cases we observed a decrease of the mass loss when both nutrients were added together. Studies regarding the effect of nitrogen on the decomposition of litter are contradictory and nitrogen addition has been reported to either increase (Hobbie 2000; Hobbie 2005) or decrease (Magill *et al.* 1998; Fog 1988) litter decomposition. The increase in decomposition has been proposed to be related to the stimulation of the microbial decomposers community in soil (Berg 1986). The decrease in decomposition has been suggested to be due to the inhibition of the production of fungal ligninolytic enzymes (Keyser *et al.* 1978; Tien *et al.* 1990; Hobbie 2000) or a microbial- mediated delay in litter decomposition (nitrogen mineralization) as long as allochthonous nitrogen is abundant in the soil (Fog 1988). It has been suggested that litter chemical composition, particularly carbon quality, is a stronger control of decomposition than nutrients (Hobbie 2000). This could explain why we were only able to observe an effect of the addition of nutrient on the relatively high quality litter, *i.e.* leaves. Furthermore, the effect of nitrogen addition only significantly increased the decomposition of leaves belowground. This suggests that: i) the effect exerted by the redox regime is stronger than the nitrogen addition and that ii) microbial communities developed under different redox regimes are limited by different nutrients throughout the peat profile. As the decomposition at the surface varied with tissue, a plausible hierarchy on the control of litter decomposition explored here (in descending order) is: i) redox regime, ii) litter composition and iii) external nutrient availability. Although the controlling factors presented here are individually important, a more dynamic control system with interactions among factors is more plausible (Aerts 1997).

Further research is needed in order to develop accurate models to predict the consequences of land use change and climate change on the litter decomposition at

the tropics. In this study we observed that roots are among the main components of tropical peat and that their decomposition is 3 to 5 times faster under aerobic conditions matching the decomposition rates of leaves. Thus, as subsidence progresses either due to the predicted reductions in the annual precipitation in the Caribbean related to climate change (Solomon *et al.* 2007) or as consequences of LUC (Couwenberg *et al.* 2009; Couwenberg *et al.* 2011), roots decomposition will play a central role defining if tropical peatlands act as carbon sinks or sources.

Chapter 5

Role of vegetation as control of greenhouse gases emissions in lowland tropical peatlands

5.1 Introduction

Greenhouse gases (GHG) emissions have become a focal topic in the framework of global warming due to their capacity to alter the radiative balance in the atmosphere (Solomon *et al.* 2007). Peatlands are wetlands where organic matter (OM), mainly derived from vegetation, was or is being accumulated due to an imbalance between production and decay of OM (Laiho 2006). Peatlands represent a dual system that can act as both a sink and a source of GHG from/to the atmosphere (Jaenicke *et al.* 2008; Rieley *et al.* 2008a). CO_2, CH_4 and N_2O represent some of the most important GHG that are interchanged between peatlands and the atmosphere (Ueda *et al.* 2000; Conrad 1996); each of them having a global warming potential of 1, 28 and 298 respectively (Solomon *et al.* 2007; IPCC 2013). Wetlands (peatlands among them) are estimated to be the most important natural source of CH_4 to the atmosphere (Solomon *et al.* 2007), emitting 0.1-0.23 Gt of CH_4 per year equivalent to 17 to 40 % of the total global CH_4 emissions (Laanbroek 2010; Solomon *et al.* 2007). Additionally, soil respiration in terrestrial ecosystems is estimated to emit *ca.* 68 GtC per year (Raich *et al.* 1992), which is high in comparison with the *ca.* 9.2 GtC estimated for the 2010 global fossil-fuel carbon emissions (Boden *et al.* 2013). In contrast, it has been estimated that peatlands globally hold *ca.* 610 GtC belowground (Page *et al.* 2011); this is equivalent to 84 % of the total carbon in the atmosphere (Falkowski 2000). Though peatlands in temperate, subarctic and boreal ecosystems have been thoroughly studied, tropi-

cal peatlands have only recently been recognized as a relevant component of the global carbon cycle (Page *et al.* 2011; Wright *et al.* 2013b).

Hitherto several environmental variables have been recognized as controllers of GHG emissions in peatlands: water table position (Moore *et al.* 1989; Chimner *et al.* 2003; Blodau *et al.* 2004; Couwenberg *et al.* 2009; Hirano *et al.* 2008), temperature (Macdonald *et al.* 1998; Raich et al. 1992), microtopography (Bubier *et al.* 1993), redox potential (Eh) (Knorr *et al.* 2009), oxygen availability (Watson *et al.* 1997), salinity (DeLaune *et al.* 1983; DeLaune 2007), pH (Dunfield *et al.* 1993) and nutrients availability (Sjögersten *et al.* 2011). These environmental variables have a close interrelationship with biotic variables such as: plant-mediated gas transport (Grosse *et al.* 1996; Thomas *et al.* 1996; Pangala *et al.* 2013b; Seiler *et al.* 1983), labile substrate input (Silvola *et al.* 1996) and nutrient bioaccumulation (Page et al. 1999). It has been recognized that aquatic rooted vegetation and trees transport CH_4 to the atmosphere, contributing with up to 95 and 87 % respectively of the total ecosystems CH_4 emissions (Dacey *et al.* 1979; Bartlett *et al.* 1988; Sebacher *et al.* 1985; Morrissey *et al.* 1993; Pangala *et al.* 2013b). For this reason, vegetation has been suggested as an important interface between the soil and the atmosphere GHG (Dacey *et al.* 1979; Bartlett *et al.* 1988).

However, establishing correlations between GHG emissions and abiotic and biotic variables is difficult as these variables are closely interrelated (Joabsson *et al.* 1999). For example, water table is directly related to the Eh and oxygen availability in the peat matrix (Knorr *et al.* 2009; Blodau *et al.* 2004). A further illustration is air and peat temperature which varies diurnally with solar radiation. Within the peat matrix, temperature affects the solubility of gases in aqueous solutions (Himmelblau 1960), microbial activity (Zeikus *et al.* 1976) and the plant-mediated transport of gases by internal pressurization and convective gas flow (Konnerup *et al.* 2010). Indeed, plant-mediated interchange of gas with the atmosphere has been found to vary diurnally as it is linked to efflux mechanisms controlled by plant transpiration processes (Kozuchowski *et al.* 1978; Dacey *et al.* 1979; Bartlett et al. 1988; Sharkey *et al.* 1991). The variables mentioned above can be antagonist, functioning both as positive or negative feedbacks to GHG emissions, *e.g.* methanogenesis inhibition by plant-mediated oxygen input (King *et al.* 1978; Armstrong *et al.* 1991; De Bont et al. 1978) and methanogenesis enhancement by root exudates (Chanton *et al.* 1995; Holzapfel-Pschorn *et al.* 1986; Kuzyakov *et al.* 2000).

Despite their importance in the global carbon cycle with an estimated carbon pool of ≈ 88.6 Gt, tropical peatlands are highly vulnerable to anthropogenic degradation (Page *et al.* 2011; Murdiyarso *et al.* 2010). For example, tropical peatlands in South East Asia (SEA) are commonly deforested, drained and burned for agricultural use (Hooijer *et al.* 2010). Land use change (LUC) affects most of the variables that control GHG emissions dramatically affecting carbon fluxes from peat to the atmosphere (Jauhiainen *et al.* 2008; Jauhiainen *et al.* 2005). It has been estimated that due to degradation of peatlands in SEA *ca.* 0.17 Gt C are released every year to the atmosphere (Couwenberg *et al.* 2009). Although LUC is widespread in the Neotropics (Wassenaar *et al.* 2007), information about its consequences on GHG emissions is scarce (Keller *et al.* 2005). To date, important gaps in our knowledge of the role of tropical peatlands on the global carbon cycle remain. The actual extent and depth of tropical peatlands is still unclear and debated, the rate of degradation is unknown on a global scale and our understanding of their role in the global carbon cycle remains limited. One of the fundamental gaps lies in the role that tropical vegetation plays as interface between the atmosphere and the peat matrix. Still is not possible to accurately predict GHG emissions from large areas of peatlands based on neither the type of tropical vegetation nor in the measurement of environmental variables (Couwenberg *et al.* 2011).

Neotropical peatlands are commonly dominated by palms or mono-specific hardwood stands representing two distinct phasic communities. For example, the *Raphia taedigera* palm and the *Campnosperma panamensis* hardwood tree form large mono-specific stands in swamps with contrasting characteristics across Central and South America (Urquhart 1999; Phillips *et al.* 1997). For this reason, we explored several aspects of the role of these types of vegetation on GHG emissions, such as the inhibition of CH_4 by plant oxygen input and the spatial and temporal variations on GHG emissions in relation to two distinct tropical phasic communities. We hypothesized that: i) *R. taedigera* reduces the CH_4 emissions due to roots oxygen input; ii) Removal of *R. taedigera* will reduce CO_2 emissions and increase CH_4 emissions; iii) *in situ* CH_4 emission is lower in *R. taedigera* (palms swamp) sites in comparison with *C. panamensis* (mixed forest) sites; and iv) in situ CH_4 emissions are higher in flooded patches of the peatlands irrespectively of the phasic community.

In order to test these hypotheses a combination of *in situ* and *ex situ* experiments were performed in the north-western region of Panama's Caribbean coast. In addition to these experiments, the loss of one of our plots due to subsistence agriculture practices offered an exceptional opportunity to monitor the effect of LUC (slash and burn agricultural practices) on GHG emissions.

5.2 Materials and Methods

5.2.1 Study sites

A full description of the study area is presented in Chapter 2. Six sites were selected for this study. Sites were selected with respect to the presence of two specific phasic communities (palm swamp and mixed forest). A vegetation survey was undertaken in order to classify the phasic communities in the peatlands; the mono-dominance was defined using the % of basal area (m^2 ha^{-1}). Three sites were dominated by *R. taedigera* (an evergreen canopy forming palm) and three were mixed forests dominated by *C. panamensis* (an evergreen canopy forming hardwood tree) (Table 5.1). Two of the sites are located in the CPD where several studies have been previously carried out (Sjögersten *et al.* 2011; Wright *et al.* 2011; Troxler 2007; Cheesman *et al.* 2012). The additional four sites were selected following satellite imagery analysis, aerial reconnaissance of the area and field campaigns held in April 2010 (Table 5.1).

All sites were freshwater with water table fluctuating from + 0.15 to - 0.4 m relative to the peat surface. *R. taedigera* sites had large amounts of leaf litter at the surface, a substantial amount of pneumatophores protruding from the surface and a dense but shallow (1.1 m) fibrous root system (Wright *et al.* 2013b). Shallow water ponds and raised areas (close to each *R. taedigera* colony) are typical components of this sites microtopography. Mixed forest sites dominated by *C. panamensis* are also characterized by large amounts of leaf litter, however pneumatophores were no longer ubiquitous at the surface. *C. panamensis* developed buttress roots (1 m depth) with lenticels (Wright *et al.* 2013b); similar to *R. taedigera* sites the microtopography at the mixed forest sites was heterogeneous characterized by shallow ponds and raised areas.

At each site, permanent 0.1 ha plots were established (20 × 50 m) for characterization of the vegetation, monitoring of physicochemical parameters and gas

flux sampling. Within each plot a water sampling well was installed to measure *in situ* dissolved oxygen, temperature and conductivity; each well consisted of a PVC pipe (ø = 50 mm) with perforations (ø = 10 mm) separated in 50 mm intervals. The pipe was inserted through the peat profile until the mineral bed was reached and was closed at the bottom so water could only enter through the lateral holes.

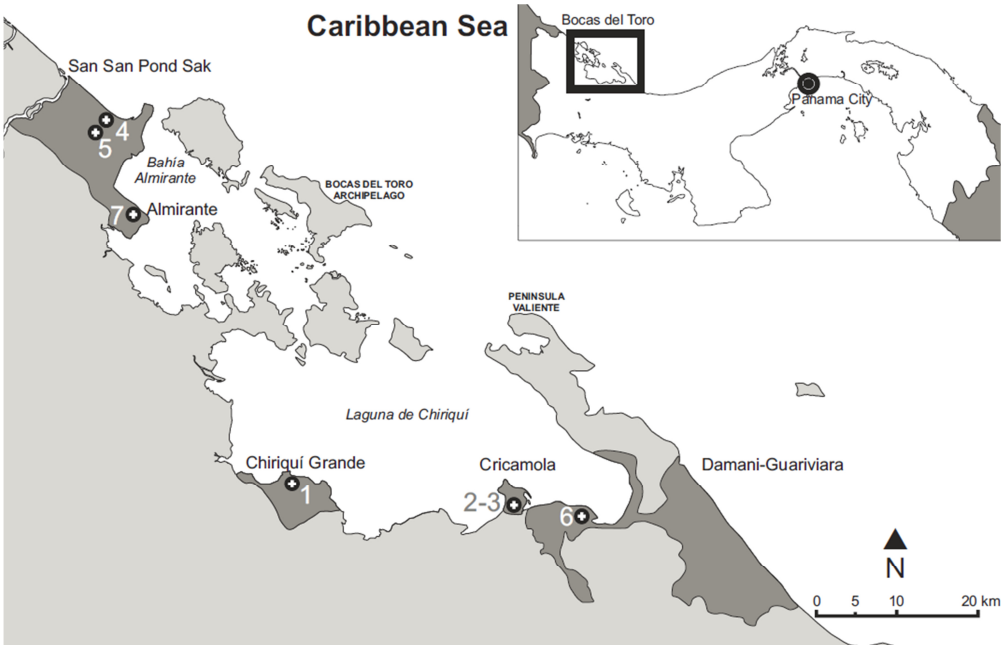

Fig. 5.1 Map of the north western region of the Caribbean coast of the Republic of Panama. Locations of the six study sites are shown and numbered according to Table 1; darker zones correspond to wetlands areas identified from aerial and satellite imagery.

Table5.1: Location of study sites

Site		Coordinates	Distance to coast (m)	Dominant vegetation	% basal area (m^2 ha^{-1})[e]
1	Chiriqui Grande	8°58'28.22"N, 82°07'52.85"W	140	*R. taedigera*	80.5
2	Cricamola River[c]	8°57'17.70"N, 81°54'41.35"W	1400	*R. taedigera*	Deforested
3	Cricamola River[d]	8°57'13.64"N 81°54'43.78"W	1500	*R. taedigera*	70.9
4	San San Pond Sak 1[a]	9°25'29.20"N, 82°24'05.60"W	500	*R. taedigera*	98.9
5	San San Pond Sak 2[b]	9°25'15.00"N, 82°24'14.64"W	1000	*C. Panamensis*	38.7
6	Damani-Guariviara	8°57'02.34"N, 81°49'32.40"W	518	*C. panamensis*	29.8
7	Almirante Bay	9°18'17.46"N, 82°21'07.14"W	200	*C. panamensis*	45.8

[a,b] San San Pond Sak sites 1 and 2 correspond to Sites 1 and 2 respectively from Sjögersten *et al*., 2010

[c] Original plot set in December 2010 and afterwards used for agriculture in March 2011

[d] New plot set in May 2011

[e] Percentage of forest basal area corresponding to the dominant vegetation: Palm swamp-*R taedigera* and Mixed forest-*C. panamensis;* San San Pond Sak data from Sjögersten *et al*., 2010

5.2.2 Vegetation inventories

In each 0.1 ha plot, all stems > 0.1 m in diameter at breast height (1.30 m DBH), where measured, marked, tagged and mapped. The forest structure and tree diversity were characterized by measuring tree height and identifying all measured individuals to the species or genera level, respectively. Diameter measurements were used to estimate species dominance via basal area at the hectare level (BA= m^2 ha^{-1}). However, given the multi-stem colony growth of *R. taedigera*, it is plausible that the BA for this specie is overestimated. Vegetation data for the San San Pond Sak sites were taken from Sjögersten et al.(2010).

5.2.3 Experimental programme

Three approaches were used to explore the role of vegetation on GHG emissions to the atmosphere: i) monitoring of *ex situ* diurnal CO_2 and CH_4 emissions from *R. taedigera* seedlings growing on peat monoliths relative to controls without seedlings, ii) monitoring of *in situ* CO_2, CH_4 and N_2O emissions from the soil surface of an anthropogenically impacted *R. taedigera* palm swamp site compared to an undisturbed site and iii) monitoring of *in situ* CO_2/CH_4 emissions from the soil surface of peatlands with two distinct phasic communities (*R. taedigera* palms swamp and *C. panamensis* dominated mixed forest). In order to conduct an *ex situ* experiment at the Smithsonian Tropical Research Institute station in Bocas del Toro (STRI-BDT), twelve peat monoliths and six *R. taedigera* seedlings were collected within the transect previously studied by Sjögersten *et al.* (2010) (9°25'34.90" N, 82°24'1.80" W). The site where peat monoliths were collected was freshwater (60 µS m^{-1}). Each monolith (ø = 0.21 m, h = 0.5 m) was collected and set up for the experiment in PVC pipes (ø = 0.21 m, h = 0.5 m). PVC pipe was introduced into the ground by carefully cutting with a blade around the pipe which was then manually pushed into the peat. Once the pipe was full of peat the lower section of the core was cut; this allowed retrieving the peat monolith within the pipe with minimal disturbance. Peat monoliths were kept upright and a PVC cap was fixed to the bottom of the pipe. The presence of the first *eophyll* (height of 0.15 to 0.2 m) was the single requisite for the selection of *R. taedigera* seedlings. Seedlings were transplanted into six of the peat monoliths; therefore there were six control peat monoliths (with peat) and six peat monoliths with *R. taedigera* seedlings. Water table was kept 50 mm above peat level simulating field flooded conditions. Experimental units were divided in two random blocks, each having three controls and three *R. taedigera* peat monoliths. Diurnal monitoring

of CO_2 and CH_4 was carried in 4 h intervals across 24 h. Each block was sampled within a single 24 h period on three occasions. Monitoring events were conducted across five months from the time seedlings were transplanted from May 2011 to November 2011. On completion, *R. taedigera* plants were carefully harvested and separated into leaves, stems and roots for gravimetric analysis of biomass.

Due to the anthropogenic disturbance on the plot located at the Cricamola River (March 2011), the effect of slash and burn practices on GHG was explored. For this reason, in addition to the original plot that was set up at the Cricamola River (December 2010), an additional plot was set up in an adjacent intact *R. taedigera* site (May 2011). This plot was located 100 m SW from the anthropogenically impacted site and was used as control. Gas samplings on the original plot were carried out in six occasions across 278 days from the plot set up (App. C). In contrast, gas samplings at the control plot were performed on four occasions across 109 days. Therefore, it was possible to sample before the site was anthropogenically impacted (0 days), when the site's vegetation was cleared (99 days), two days after the site was burned (169 days) and then in three random occasions through rice growth 216, 243 and 278 days after the original plot establishment.

Spatial and temporal variation in CO_2 and CH_4 fluxes in the region with respect to the phasic communities were explored by a monitoring campaign held over 9 months (December 2010 to September 2011). The six sites (Table 5.1) were monitored at different dates in six time blocks (App. C). Time blocks were distributed through the year with the intention of observing temporal fluctuations of GHG. This allowed monitoring GHG emissions under contrasting water table levels. In addition, gas samples were collected from flooded zones (shallow ponds) if present and non-flooded zones within the plot, allowing for the assessment of heterogeneity of GHG emissions as a function of microtopography.

5.2.4 *In situ* gas flux measurements

In situ gas fluxes were determined from the surface of peat in the case of non-flooded zones and on top of the shallow ponds when flooded zones were present. Gas samples were collected between 10:00 and 16:00 hrs on every occasion (App. C).The exact sampling location within the plot was randomly chosen. Gas collection for flux estimation was performed using the closed chamber technique (Sjögersten *et al.* 2011). Plastic chambers had an area of 0.075 m^2 and were *ca.* 0.1 m high, with a total volume of 7 L. Each chamber had a sampling port equipped

with a Suba-Seal® rubber septa (Fisherbrand, Loughborough, UK). Small vegetation and fallen branches were removed before the installation of the chamber. Peat disturbance was avoided as much as possible during the installation of the chambers but slight pressure was applied in order to ensure a tight seal. For each sampling, three chambers were deployed simultaneously not further than 5 m from each other. Once installed and prior to the collection of gas samples, the chamber headspace was homogenised by repeatedly pumping the air within the chamber with a 20 mL syringe equipped with a hypodermic needle. Afterwards, gas samples were collected from each chamber after 0, 2, 10 and 20 min using a 20 mL syringe equipped with a thin needle (25 Gx1'', TERUMO, UK). Gas samples were injected into pre-vacuumed 12 mL borosilicate glass vials sealed with a screw cap-septum (Exetainer; LABCO, UK), leaving each vial with overpressure. All samples were shipped to the University of Nottingham for gas chromatography analysis. Vials were discarded if an overpressure was no longer present (< 5 %, n = 864). CO_2, CH_4, and N_2O concentrations were determined using a single injection system with a 1 mL sample loop that passed the gas sample using N_2 as carrier through a non-polar methyl silicone capillary column (CBP1-W12-100, 0.53 mm I.D., 12 m, 5 mm; Shimadzu UK LTD, Milton Keynes, UK) and porous polymer packed column (HayeSep Q 80/100). Thermal conductivity (TCD) and flame ionization (FID) detectors were used to measure CO_2 and CH_4, respectively; whilst N_2O was measured with an electron capture detector (ECD). Flux calculations were based on the linear accumulation of gases within the closed chamber; therefore gas concentrations that did not follow a linear trend were discarded for the calculation of gas fluxes. CO_2 fluxes within the anthropogenically impacted site (*i.e.* Cricamola River) were also measured using a portable Infrared Gas Analyzer (IRGA; EGM-1, PP Systems, USA) equipped with its own gas sampling chamber (SRC-1; PP Systems, USA).

5.2.5 *Ex situ* gas flux measurements

The closed chamber technique was used in parallel to the *in situ* gas sampling but with larger transparent chambers made of polycarbonate ($\approx$ 15.7 L; ø = 0.2 m, h = 0.5 m). Gas sampling for the determination of diurnal GHG fluxes was done in 4 hr intervals within 24 hr. During each sampling event the chamber was placed on top of the peat monoliths, achieving a tight seal due to the high water table within the PVC pipe. Chambers were equipped with a battery powered fan (50 $\times$ 50 mm) that homogenized the air in the chamber's headspace. Gas samples were taken after 0, 10, 20 and 40 min after the chamber was placed on top of the peat

monoliths. Gas samples were processed as previously described.

5.2.6 Estimation of root respiration

Soil respiration was estimated i) from a combination between *ex situ* and *in situ* CO_2 flux data from San San Pond Sak 1 and ii) from the before and after observation at the LUC impacted plot. For the first approach we assumed that the daylight hours fluxes from *in situ* San San Pond Sak 1 included the whole soil respiration components (Soil respiration = soil organisms respiration + root respiration). Then the *ex situ* flux from the control peat monoliths from San San Pond Sak 1 were subtracted from the *in situ* fluxes considering that the peat monoliths were equivalent to using the trenching technique for estimating root respiration (Root respiration = soil respiration from SSPS1*in situ* – soil respiration from SSPS1 peat monoliths *ex situ*) . The second approach was the subtraction of the LUC CO_2 fluxes (when *R. taedigera* was cleared) from the CO_2 fluxes previous to the LUC (Root respiration at Cricamola = soil respiration before LUC_{day0} – soil respiration after *R. taedigera* was $cleared_{day\ 99}$).

5.2.7 Physicochemical parameters

Simultaneously to the collection of gas samples, dissolved oxygen (DO; ppm) and temperature (°C) in the surface layers of the peat were measured *in situ* at the sampling wells installed within each plot using a portable multiparametric probe (YSI 556 MPS, USA). For the *ex situ* experiment, dissolved oxygen was measured using a DO microprobe (Lazar Research Laboratories Inc., USA) at 0, 20 and 40 mm away from three roots in each peat monolith with *R. taedigera*; measurements were also conducted on the control peat monoliths. Temperature was recorded in the peat monolith using portable thermo-couples with data logging capabilities (Tinytag Talk 2, Tinytag, UK). Diurnal solar irradiance (µmol m^{-2} s^{-1}) was measured with a portable pyranometer (LI-1400, LI-COR, USA).

5.2.8 Peat sampling and characterization

Three soil samples from the peat 0.1 m top layer (0.1 × 0.1 × 0.1 m) were collected from each plot. Samples were wrapped in aluminium foil and placed in plastic boxes for later transportation ($<$ 3 h) to the laboratory at the Smithsonian Tropical Research Institute (STRI), BDT. All samples were refrigerated until shipped to the University of Nottingham.

Water holding capacity (WHC) was determined by gravimetric analysis of the water mass loss of 10 g fresh peat samples after oven drying peat samples at 70 °C for 70 h (Wright *et al.* 2011). Loss on ignition (LOI), as an indirect measurement of soil organic matter content (SOM), was determined by gravimetric analysis of mass loss from dry peat samples placed in the muffle furnace (Weiss-Gallenkamp, Loughborough, UK) for 7 h at 550 °C. Peat pH was determined in a 1:2.5 peat fresh weight (fw)-deionized water solution (pH meter-pH 209, Hanna Instruments, Leighton Buzzard, UK) and conductivity was simultaneously determined from the same solution (Conductivity meter-HI9835, Hanna Instruments, Leighton Buzzard, UK). Total carbon (C), nitrogen (N) and sulfur (S) were determined from 0.5 g_{dw} homogenised peat samples (homogenization was carried out in a Planetary Ball Mill, Retsch-PM400, Castleford, UK) using a total element analyser (Flash EA 1112,CE Instruments, Wigan, UK). Peat ashes from loss on ignition were dissolved in 6M HNO_3 to estimate the peat phosphorus content by spectrophotometry using the molybdate-ascorbic acid method (Andersen 1976).

5.2.9 Statistical analyses

Analysis of variance on gas fluxes was performed using the Residual Maximum Likelihood method (REML). Gas fluxes were transformed ($\log_{10}$) to fulfil the normality requirement of REML. Linear mixed models were used to compare gas production rates. Level of significance of the differences between the fixed effects was estimated by Wald tests using an F distribution. Significance was attributed at $P < 0.05$. For the *ex situ* experiment, the presence of *R. taedigera* was used as fixed factor whilst the specific peat monolith and the sampling date were included as random factors. For the analysis of the effect of land use change (LUC) on gas fluxes, the anthropogenic impact and the sampling dates were used as fixed factors without a blocking design. *In situ* monitoring was analysed by introducing the phasic community and the flooded vs non-flooded area as fixed factors whilst sites and sampling time blocks were used as random factors. Time was used as fixed factor when the analysis was focused on temporal variation. Balanced data was analysed by one-way ANOVAs (*e.g. ex situ* dissolved oxygen and *R. taedigera* tissues). Results through text and graphs are presented as mean ± SE. Relationships between gas fluxes and environmental factors (water table, temperature and dissolved oxygen) were explored using regression analyses. The % of variance accounted by regression statistical models is referred to as σ^2 in text and figures. All statistical analysis were performed in GenStat (VSN International 2011).

5.3 Results

5.3.1 *Ex situ* diurnal CO_2/CH_4 fluxes

Ex situ CO_2 emissions in control peat monoliths did not follow a diurnal pattern ($F_{2,28} = 0.65$, $P > 0.05$) (Fig. 5.2a). In contrast, CO_2 fluxes from peat monoliths with *R. taedigera* showed a concave dial pattern with negative fluxes during daylight (*i.e.* photosynthetic assimilation). This trend was modelled with a quadratic function (CO_2 (mg m^{-2} h^{-1}) = 8.18 × Hr of $Day_{0\text{-}24}{}^2$ – 193.7 × Hr of $Day_{0\text{-}24}$ + 770; $F_{2,44} = 7.96$, $P < 0.001$), that accounted for 23 % of the variance (Fig. 5.2a).

Ex situ CH_4 fluxes in both control and *R. taedigera* peat monoliths were highest during daylight following a convex pattern across the day (Fig. 5.2b). This pattern was also modelled with a quadratic function that presented a significant treatment effect when temperature was added as covariate (Treatment: $F_{1,15} = 5.5$, $P < 0.05$; Quadratic term (x^2): $F_{1,41} = 4.5$, $P < 0.05$). However, when fitting solar irradiance in the model, it absorbed the significant variation previously attributed to the quadratic term in the model (Quadratic term (x^2); $F_{1,34} = 2.59$, $P > 0.05$).

The CO_2 and CH_4 fluxes showed maximum differences between control and *R. taedigera* monoliths during daylight (9:00 to 16:00). CH_4 fluxes during daylight were higher in control peat monoliths in comparison with those with *R. taedigera* (Fig. 5.2c); in contrast with the diurnal pattern, this difference was not significant ($\log_{10}CH_4$ (mg m^{-2} h^{-1}), Treatment: $F_{1,10} = 0.36$, $P > 0.05$). During daylight hours, CO_2 uptake becomes evident by the negative fluxes and significant difference can be observed between control and *R. taedigera* monoliths ($F_{1,36} = 12.34$, $P < 0.001$) (Fig. 5.2c).

During daylight, DO varied significantly depending on the distance relative to *R. taedigera* roots; with highest oxygen concentrations closer to the roots and the lowest (near to zero) when measurements were conducted at 40 mm (Fig. 5.3).

R. taedigera dry weight biomass at the end of the assays was distributed 78 ± 8 % above ground (leaves and stems, 25.7 ± 2.8 g_{dw}) and 19 ± 3 % below ground (roots, 6.2 ± 0.8 g_{dw}) (Fig. 5.4). Alive roots at the end of the experiment occupied in average a volume of 95 ± 9 mL within each peat monolith with *R. taedigera*. This is equivalent to ≈ 0.6 % of the total peat monolith volume.

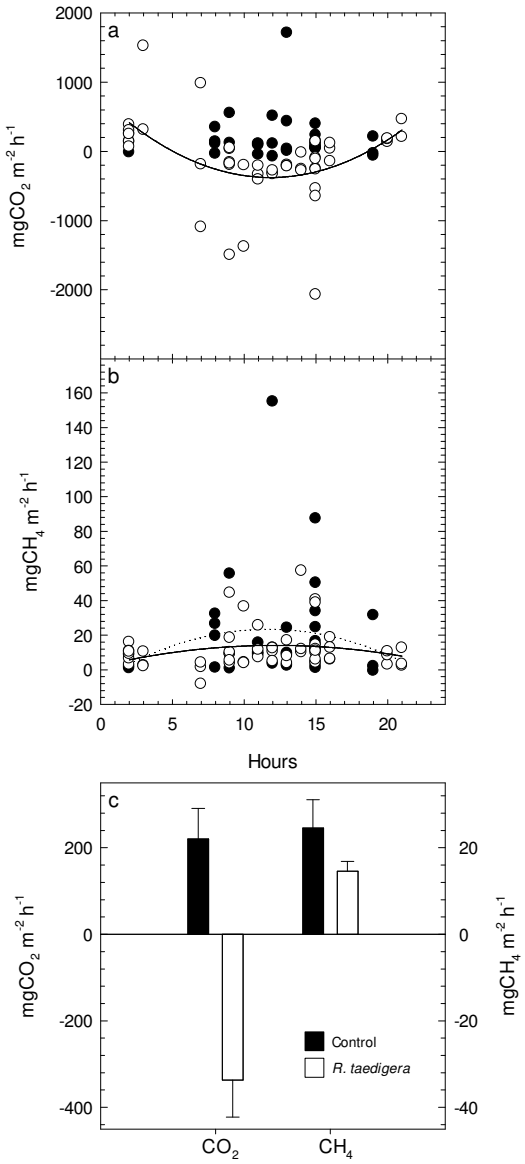

Fig. 5.2 Diurnal fluxes of CO_2 (a) and CH_4 (b) from *ex situ* experiment. Closed symbols correspond to diurnal flux from control monoliths (●) whilst open symbols correspond to monoliths with *R. taedigera* (○). Dotted (···) and solid (—) lines represent the quadratic models describing the fluxes from control and *R. taedigera* monoliths respectively. Mean ± SE of CO_2 and CH_4 fluxes from daylight hours (9:00 to 16:00) are presented in figure c. Statistical analyses are presented in text.

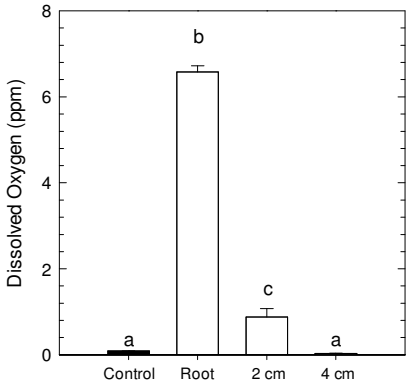

Fig. 5.3 Dissolved oxygen concentration in relationship to distance from *R. taedigera* root. Tukey multiple comparison test are indicated by letters; different letters indicate a significant difference. One-way ANOVA output is: Dissolved oxygen (ppm), Distance from root: $F_{3,200} = 663$, $P < 0.001$.

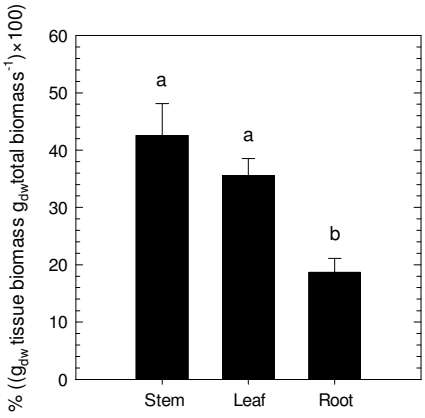

Fig. 5.4 Biomass (dry weight) from different tissues of *R. taedigera* plants used for *ex situ* experiment. Tukey multiple comparison test are indicated by letters; different letters indicate a significant difference. One-way ANOVA output is: Biomass (%), Tissue: $F_{2,10} = 19.76$, $P < 0.001$.

5.3.2 Land use change effect on CO_2 and CH_4 fluxes

After the LUC, DO declined in the peat matrix of the impacted plot and was consistently higher in the control plot (Fig. 5.5a). Temperature in the peat surface was also affected by the anthropogenic impact; temperature was significantly higher in the surface of peat at the impacted plot (Fig. 5.5b). Once rice was seeded, its height was registered at each gas sampling (Fig. 5.5c). $Log_{10}CO_2$ flux was significantly higher in the control plot and varied significantly through time (Fig. 5.6a). The $log_{10}CH_4$ fluxes were significantly lower at the control plot through time; however $log_{10}CH_4$ flux values from the impacted plot declined to almost converge with those from the control plot at the end of the study period (Fig. 5.6b). $Log_{10}N_2O$ flux also differed significantly between the impacted and the control plot; the temporal trends in fluxes from the plots were opposite (Fig. 5.6c). Overall mean CO_2 fluxes were lower in the impacted plot whilst the mean CH_4 and N_2O fluxes were higher in the impacted plot in comparison with the control plot (Fig. 5.7).

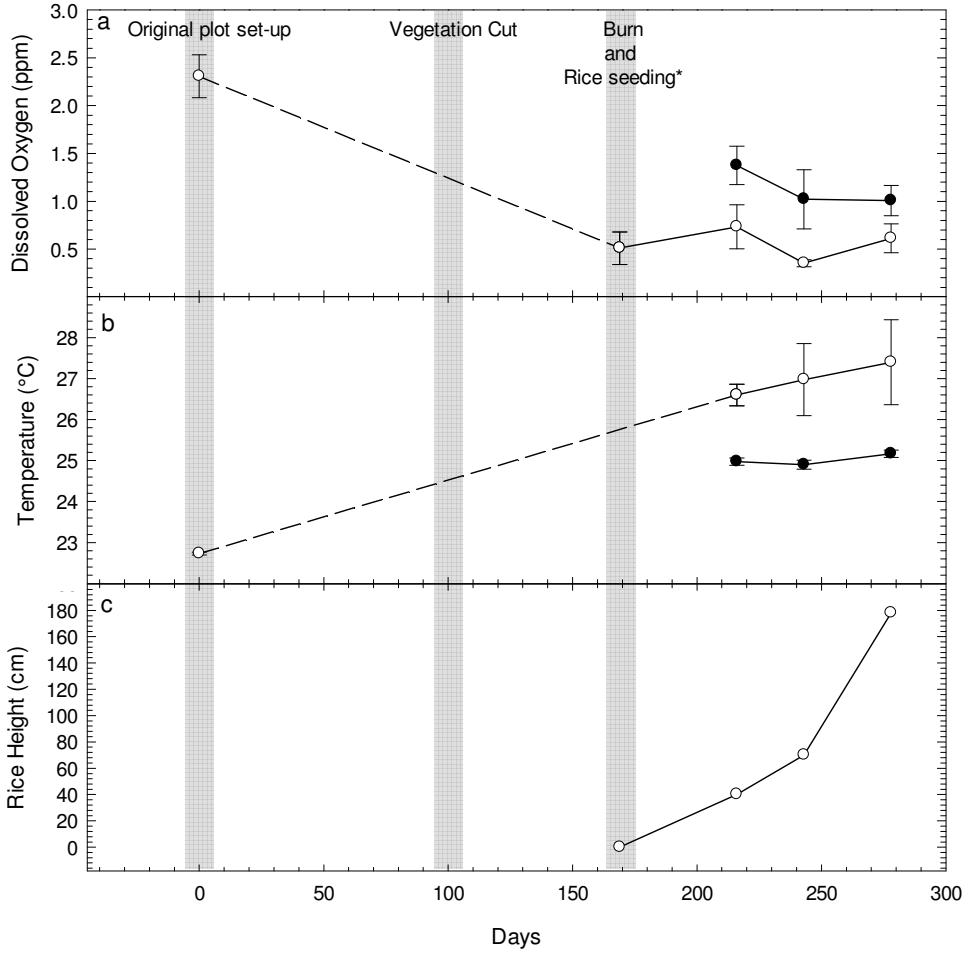

Fig. 5.5 *In situ* Dissolved oxygen (top 50 cm), surface temperature and rice height (cm) at anthropogenically impacted site. Symbols represent mean ± standard error. Control and anthropogenically impacted plot are presented as closed (●) and open (○) symbols respectively. Dashed lines connect the samplings before the original plot was subjected to disturbance. Statistical analyses only include post disturbance samplings as to compare both Control and Anthropogenically impacted plot. REML outputs are:

a) Dissolved oxygen (ppm) Anthropogenic impact: $F_{1,17} = 12.15$, $P < 0.01$, Time: $F_{2,17} = 1.74$, $P < 0.05$, Anthropogenic impact.Time: $F_{2,17} = 0.26$, $P > 0.05$;

b) Surface temperature (°C), Anthropogenic impact: $F_{1,17} = 16.59$, $P < 0.001$, Time: $F_{2,17} = 0.37$, $P > 0.05$, Anthropogenic impact.Time: $F_{2,17} = 0.14$, $P > 0.05$

*Control plot set-up

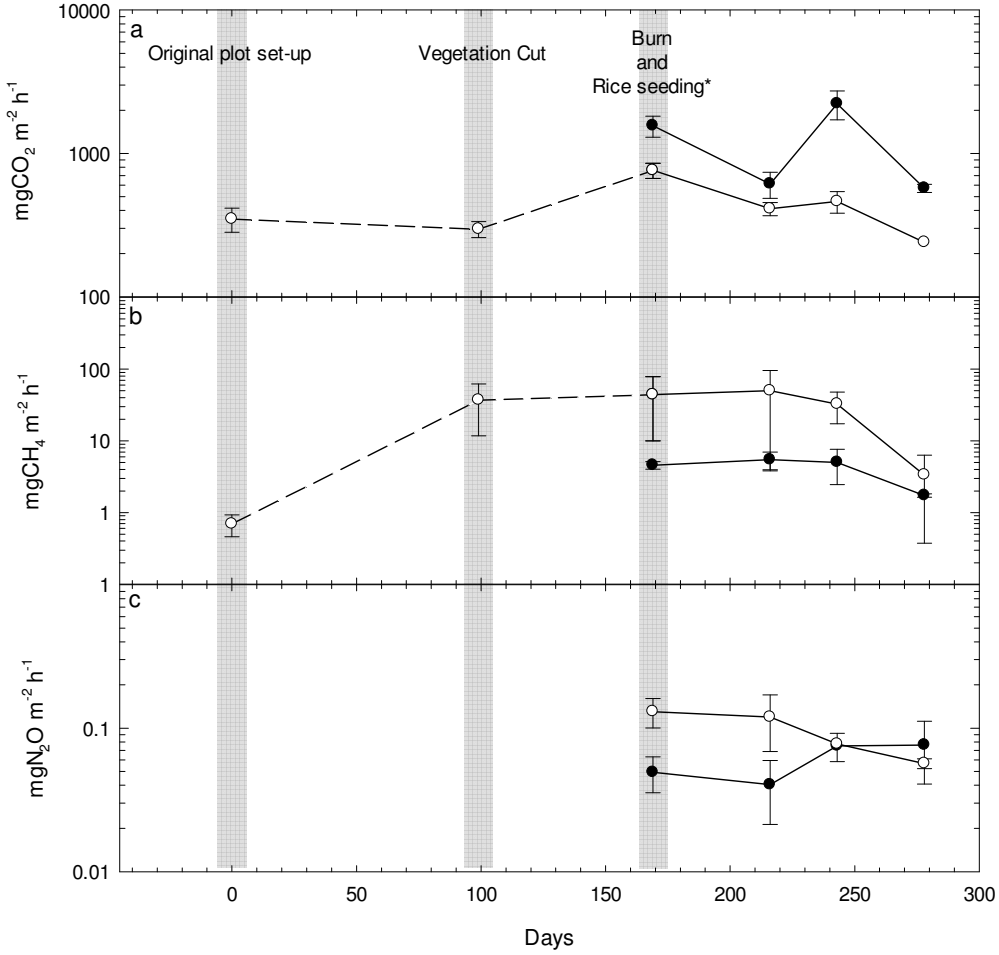

Fig. 5.6 *In situ* CO_2, CH_4 and N_2O emissions (mg m^{-2} h^{-1}) from peat surface at anthropogenically impacted site. Symbols represent mean ± standard error. Control and anthropogenically impacted plot are presented as closed (●) and open (○) symbols respectively. Dashed lines connect the samplings before the original plot was subjected to disturbance. Statistical analyses only include post disturbance samplings as to compare both Control and Anthropogenically impacted plot. REML outputs are:

a) $\log_{10}$ CO_2, Anthropogenic impact: $F_{1,107} = 23.12$, $P < 0.001$, Time: $F_{3,107} = 3.98$, $P < 0.01$, Anthropogenic impact.Time: $F_{3,107} = 2.79$, $P < 0.05$;

b) $\log_{10}$ CH_4, Anthropogenic impact: $F_{1,30} = 4.02$, $P = 0.05$, Time: $F_{3,30} = 2.83$, $P = 0.05$, Anthropogenic impact.Time: $F_{3,30} = 1.02$, $P > 0.05$;

c) $\log_{10}$ N_2O , Anthropogenic impact: $F_{1,21} = 4.68$, $P < 0.05$, Time: $F_{3,21} = 0.89$, $P > 0.05$, Anthropogenic impact.Time: $F_{3,21} = 0.35$, $P > 0.05$
*Control plot set-up.

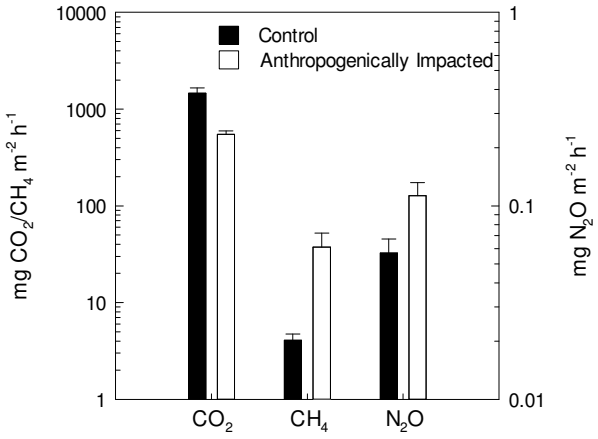

Fig. 5.7 CO_2, CH_4 and N_2O surface emissions in control and anthropogenically impacted plots. Error bars correspond to standard error. Output from REML analyses are:

$\log_{10}$ CO_2 (mg m^{-2} h^{-1}), State of the plot: $F_{1,118} = 26.24$, $P < 0.001$

$\log_{10}$ CH_4 (mg m^{-2} h^{-1}), State of the plot: $F_{1,41} = 5.89$, $P < 0.05$

$\log_{10}$ N_2O (mg m^{-2} h^{-1}), State of the plot: $F_{1,26} = 5.07$, $P < 0.05$

5.3.3 *In situ* CO_2 and CH_4 flux measurements

Vegetation surveys revealed a significant difference between the basal area from the *R. taedigera* (110 ± 7 m^2 ha^{-1}) and the *C. panamensis* sites (25 ± 6 m^2 ha^{-1}) ($F_{1,4} = 87.89$, $P < 0.001$). The highest and the lowest basal areas were recorded at Cricamola River (124.5 m^2 ha^{-1}) and San San Pond Sak 2 (13 m^2 ha^{-1}) sites respectively. As previously mentioned, three sites were dominated by *R. taedigera* and three by *C. panamensis*, this was reflected in their % of basal area within each plot (Table 5.1).

DO *in situ* varied with depth describing a declining profile with highest values near the peat surface; this profile did not vary significantly between phasic communities (Fig. 5.8a). Temperature did not significantly vary with depth nor with phasic community (Fig. 5.8b). A summary of the main physicochemical characteristics and nutrients of the surface peat are presented in Table 5.2.

Both $\log_{10}CO_2$ and $\log_{10}CH_4$ fluxes varied significantly during the monitoring period from December 2010 to September 2011, but showed no obvious seasonal trend (Fig. 5.9). $\text{Log}_{10}CO_2$ and $\log_{10}CH_4$ fluxes from the surface did not vary significantly between the phasic communities throughout the monitoring period (Fig. 5.10). However a significant difference was observed in both $\log_{10}CO_2$ and $\log_{10}CH_4$ with respect to the flooded vs. non flooded condition of the area that was sampled (Fig. 5.10a,b). $\text{Log}_{10}CO_2$ fluxes were highest from non-flooded areas and comparatively lower in those areas that were flooded (Fig. 5.10a). In contrast, $\log_{10}CH_4$ showed highest fluxes when estimated from flooded areas and lowest in the non-flooded areas (Fig. 5.10b).

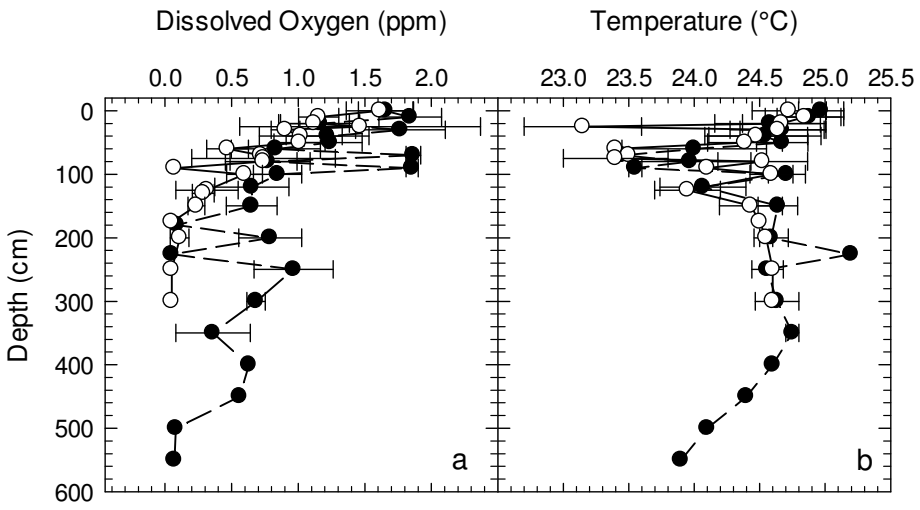

Fig. 5.8 Dissolved oxygen (ppm) and temperature (°C) through peat profiles of Mixed forest (●) and Palm swamp(○) phasic communities. Symbols represent mean ± standard error. REML outputs throughout the peat cores are:

a) Dissolved oxygen (ppm), Depth: $F_{27,204} = 3.33$, $P < 0.001$, Phasic Community: $F_{1,4} = 0.63$, $P > 0.05$, Depth.Phasic Community: $F_{14,204} = 0.42$, $P > 0.05$;

b) Temperature, Depth: $F_{25,139} = 2$, $P < 0.01$, Phasic Community: $F_{1,4} = 0.44$, $P > 0.05$, Depth.Phasic Community: $F_{14,139} = 0.25$, $P > 0.05$

Table 5.2: Physicochemical parameters of surface peat

Site		pH	Conductivity	Bulk Density	Water holding capacity	Loss on ignition	Total elements			
							C	N	S	P
			$\mu S\ m^{-1}$	$g_{dw}\ cm^{-3}$	$g\ g_{fw}^{-1}$	$g\ g_{dw}^{-1}$	$mgC\ g_{dw}^{-1}$	$mgN\ g_{dw}^{-1}$	$mgS\ g_{dw}^{-1}$	$mgP\ g_{dw}^{-1}$
1	Chiriqui Grande	4.79 ± 0.08	142 ± 26	0.06 ± na	0.91 ± 0	0.89 ± 0.03	356 ± 120	12.7 ± 5.3	3.9 ± 1.6	0.48 ± na
2	Cricamola River[c]	5.52 ± 0.75	108 ± 15	0.13 ± na	0.83 ± 0.01	0.51 ± 0.12	458 ± 250	22.9 ± 18.2	4.7 ± 1.6	0.22 ± na
3	Cricamola River[d]	na	na	na	na	na	na	na	na	na
4	San San Pond Sak 1[a]	5.05 ± 0.23	64 ± 5	0.11 ± na	0.90 ± 0.02	0.92 ± 0.02	502 ± 200	12.1 ± 5.5	1.3 ± 0.7	0.27 ± na
5	San San Pond Sak 2[b]	5.34 ± 0.53	62 ± 25	0.11 ± na	0.92 ± 0	0.94 ± 0	506 ± 250	20.3 ± 12.3	25.2 ± 12	0.21 ± na
6	Damani-Guariviara	5.38 ± 0.55	55 ± 18	0.11 ± na	0.90 ± 0.01	0.92 ± 0.02	536 ± 190	15.8 ± 1.5	57.7 ± 13	0.05 ± na
7	Almirante Bay	5.59 ± 0.09	57 ± 10	0.09 ± na	0.90 ± 0.01	0.93 ± 0.01	470 ± 40	20.9 ± 2.9	2.1 ± 0.1	0.21 ± na
	F	0.39	3.42	$t_5 = -0.02$	12.32	10.88	0.42	0.25	10.70	$t_5 = -0.03$
	P	NS	NS	NS	< 0.001	< 0.001	NS	NS	< 0.001	NS
	LSD (5 %)	1.5	60		0.03	0.15	505.5	28.7	21.5	

Values are the mean ± 1 standard error of three samples, excluding the bulk density and phosphorus, which were measured from a single sample

Significant differences among sites are indicated by the *F*, t, *P* and leas significant differences (LSD, 5 %) accordingly. fw and dw are fresh and dry weight respectively. NS, not significant. na, not avaiable

[a,b] San San Pond Sak sites 1 and 2 correspond to Sites 1 and 2 respectively from Sjögersten *et al*., 2010

[c] Original plot set in December 2010 and afterwards used for agriculture in March 2011

[d] New plot set in May 2011

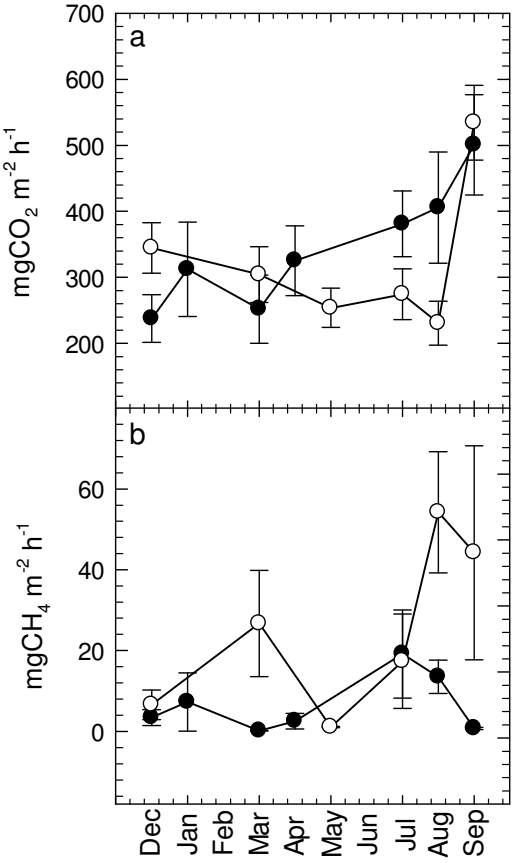

Fig. 5.9 *In situ* CO_2 and CH_4 surface fluxes (Dec 2010 to Sept 2011). Mixed forest (●) and Palm swamp (○) phasic communities. Symbols represent mean ± standard error. REML outputs are:

a) $\log_{10}$ CO_2 (mg m^{-2} h^{-1}), Time: $F_{7,132} = 3.18$, $P < 0.01$

b) $\log_{10}$ CH_4 (mg m^{-2} h^{-1}), Time: $F_{7,126} = 7.82$, $P < 0.001$

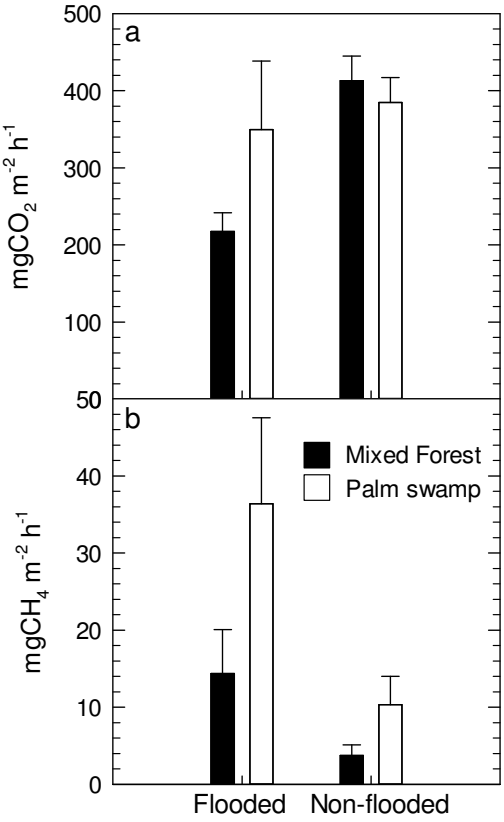

Fig. 5.10 CO_2 and CH_4 surface emissions from the palm swamp (*R .taedigera*) and mixed forest (*C. panamensis*). Samples were taken over flooded and non-flooded patched within the plots. Error bars correspond to SE. Output from REML analyses are:

a)

$\log_{10}$ CO_2 (mg m^{-2} h^{-1}), Phasic community: $F_{1,4} = 1.14$, $P > 0.05$

$\log_{10}$ CO_2 (mg m^{-2} h^{-1}), Flooding state: $F_{1,118} = 23.67$, $P < 0.001$

$\log_{10}$ CO_2 (mg m^{-2} h^{-1}), Phasic community.Flooding state: $F_{1,120} = 3.51$, $P = 0.06$

b)

$\log_{10}$ CH_4 (mg m^{-2} h^{-1}), Phasic community: $F_{1,4} = 0.74$, $P > 0.05$

$\log_{10}$ CH_4 (mg m^{-2} h^{-1}), Flooding state: $F_{1,117} = 9.42$, $P < 0.01$

$\log_{10}$ CH_4 (mg m^{-2} h^{-1}), Phasic community.Flooding state: $F_{1,117} = 0$, $P > 0.05$

5.3.4 Effect of environmental variables on *in situ* GHG fluxes

LUC at Cricamola affected environmental variables such as soil temperature and DO in the top 0.5 m of the peat profile that are closely related with GHG fluxes. Temperature did not show a significant correlation with CO_2, CH_4 or N_2O fluxes. In contrast, DO in the top 0.5 m did show a near significant correlation with gas fluxes. The relationship between $\log_{10}CO_2$ and $\log_{10}CH_4$ fluxes with DO was described by quadratic functions ($\log_{10}CO_2$ = - 0.46 × DO^2 + 1.02 × DO + 2.28; $\log_{10}CH_4$ = 1.27 × DO^2 - 3.16 × DO + 2.34) (Fig. 5.11a,b). High DO values were correlated to high $\log_{10}CO_2$ fluxes but low $\log_{10}CH_4$ fluxes. The $\log_{10}N_2O$ relationship with DO was linear ($\log_{10}N_2O$ = - 0.57 × DO - 0.61) (Fig. 5.11c), where $\log_{10}N_2O$ decreased as DO increased. The DO and soil temperature at the impacted plot significantly affected the $\log_{10}CH_4$ fluxes ($\log_{10}CH_4$ = - 2.54 DO – 0.52 Temp + 17.79; $F_{2,21}$ = 11.23, $P < 0.001$) accounting for 47 % of the observed variance.

Water table depth, DO in the top 0.5 m and surface temperature were correlated (linear and polynomial) to both *in situ* $\log_{10}CO_2$ and $\log_{10}CH_4$ fluxes from all sites. For $\log_{10}CO_2$ fluxes, water table depth ($\log_{10}CO_2$ = 3.4E-5 × WT^3 + 1.2 E-3 × WT^2 - 5.2E-3 × WT + 2.4), DO in the top 0.5 m ($\log_{10}CO_2$ = - 0.13 × DO^2 + 0.58 × DO + 2) and surface temperature ($\log_{10}CO_2$ = 0.4 × Temp - 7.62) accounted for 31.7, 25.7 and 15.8 % of the variance in the models respectively (Fig. 5.12 a,b,c). $Log_{10}CO_2$ fluxes were low at very low water table levels (- 0.4 m) increasing as the water table increased (- 0.3 to – 0.2 m) and declined as the water table got closer to the surface and above. In relation with DO in the top 0.5 m, $\log_{10}CO_2$ showed a convex shape; with respect to temperature, the highest $\log_{10}CO_2$ fluxes coincided with higher temperature values. In the case of $\log_{10}CH_4$ fluxes, water table depth did not show a significant correlation but data was distributed in a funnel shape with a greater range of fluxes with higher levels of water table. In contrast, DO in the top 0.5 m ($\log_{10}CH_4$ = 0.36 × DO^2 - 1.4 × DO + 1.4) and surface temperature ($\log_{10}CH_4$ = - 2.3 × Temp + 58.5) accounted for 7.3 and 29.1 % of the variance in the models respectively (Fig. 5.12d,e,f). The correlation between $\log_{10}CH_4$ and DO in the top 0.5 m showed a convex shape whilst the correlation with temperature described a negative linear relationship with lowest $\log_{10}CH_4$ fluxes found when temperatures were highest.

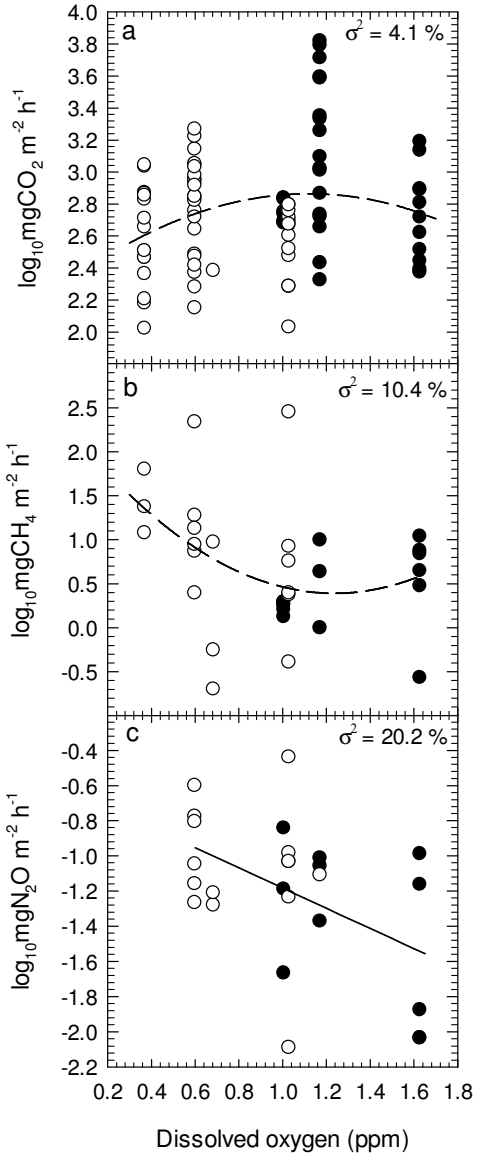

Fig. 5.11 Relationship between GHG emissions and DO

a) $\log_{10} CO_2$ flux and Dissolved oxygen (top 50cm) ($F_{2,87} = 2.91$, $P = 0.06$);

b) $\log_{10} CH_4$ flux and Dissolved oxygen (top 50cm) ($F_{2,30} = 2.86$, $P = 0.07$);

c) $\log_{10} N_2O$ flux and Dissolved oxygen (top 50cm) ($F_{1,24} = 7.33$, $P < 0.05$);

Control and anthropogenically impacted plot are presented as closed (●) and open (○) symbols respectively. Solid and dashed lines correspond to the linear and quadratic models that were significant and near significant respectively.

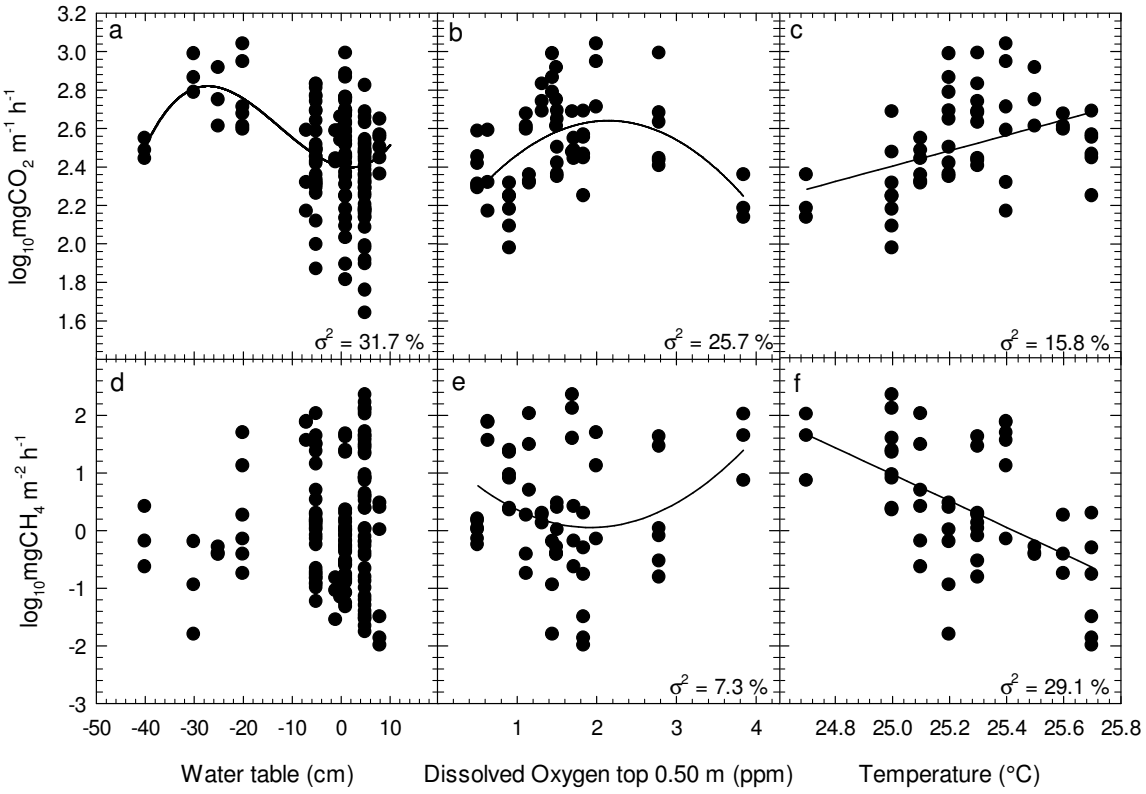

Fig. 5.12 Relationship between *in situ* CO_2 and CH_4 fluxes and water table, temperature and dissolved oxygen. Models are presented as solid lines. Significance of the model is presented below. Variance accounted by the model is presented in the graphs (σ^2).

a) $\log_{10}$ CO_2 flux and Water table ($F_{3,58} = 10.43$, $P < 0.001$);

b) $\log_{10}$ CO_2 flux and Dissolved oxygen in top 50 cm ($F_{2,56} = 11.02$, $P < 0.001$);

c) $\log_{10}$ CO_2 flux and Temperature ($F_{1,51} = 10.75$, $P < 0.01$);

d) $\log_{10}$ CH_4 flux and Water table (Model was not significant);

e) $\log_{10}$ CH_4 flux and Dissolved oxygen in top 50 cm ($F_{2,54} = 3.19$, $P < 0.05$)

f) $\log_{10}$ CH_4 flux and Temperature ($F_{1,49} = 21.53$, $P < 0.001$)

5.4 Discussion

We have shown that vegetation exerts a direct control on GHG fluxes from tropical lowland peatlands. In both *ex situ* and *in situ* measurements, fluxes of CO_2 and CH_4 varied with vegetation activity. *Ex situ* CO_2 fluxes presented a diurnal pattern that reflected the photosynthetic activity by *R. taedigera* seedlings. Diurnal patterns of *in situ* CO_2 fluxes were not measured in this study; however previous measurements of GHG fluxes from the peat surface in the same study area have found diurnal patterns presumably related to root respiration and the exudation of photoassimilates by the rhizosphere (Wright *et al.* 2013b; Tang *et al.* 2005). During daylight *ex situ* and *in situ* root respiration contributed with 17 and 15 % of the total soil respiration respectively. These values are low in comparison with previous studies from northern hemisphere forests, wetlands and paddy fields estimating that root respiration contributes with 30 to 98 % of the total soil respiration (Schlesinger 1977; Hergoualc'h *et al.* 2011; Murdiyarso *et al.* 2010; Silvola *et al.* 1996; Hanson *et al.* 2000); but are similar to the 21 % estimated by Jauhiainen *et al.* (2011) in *Acacia* plantations on peatlands and the 24 % estimated by Silver *et al.* (2005) in tropical forests. The difference can plausibly be attributed to several factors including the type of vegetation, the degree of peat disturbance, peat respiration and the water logging conditions.

The higher soil respiration values observed at the control plot adjacent to the anthropogenically impacted plot at Cricamola supported our hypothesis (ii) predicting a decrease in the CO_2 fluxes following the clearance of *R. taedigera* for LUC. We attributed this to the removal of *R. taedigera* roots respiration after LUC. However, the reports on the effect of LUC on soil respiration are contradictory as reviewed by Raich & Schlesinger (1992). It has been reported that the main consequence of LUC on soils respiration is related to the alteration of water table levels (Furukawa *et al.* 2005; Hatala *et al.* 2012; Hirano *et al.* 2012). As the impacted plot in our study was not subjected to drainage, it was not possible for us to assess the effect of such alteration. Thus, it is plausible that in non-drained tropical peatlands, the direct effect of LUC is a reduction in soil respiration.

Vegetation controlled both *ex situ* and *in situ* CH_4 fluxes to some degree. *Ex situ* CH_4 fluxes during daylight were lower in the monoliths with *R. taedigera* than in the control (Fig. 5.2b,c). Simultaneous measurements of DO in the rhizosphere confirmed that O_2 diffused from roots to the peat matrix (Fig. 5.3). This suggests

that the input of O_2 by *R. taedigera* rhizosphere to the peat matrix enhanced CH_4 oxidation (Gerard *et al.* 2011; De Bont *et al.* 1978; King 1996; Calhoun *et al.* 1997) and/or partially inhibited methanogenesis (Holzapfel-Pschorn *et al.* 1986; Grosse *et al.* 1996), reducing CH_4 fluxes by *ca.* 40 % in comparison to the controls (Fig. 5.2c). This supports hypothesis (i) which predicted a reduction on CH_4 emissions due to *R. taedigera* O_2 input to the peat matrix.

LUC also affected CH_4 fluxes, we observed that pre-disturbance fluxes were 90 % lower in comparison to the fluxes observed after the vegetation in the plot was cleared (Fig. 5.6b); this was consistent with hypothesis (ii). However, several explanations can account for this increase in CH_4 flux. For example, once vegetation was cleared, the microenvironment below *R. taedigera* canopies was no longer present, thus temperature increased at the peat surface (Fig. 5.5b), decreasing O_2 and CH_4 solubility thus exacerbating the anaerobic conditions and increasing CH_4 production. Additionally, by clearing the *R. taedigera*, the input of O_2 to the peat matrix stopped. Therefore, biologically enhanced CH_4 oxidation and methanogenesis inhibition (as observed *ex situ*) ceased, increasing CH_4 emissions. Indeed, DO in the top 50 cm of the peat matrix and temperature in the peat surface accounted for 47 % of the variance of the CH_4 fluxes in the anthropogenically impacted plot; this gives additional support to hypothesis (i).

The DO concentrations measured *in situ* (*i.e.* oxygenation of the peat matrix throughout the rhizosphere) (Fig. 5.8) suggests that CH_4 emissions observed *in situ* are strongly affected by the vegetation O_2 input (Fig. 5.10b). The decline in CH_4 fluxes with rice growth (Fig. 5.6b) may be attributed to the gradual increase of CH_4 oxidation and methanogenesis inhibition due to the input of O_2 by rice aerenchymatous root system (Gerard *et al.* 2011; De Bont *et al.* 1978; King 1996). Alternatively, the declining fluxes are due to the increasing capacity of vegetation to mediate CH_4 fluxes to the atmosphere hence underestimating CH_4 fluxes estimations.

A similar decline was observed in N_2O fluxes from the impacted plot (Fig. 5.6c). Natural and induced fire events have been observed to affect the balance of mineral nutrients balance in soil (Wan *et al.* 2001). A high ammonium (NH_4^+) pulse is usually observed immediately after forests have been affected by fires (Smithwick et al. 2005); NH_4^+ is converted into more oxidized forms of nitrogen by microbial nitrification (*i.e.* NO_2^-, NO_3^-). N_2O is produced as an intermediate

of NO_3^- denitrification (Conrad 1996). Thus, it is plausible that the decline of N_2O fluxes at the impacted site (Fig. 5.6c) is related to the depletion of NO_3^- available for denitrification. This has to be considered in the light of the decline of CH_4 fluxes as NO_3^- is toxic to methanogenesis and methane can be oxidized under anaerobic conditions coupled to denitrification (Modin *et al.* 2007; Jetten 2008; Conrad 1999). Consequently, LUC and particularly slash and burn practices could represent short term N_2O sources.

The *in situ* CO_2 fluxes here reported (217 to 412 $mgCO_2\ m^{-2}\ h^{-1}$) (Fig. 5.10a) are comparable with those reported in tropical wetlands of Hawaii (131 to 401 $mgCO_2\ m^{-2}\ h^{-1}$) (Chimner 2004), Indonesia (139 to 689 $mgCO_2\ m^{-2}\ h^{-1}$) (Furukawa *et al.* 2005; Jauhiainen *et al.* 2005; Hooijer *et al.* 2010) and previous studies within the same study area in Panama (150 to 500 $mgCO_2\ m^{-2}\ h^{-1}$) (Sjögersten *et al.* 2011; Wright *et al.* 2011; Wright *et al.* 2013b). Likewise, the *in situ* CH_4 fluxes (3.7 to 36.8 $mgCH_4\ m^{-2}\ h^{-1}$) (Fig. 5.10b) fall within the range of emissions (-1 to 50 $mgCH_4\ m^{-2}\ h^{-1}$) reported for tropical peatlands in the Amazon, Indonesia, Hawaii, Costa Rica and Panama (Bartlett *et al.* 1988; Furukawa *et al.* 2005; Jauhiainen *et al.* 2005; Wright *et al.* 2011; Sjögersten *et al.* 2011; Wright *et al.* 2013b; Nahlik *et al.* 2011). *In situ* $\log_{10}CO_2$ and $\log_{10}CH_4$ fluxes were correlated to the DO concentrations in the peat matrix (Fig. 5.12b,e). Additionally, the water table was a good predictor of $\log_{10}CO_2$ fluxes (Fig. 5.12a). Under low water table conditions the CO_2 fluxes are low and as the water table rises close to the peat surface the CO_2 fluxes increase; once the water table reaches or is above the surface the range of CO_2 fluxes widens and shows its lowest values. In contrast, water table was not a good predictor of CH_4 fluxes; as water table increased so did the range of CH_4 fluxes. Therefore, low CH_4 fluxes were observed under both low and high water tables but the highest CH_4 fluxes were only present under high water table levels (Fig. 5.12d).This is consistent with previous reviews addressing the relationship between CH_4 emissions and water table in tropical peatlands (Couwenberg *et al.* 2009). Furthermore, the $\log_{10}CH_4$ fluxes varied significantly between flooded and non-flooded patches (Fig. 5.10b). This supports hypothesis (iv) (predicting higher CH_4 fluxes from flooded patches in comparison with non-flooded ones) and confirms that water table is one of the most important factors regulating GHG emissions in tropical peatlands as it also is in temperate and boreal ecosystems (Moore *et al.* 1989; Chimner *et al.* 2003; Blodau *et al.* 2004; Couwenberg *et al.* 2009; Hirano *et al.* 2008). The most likely reason for observing higher $\log_{10}CH_4$ fluxes in flooded patches is the role of wa-

ter as natural mass transfer barrier for impeding O_2 transport into the peat matrix.

The relationship between the peat surface temperature and the $\log_{10}CO_2$ and $\log_{10}CH_4$ suggests that as temperature increased $\log_{10}CO_2$ fluxes also increased but $\log_{10}CH_4$ fluxes decreased. This is apparently contradictory with previous works focused on the effect of temperature on methanogenesis (Macdonald *et al.* 1998; Raich et al. 1992; Zeikus *et al.* 1976). However, considering that our CH_4 flux measurements are the result of methanogenesis and methanotrophic processes and that peat temperature is affected by different environmental factors such as water table, it is not possible to explain the observed relationship. Additional experimental work will be required so as to fully understand the relationship between *in situ* CH_4 emissions and peat temperature.

It was expected that *R. taedigera* extensive aerenchymatous root system with the capacity of developing pneumatophores, which is not present in the mixed forest sites, would contrastingly affect *in situ* CO_2 and CH_4 emissions. It has been observed that pneumatophores and prop roots stimulate aerobic soil respiration in tropical peatlands (Couwenberg *et al.* 2009; Kitaya *et al.* 2002; Chimner *et al.* 2004) and that vegetation can reduce CH_4 emissions (Gerard *et al.* 2011; Holzapfel-Pschorn et al. 1986). However, our data do not support hypothesis (iii) predicting lower *in situ* CH_4 emissions at the *R. taedigera* sites in comparison with the mixed forest sites (Fig. 5.10b). In fact no significant difference was observed between phasic communities (Fig. 5.10). This may be due to the fact that root exudates are an important source of labile organic matter that can be used to produce CH_4 (Chanton *et al.* 1995) and the amount of root exudates that is input into the soil matrix is correlated with the extension of the root mat (Seiler *et al.* 1983). Therefore, it is possible that the amount of root exudates produced by *R. taedigera* compensated for the reduction of CH_4 emissions by the roots oxygen input to the peat matrix. Based on the aforementioned observations, it is plausible that the apparent lack of significant difference between the *in situ* GHG emissions from the two phasic communities is due to the experimental approach (*i.e.* measuring GHG at the peat surface) rather than a real lack of difference in the GHG emissions between the two phasic communities. For example, it is possible that the difference in emissions does exist, but has to be assessed at the vegetation canopies rather that at peat surface. Thus it is not possible to reject the hypothesis by exclusively considering peat surface fluxes only.

If plant-mediated CH_4 emissions are significant (Pangala *et al.* 2013b), measuring CH_4 fluxes at the surface underestimates the net amount of CH_4 emissions to the atmosphere. Indeed, the covariation of the diurnal CH_4 fluxes with temperature and solar irradiance suggest that *R. taedigera* might be capable of using a pressurized flow-through ventilation mechanism controlled by temperature to transport gases (thermal transpiration and hygrometric pressure; thermo-osmosis) (Chanton *et al.* 1993). This mechanism has been described in aquatic plants (Dacey 1980) and wetland trees (Grosse *et al.* 1992). However, diurnal patterns in CH_4 fluxes can occur even if the plant solely uses molecular diffusion to transport gases (*e.g.* rice) (Chanton *et al.* 1997). Further research is required to establish the mechanisms through which tropical peatland plants such as *R. taedigera* and *C. panamensis* mediate the gas transport from the peat matrix to the atmosphere. Thus, given that plant-mediated CH_4 emissions are the dominant pathway in some ecosystems, transporting 75 to 95 % of the total CH_4 emitted (Cicerone *et al.* 1981; Dacey *et al.* 1979; Seiler *et al.* 1983; Schütz *et al.* 1989), this underestimation could be of importance in global CH_4 emission budgets from tropical peatlands.

Chapter 6

General discussion

The study into the controls of carbon turnover in lowland tropical peatlands aimed to improve our understanding of the role of these ecosystems in the global carbon cycle. This involves the past, present and future role of lowland tropical peatlands in the carbon cycle within the framework of the global climate change (*e.g.* droughts, warming, and increasing concentration of GHG in the atmosphere) and considering the current anthropogenic threats (*e.g.* LUC). In the following section, the role of lowland tropical peatlands in the north western region of Panama within the regional and global carbon cycle is discussed under the light of the data presented in this thesis. In addition, the need for a new conceptual framework to study lowland tropical peatlands is discussed.

6.1 Role of lowland tropical peatlands on the global carbon cycle and carbon balance

The carbon balance of an ecosystem is integrated by the input and output variables. In a peatland, the input consists of NPP whilst the output involves the decomposition and displacement of plant material derived from NPP. The difference between inputs and outputs determines if the peatland is acting as a net carbon sink or source.

The lowland tropical peatlands in the northwestern region of Panama have accumulated large amounts of carbon belowground over millennia. The basal date obtained from a core at the Damani - Guariviara wetland (5330 ± 40 to 5920 ± 40 cal yr BP) is consistent with the basal date available from SSPS (*ca.* 4540 cal yr BP) (Phillips *et al.* 1997), suggesting that the peat accumulation in

the region started during the mid-Holocene. Indeed the presence of marine fossils in the marine clay underlying the peat at the Damani – Guariviara wetland indicates that coastal peatlands in the region developed following the sea level stabilization, *ca.* 8 to 4 ka (Yu *et al.* 2010; Dommain *et al.* 2011). Following the sea level stabilization, mangroves colonized the coasts as confirmed by the fossil pollen and macrofossils found at SSPS (Phillips *et al.* 1997); and the macrofossils and Taraxerol (a biomarker for mangroves; (Versteegh *et al.* 2004)) found at the Damani – Guariviara wetland. Afterwards, the succession of phasic communities developed the stratigraphic profiles and swamp catena observed in SSPS (Phillips *et al.* 1997).

The latest estimation of 2.38 GtC for the peat carbon pool of the whole Republic of Panama (Page *et al.* 2011) is based on: i) the area of histosols in Panama included in the Bord na Móna (1984) report for "Fuel peat in developing countries" (7870 km^2) and ii) the average peat thickness (6 m) from Phillips *et al.* (1997) obtained in the CPD peatland. This is likely to be an overestimation because of the application of the total histosols area in Panama as if they were peat (Soil Survey Staff 1999) and because 6 m is unlikely to be the average depth of the peat deposits in the country. In this thesis, the description of new peatlands in the region allowed improved peat carbon pool estimates for the lowland tropical peatlands in the north western region of the Republic of Panama. In order to develop the estimate, the area of the wetlands in the region was estimated from the analysis of satellital imagery and the vegetation cover map published by the National Environmental Agency of Panama (ANAM) (Autoridad Nacional del Ambiente (2000); App. D); the peat dry mass, carbon content and bulk density was measured in peat cores (App. A); and the peat depths were taken from isopachous maps of the CPD (Cohen *et al.* 1989) and direct measurments in field. The estimate for the peat carbon pool in the north western region of Panama calculated in this thesis is around 0.025 to 0.064 GtC (for further details on the calculations see App. D). This estimate is 2 to 5 times lower than the currrent estimate for the same area (*ca.* 0.11 GtC) based on Page *et al.* (2011) data. Despite the high uncertainty reflected in the difference between estimates, the peatlands located in north western region of Panama represent a large peat carbon pool.

The current carbon balance of the peatlands in the north western region of Panama can be estimated making certain assumptions; for instance, NPP and fluvial organic carbon fluxes have not been measured in the region. Thus, a pre-

liminary carbon balance can be estimated from the NPP figures available in the literature and in the gaseous carbon fluxes provided in this thesis (Chapter 5). The annual net primary productivity of tropical forests is higher than that of boreal-temperate forests and accounts for approximately one third of the global NPP (Jenny *et al.* 1949; Field 1998). The carbon input from the total aboveground NPP in tropical forest is high, with values ranging from 1000 - 1279 gC m^2 y^{-1} (Chimner *et al.* 2005; Nebel *et al.* 2001). It has been estimated that the aboveground NPP represent 90 % of the total NPP (Chimner *et al.* 2005), with fine root biomass contributing with the remaining 10 %. Therefore, by taking the average of the values reported for aboveground NPP in tropical forests and adding 10 % to account for the belowground biomass, a conservative estimate of the total NPP (aboveground and belowground) in lowland tropical forests would be *ca.* 1250 gC m^2 y^{-1}. The average carbon fluxes (TCfluxes; CO_2 and CH_4) from the six study sites throughout the monitoring campaign (including autotrophic root respiration) were 888 ± 57 gC m^2 y^{-1}. This results in a Net Ecosystem Production (NEP; NEP = NPPtotal – TCfluxes) of 365 gC m^2 y^{-1}, suggesting that the peatlands in the region are currently accumulating carbon. However, this estimate has to be considered with caveats; for instance, the information on NPPtotal in tropical peatlands is limited and needs refining. Similarly, the study of previously ignored components of the carbon balance have to be quantified, *e.g.* herbivory (Malhi et al. 2011) and the fluvial organic carbon flux (Moore *et al.* 2013; Moore *et al.* 2011).

The long-term apparent rate of carbon accumulation (LORCA) calculated from the basal dates of the peat cores at SSPS and the Damani – Guariviara wetland ranged from 43 to 55 gC m^{-2} y^{-1}, representing 13 % of the NEP presented above. This suggests that 87 % of the NEP is lost through other mechanisms besides gas fluxes; confirming the need for more accurate NEP estimates (including fluvial organic carbon fluxes and herbivory), as well as more detailed estimates of the LORCA in the Neotropics. Until these gaps are filled, we will not be able to improve the estimates of the carbon balance in the lowland tropical peatlands of the region or make well constrained comparisons with other tropical peatlands in the world.

6.2 The need for a new conceptual framework to study lowland tropical peatlands

Tropical and temperate-boreal peatlands are similar in several aspects (Andriesse 1988); in both systems the conditions result in an imbalance between plant production and decomposition and the consequent accumulation of peat. Since the underlying processes driving this imbalance are similar (*i.e.* water logging hindering rapid decomposition of plant material), up until now the same conceptual framework has been used to study both tropical and temperate-boreal peatlands indistinctly. The diplotelmic model developed by Ivanov (1981) considered two major layers with distinct structural and functional characteristics; an active layer (surface) and an inactive-inert layer (subsurface) (Joosten *et al.* 2007). These concepts were renamed by Ingram (1978) as acrotelm (acros: upper) and catotelm (kata: under) in order to stress the position of these layers in the peat profile from a structural point of view (Couwenberg *et al.* 1999). Subsequently, these concepts have been redefined from a functional point of view , the acrotelm being a zone were water flows relatively free and the catotelm zone were the water remains relatively stagnated (Couwenberg *et al.* 1999). The diplotelmic model was originally developed to describe the boreal-temperate peatlands were peat is mainly formed by non-vascular plants such as Sphagnum moss, which lack roots (Clymo 1987). In boreal-temperate ecosystems, microorganisms in the acrotelm use the oxygen that diffuses from the atmosphere faster than it is replaced, thus the acrotelm is aerobic with a positive redox regime and the acrotelm is anaerobic with a negative redox regime (Clymo 1984).

Though this conceptual framework has been modified to be applied to lowland tropical peatlands, in the tropics peat is formed mainly by vascular plants (Andriesse 1988). In addition, the acrotelm of lowland tropical peatlands is situated above the peat surface, including the freshly fallen litter and the vegetation mass up to the height of the highest annual water table, *e.g.* buttress roots (Joosten *et al.* 2007). The acrotelm also includes the zone of chemical, biological, and physical influence generated by root growth and activity (rhizosphere) (Pinton *et al.* 2007); where vascular plants have developed structural adaptations to aerate their roots which are under permanent waterlogging conditions (Armstrong 1979; Armstrong *et al.* 1991; Armstrong 1967). Thus the rhizosphere influences the rates of carbon turnover in the peat profile, creating a root zone-influenced layer (Rieley 2007).

In this thesis, evidence of the influence of the rhizosphere in the carbon turnover were observed in the *ex situ* respirometric assays (Chapter 3), the *in situ* litterbags translocation experiment (Chapter 4) and the monitoring of LUC (Chapter 5). The *ex situ* respirometric assays under anaerobic conditions showed a high methanogenic activity in the upper peat layers (2 m) and near negligible activity in the deeper layers; this was attributed to a difference in the peat chemical composition as the rhizosphere influence was not present. An alternative explanation is that the upper peat layers had a higher inoculum of decomposing microorganisms, as it has been observed that microbial diversity and activity is higher in the upper layers of the peat profiles (Jackson *et al.* 2009). However, when the assay was carried out under aerobic conditions the overall microbial activity (CO_2 production) was no longer restricted to the upper layers. This indicate that methanogenesis is strongly controlled by the availability of high quality (easily degradable) substrate (Wright *et al.* 2011), whilst the overall microbial activity is strongly influenced by the redox regime. It has been shown that in peatlands, the highest methane production is allocated in the upper peat layers, in spite of the high redox potentials that have been observed at this depth (Wright *et al.* 2011). This corresponds to the rhizosphere-influence zone; in tropical forests, as much as 85 % of the root active rhizosphere can be found in the upper 0.3 m of the soil profile (Greenland et al. 1960) and in tropical peatlands a large amounts of live root biomass can be found down to 1.1 m (Wright *et al.* 2011). It has been suggested that easily degradable substrates released by the roots of vascular plants in peatlands enhance methanogenic activity in the upper peat layers (Laing *et al.* 2010; Chanton *et al.* 1995; Holzapfel-Pschorn *et al.* 1986; Kuzyakov *et al.* 2000). This is important for the GHG emissions, as variations of a few decimetres in the water table affects the biogeochemical processes due to the change in redox regime and the availability of an aqueous phase to transport the root exudates to the microorganisms in the soil.

The variation in litter decomposition due to the allochthonous – autochthonous effect is also related to the rhizosphere – influence zone, as it has been observed in tropical peatlands that different phasic communities develop associations with distinct microbial consortiums (Troxler *et al.* 2012). These associations have been suggested to have a direct effect on nutrients turnover, participating in the control of nutrient release to avoid competition from fast-growing deciduous species (Cornelissen *et al.* 1999).

Monitoring the effects of LUC also gave evidence to support the need for a new conceptual framework including the rhizosphere as a central player in the carbon turnover in tropical peatlands. As the activity of the rhizosphere was affected by LUC, so were the biogeochemical processes involved in the GHG emissions. Furthermore, as the rhizosphere is the interface between the aboveground biomass and the peat (Rieley 2007), the rhizosphere could represent a bottle neck in the plant – mediated gas transport to the atmosphere. Thus the structure of the rhizosphere is fundamental to understand the recently recognized role of tropical vegetation in transporting large amounts of GHG to the atmosphere (Pangala *et al.* 2013b; Pangala *et al.* 2013a).

Thus, a new conceptual framework that does not oversimplify the structural and functional components of a tropical peatlands to acrotelm and catotelm layers is necessary. From the work presented in this thesis, it is possible to suggest that aspects such as i) the factors controlling the peat profile functional hydrology (redefinition of acrotelm and catotelm), ii) the interdependent relation between microbial communities and vegetation and iii) the direct role of vegetation (rhizosphere and plant-mediated gas transport) on the carbon turnover must be included in the new conceptual framework to study lowland tropical peatlands. This will change the currently reductivist approach to a holistic scientific approach. Within this framework, new and more challenging questions about the carbon turnover processes in tropical peatlands can be generated from a holistic ecological point of view.

6.3 The future of lowland tropical peatlands in the north-western region of Panama

There are three interdependent factors that are necessary for a peatland to be a carbon net sink: i) hydrology, ii) peat structure and composition and iii) peat forming vegetation (Joosten *et al.* 2007). In the north western region of Panama, these three factors are currently threatened by LUC and climate change.

A reduction of precipitation (Campbell *et al.* 2011) and warming in most of the Caribbean due to climate change has been projected to occur by the end of the century (Meehl *et al.* 2012; Solomon *et al.* 2007). Dryer and warmer conditions could affect the constant water input that is necessary to keep the peatlands

waterlogged. Previous observations at the CPD have recorded a maximum water table drawdown of 0.25 m (Wright 2011); in this thesis a maximum drawdown of 0.4 m was observed. With a reduction in precipitation, a further and sustained lowering of the water table is expected.

By monitoring *in situ* GHG emissions across one year (Chapter 3), it was possible to quantify the effect of the water table on the carbon turnover. Under flooded conditions (water table at or above the surface; 0 to 0.15 m), the CH_4 emissions were *ca.* 4 times higher in comparison with those where the water table was below the surface (-0.01 to -0.4 m). In contrast, CO_2 emissions were *ca.* 1.5 times higher when the water table was below the surface. The Global Warming Potential (GWP) is a metric use to transfer emissions of different gases to a common scale, allowing a comparison in terms of their relative contribution to global warming. When converted to CO_2 equivalents (CO_{2eq}) (CH_4 GWP = 34; IPCC (2013), unpublished data), the flooded conditions represent a greater source of CO_{2eq} than the non-flooded conditions. Under flooded conditions CH_4 fluxes contributed with *ca.* 75 % of the Total CO_{2eq} (TCO_{2eq} = CH_4- CO_{2eq}+ CO_2) (Flooded: CH_4- CO_{2eq} = 843 ± 200 mg m^{-2} h^{-1}; CO_2- CO_{2eq} = 280 ± 44 mg m^{-2} h^{-1}); in contrast, under non flooded conditions CH_4 contributed with *ca.* 34 % of the TCO_{2eq} (Non Flooded: CH_4- CO_{2eq} = 213 ± 53 mg m^{-2} h^{-1}; CO_2- CO_{2eq} = 402 ± 23 mg m^{-2} h^{-1}). This confirms that the water table exerts a strong control over GHG emissions (Moore *et al.* 1989; Chimner *et al.* 2003; Blodau *et al.* 2004; Couwenberg *et al.* 2009; Hirano *et al.* 2008) and that the control is strong enough to invert the relative importance of the two main GHG that are emitted by peatlands.

Water table drawdown could also trigger the irreversible process of subsidence. In tropical peatlands, subsidence rates are high during the first five years after drainage reaching up to 1.5 m (Wösten *et al.* 1997); afterwards, the subsidence rate has been estimated to be lower and constant (*ca.* 0.05 m y^{-1}; 5 m in 100 y) (Hooijer et al. 2012; Couwenberg *et al.* 2009). It has been estimated that *ca.* 13.3 t ha^{-1} y^{-1} of CO_{2eq} (calculated with the IPCC 4AR global warming potentials (Solomon *et al.* 2007); the estimate are likely to be higher with the new methane GWP of 34 (IPCC (2013), unpublished report)) could be potentially released for each cm of peat lost by subsidence (Wösten & Ritzema 2001 cited by Hooijer et al. 2012). Under those scenarios, shallow peatlands (1.5 m) like those located at Chiriquí Grande could be lost in less than a decade of severe droughts.

Simultaneously with the predicted temperature increase in the region, the CO_2 concentration in the atmosphere will continue to increase. These two factors will have a direct impact on the NPP (Cernusak *et al.* 2013). However CO_2 fertilization may only be short lived as other nutrients (nitrogen and phosphorus) may become limiting (Cernusak *et al.* 2013; Norby *et al.* 2010). Additionally, as photosynthesis is enhanced by CO_2 fertilization, the chemistry of the foliar tissue will change, increasing the amount of non-structural carbohydrates and decreasing its nitrogen content (Ceulemans *et al.* 1994; Poorter *et al.* 1997). These structural alterations affect plant material resistance to decomposition and consequently the carbon turnover in the system (Gleadow *et al.* 1998). Further studies are required to evaluate the effect of the increase of CO_2 concentration in the atmosphere on the resistance of the litter of *R. taedigera*, *C. panamensis* and a wider range of peat forming plants to decomposition.

In this thesis, it was possible to monitor the effect of LUC on GHG emissions. In terms of CO_{2eq}, the anthropogenic impact increased CO_{2eq} emissions from the *R. taedigera* swamp at Cricamola by *ca.* 20 t CO_{2eq} ha^{-1} y^{-1}. This increase is equivalent to the loss of a 2 cm of peat layer by subsidence (Hooijer *et al.* 2012). Furthermore, the relative contribution of CO_2, CH_4 and N_2O varied with LUC. At the pristine site, CO_2, CH_4 and N_2O contributed with *ca.* 90, 9 and 1 % of the TCO_{2eq} respectively. In contrast, in the anthropogenically impacted plot, CO_2, CH_4 and N_2O contributed with *ca.* 29, 69 and 2 % of the TCO_{2eq} respectively. These differences were attributed to alterations in the autotrophic root respiration and the cessation of plant-mediated gas transport (CH_4 and O_2) between the peat and the atmosphere. It is important to stress the fact that LUC transforms the peatland from a net carbon sink into a net source, as the input component in the carbon balance is removed (fresh litter).

6.4 General conclusions

Throughout this thesis it was possible to explore different controls of carbon turnover in lowland tropical peatlands in the north western region of Panama. The different composition of the plant material due to different botanical origins and tissues exerted a clear influence in the first stages of peat formation (Chapter 4). Once peat was formed, its decay was mainly controlled by the redox regime and by the degree of peat humification (Chapter 3). The interaction between the

hydrology and the autochthonous vegetation in the region resulted in the accumulation of significant amounts of carbon over thousands of years. Vegetation exerted a direct and indirect control on the carbon turnover of the system. The composition of plant litter is an important control for litter decay. The influence of vegetation in shaping the structure of the peat profile influences the redox regime and thus the biogeochemical processes under which litter decomposition occurs. The relationship between the vegetation and specific microbial consortia affects the rate of litter decomposition (Chapter 4). The input of labile substrates and oxygen through the rhizosphere affects the redox regime and the microbial activity in the peat profile (Chapter 5). Important gaps remain regarding the carbon turnover processes and controls in lowland tropical peatlands; particularly in relationship to climate change and LUC. These gaps will have to be filled in order to understand the present and future role of lowland tropical peatlands in the currently uncertain global carbon balance.

6.5 Future research

- The current estimates of carbon accumulation rates in the peatlands of the north western region of Panama are highly uncertain as only two basal dates exist for the region. Further studies in the region are required to take full advantage of the value of peatlands as palaeoecological records. For instance, it is important to study the marine genesis of these ecosystems and the poorly understood process of phasic community succession. This could reveal if some phasic communities accumulate peat faster or produce peat with a more stable composition.

- Biogeochemical processes occurring through the peat profile are poorly understood. For instance, the anaerobic oxidation of methane and the methanotrophy in general have not been properly quantified *in situ*. As methane production and methane consumption respond differently to the increase in temperature, it is important to define the contribution of each process to the overall carbon balance in the system.

- Changes in the composition of plant litter are expected as the regional temperature and global atmospheric CO_2 increase and as precipitation decreases. The effect of changes in plant litter composition should be evaluated, to determine if such changes would be a positive or negative feedback to peat accumulation.

- In Chapter 4 it was suggested that vegetation develops specific relationships with the microbial community. This relationship could help the current phasic community to be more competitive by administrating the release of nutrients to the peat. Research focused on the interdependence between microbial and phasic communities is required to improve our understanding of the biotic processes regulating the flow of nutrients and carbon through different trophic niches within the ecosystem.

- Water table was found to be one of the main controls of the carbon turnover. However, the uncertainty in the measurements presented in Chapter 5 suggests that samplings should have greater spatial and temporal replication. The introduction of automatic gas samplers could increase the body of data and reduce the variability. Additionally, research must be undertaken to assess the use of water table estimations from telemetry approaches as proxy for GHG emissions from large peatlands areas.

- It has been recognized that trees in tropical peatlands are important conduits of GHG. Currently, all the measurements in the region have been performed at the surface and as suggested in Chapter 5 they could be severely underestimated. In order to address this knowledge gap research that evaluates the contribution of peatlands trees to the overall GHG emissions must be undertaken.

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Appendices

- Appendix A: Physicochemical characterization of peat cores
- Appendix B: Principal component analysis latent vectors
- Appendix C: Sampling and monitoring dates of in situ GHG emissions
- Appendix D: Carbon pool calculations

Appendix A: Physicochemical characterization of peat cores

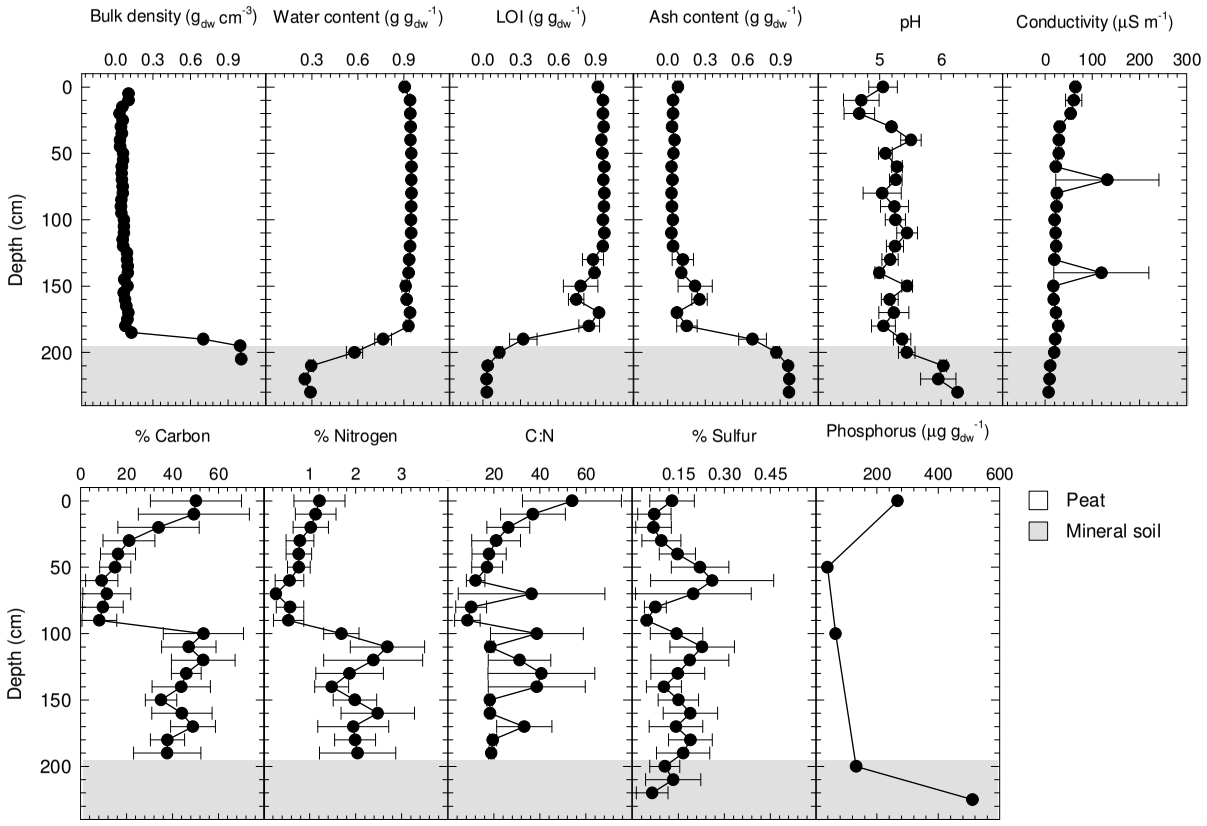

Fig. A.1 San San Pond Sak 1 (*R. taedigera* palm swamp)

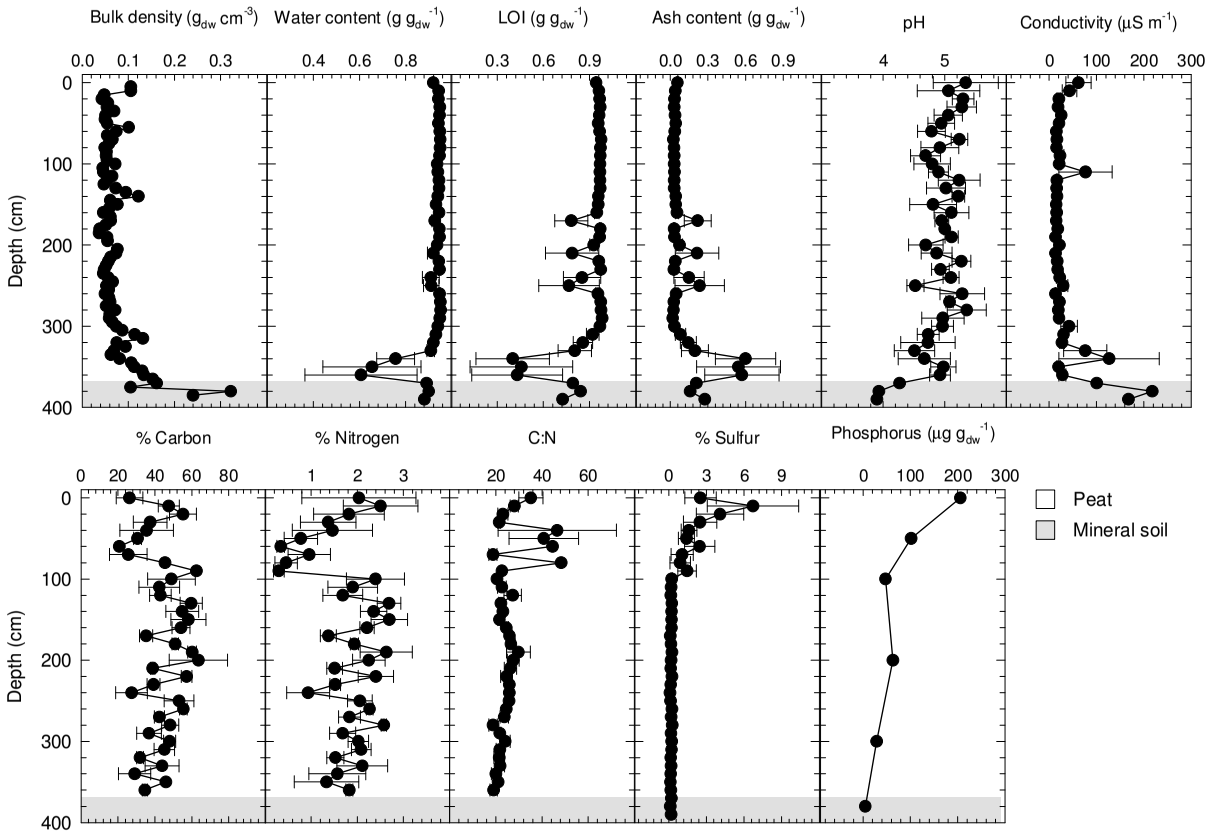

Fig. A.2 San San Pond Sak 2 (Mixed forest)

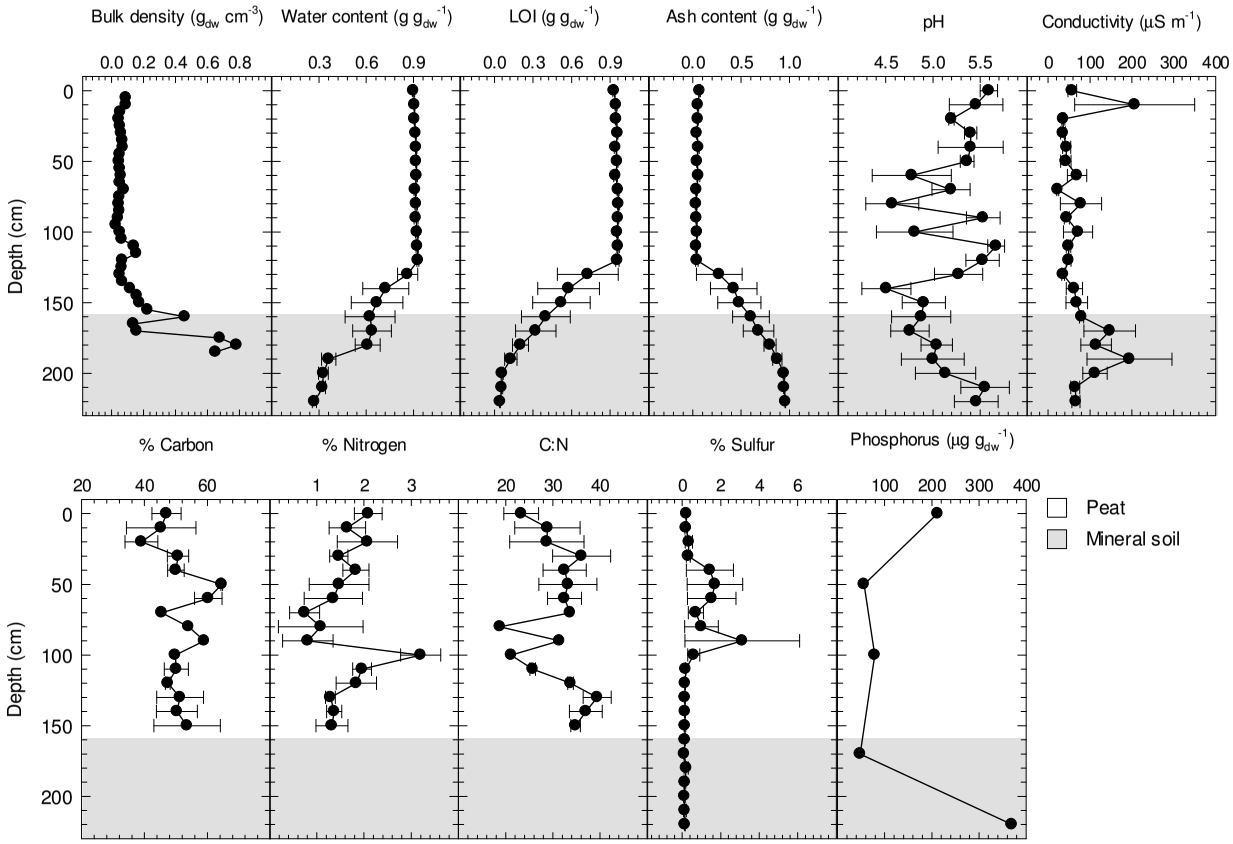

Fig. A.3 Bahia Almirante (Mixed forest)

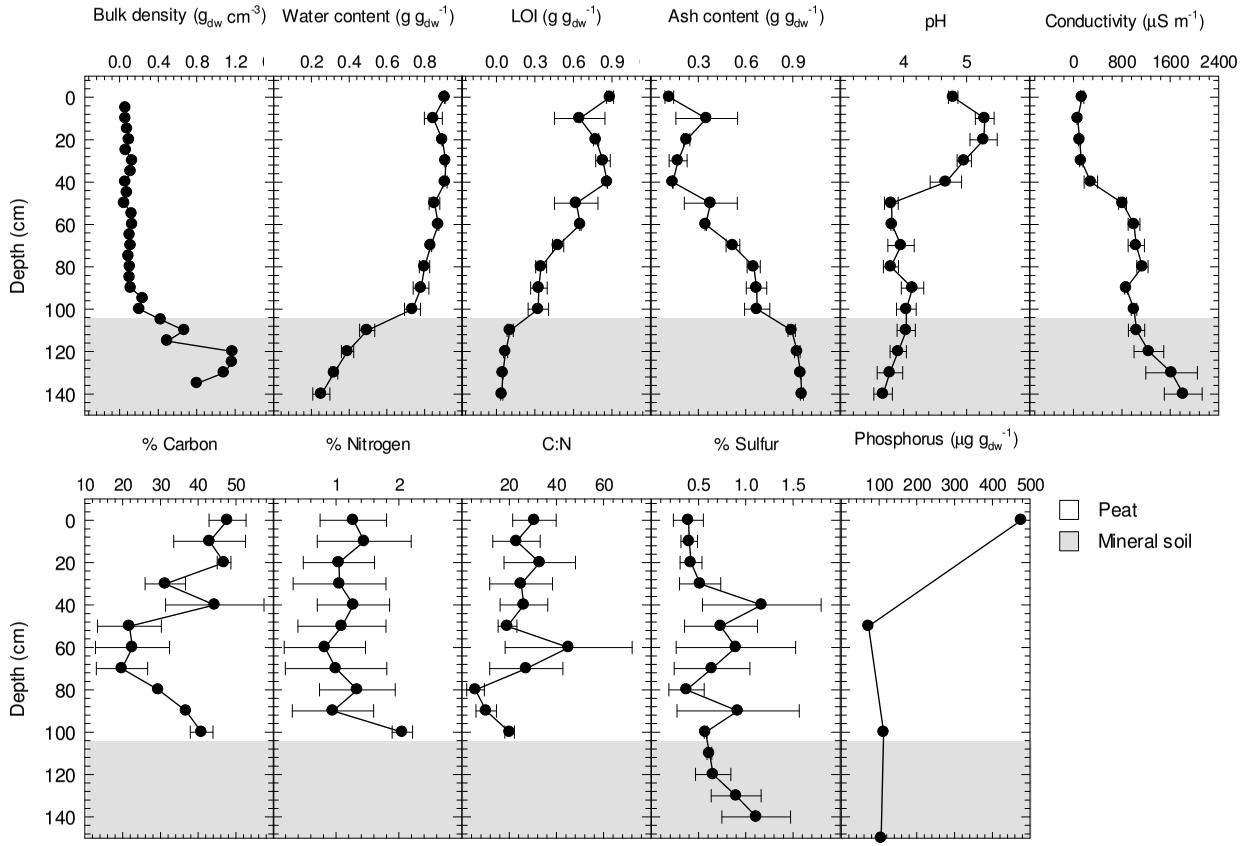

Fig. A.4 Chiriqui Grande

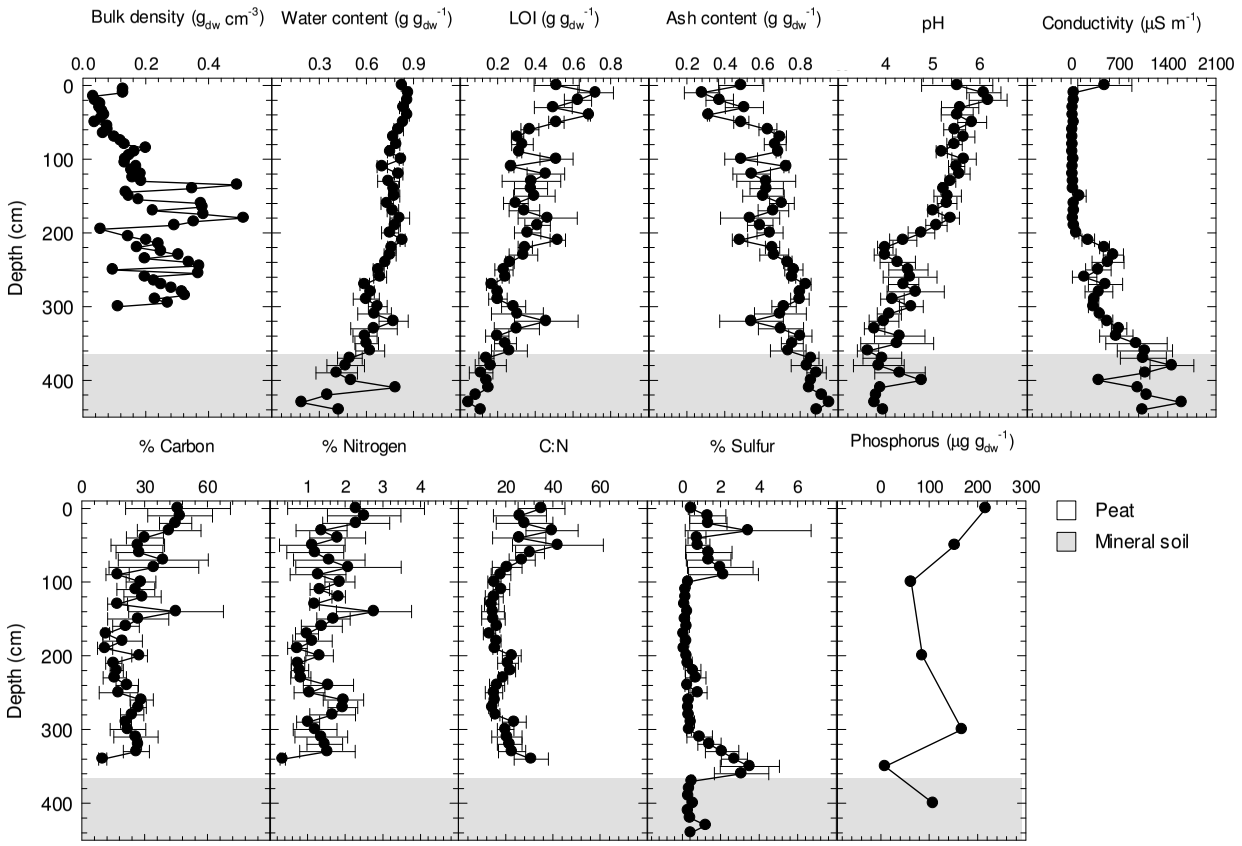

Fig. A.5 Cricamola River (*R. taedigera* palm swamp)

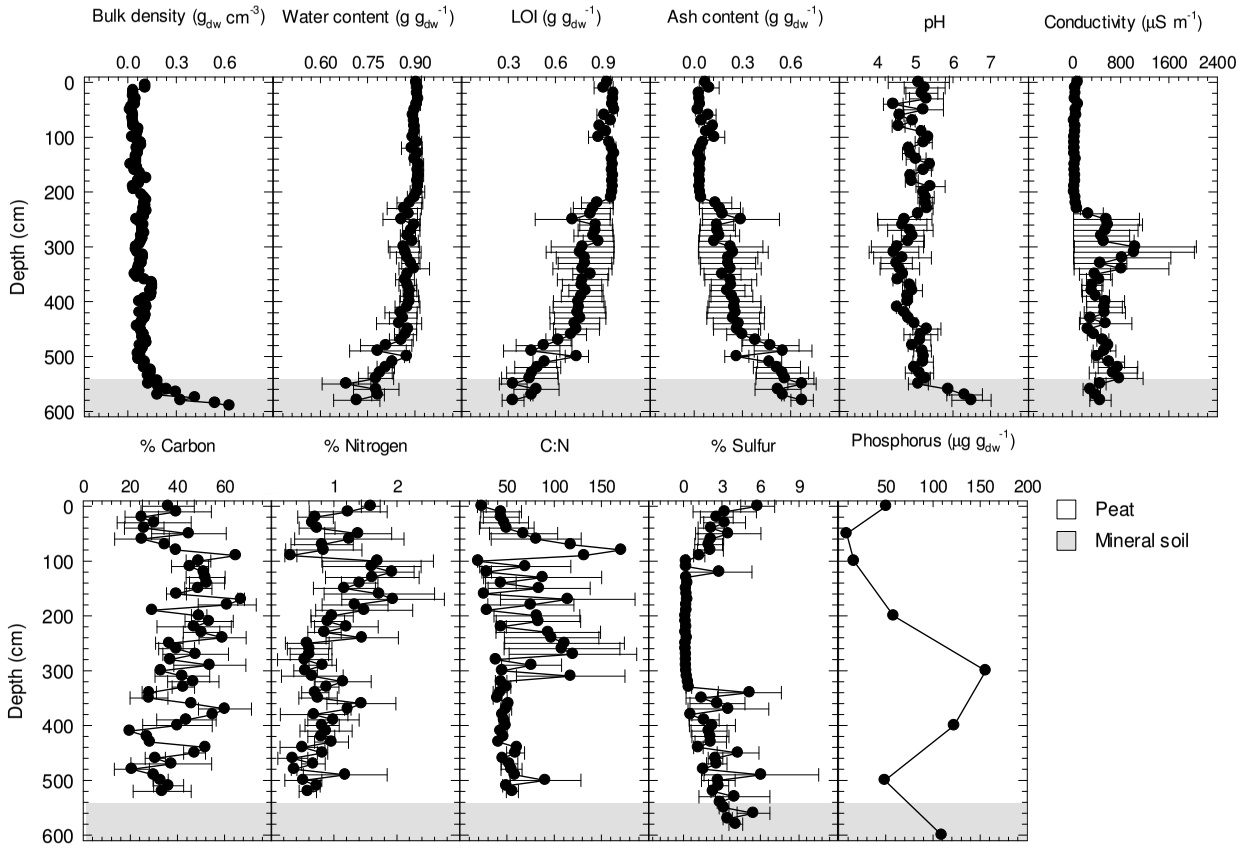

Fig. A.6 Damani – Guariviara (Mixed forest)

Appendix B: Principal component analysis latent vectors

Table B.1. Main latent vectors of Principal Component Analysis (PCA): San San Pond Sak 1

Compound	PC - 1	Compound	PC - 2
HexacoseneF	0.246	C31 FAMEF	0.266
C25 FAMEF	0.237	C26 FAMEF	0.250
C20 FAMEF	0.237	VeratroleL	0.248
C9 FAMEF	0.234	Trimethyl gallic acid methyl esterL	0.240
Methyl naphthalene	0.234	C30 FAMEF	0.239
Terpenoid	0.232	1,3,5 Trimethoxy-2-methylbenzeL	0.225
C22 FAMEF	0.231	C 28FAMEF	0.224
CresolP	0.231	C 15FAMEF	0.202
Methylated glucoseS	0.230	Dimethoxy acetophenoneL	0.201
3,4,5 TrimethoxybenzaldehydeL	0.228	C 17FAMEF	0.186

Proposed precursor: [L], Lignin; [F], Fatty Acid Methylated; [S], Carbohydrate; [C], Chlorophyll; [P], Phenol

Table B.2. Main latent vectors of Principal Component Analysis (PCA): Chiriquí

Compound	PC - 1	Compound	PC - 2
C22 FAMEF	0.242	C18 FAMEF	0.278
HexacoseneF	0.239	VeratroleL	0.271
C20 FAMEF	0.235	C16 FAMEF	0.268
Methyl naphthalene	0.227	C31 FAMEF	0.267
C14 FAMEF	0.227	Trimethyl gallic acid methyl esterL	0.261
C9 FAMEF	0.223	2,4,6 Trimethoxybenzoic acidL	0.248
Terpenoid	0.223	Trimethoxybenzene	0.239
Cresol	0.221	1,3,5 Trimethoxy 2-methylbenzeL	0.221
Prist-1-eneC	0.221	HomoveratroleL	0.201
Methylated glucoseS	0.220	C17 FAMEF	0.193

Proposed precursor: [L], Lignin; [F], Fatty Acid Methylated; [S], Carbohydrate; [C], Chlorophyll; [P], Phenol

Table B.3. Main latent vectors of Principal Component Analysis (PCA): San San Pond Sak 2

Compound	PC - 1	Compound	PC - 2
C15 FAMEF	0.213	CresolP	0.295
C24 FAMEF	0.206	Taraxerol	0.295
C22 FAMEF	0.205	3,4,5 TrimethoxybenzaldehydeL	0.293
C25 FAMEF	0.197	Methylated glucoseS	0.288
C31 FAMEF	0.196	C9 FAMEF	0.275
C20 FAMEF	0.195	Methyl naphthaleneF	0.267
C30 FAMEF	0.190	Terpenoid	0.267
C23 FAMEF	0.188	HexacoseneF	0.237
C28 FAMEF	0.187	C14 FAMEF	0.169
HomoveratroleL	0.183	Pentamethoxyheptanoic acidS	0.155

Proposed precursor: [L], Lignin; [F], Fatty Acid Methylated; [S], Carbohydrate; [C], Chlorophyll; [P], Phenol

Table B.4. Main latent vectors of Principal Component Analysis (PCA): Almirante

Compound	PC - 1	Compound	PC - 2
HexacoseneF	0.235	VeratroleL	0.270
C25 FAMEF	0.235	Trimethyl gallic acid methyl esterL	0.265
C14 FAMEF	0.232	C18 FAMEF	0.260
C12 FAMEF	0.231	2,4,6 Trimethoxybenzoic acidL	0.243
Prist-1-eneC	0.231	C16 FAMEF	0.243
C20 FAMEF	0.226	TrimethoxybenzeneL	0.210
C15 FAMEF	0.216	C17 FAMEF	0.205
C22 FAMEF	0.213	1,3,5 Trimethoxy 2-methylbenzeL	0.198
C23 FAMEF	0.212	HomoveratroleL	0.188
Pentamethoxyheptanoic acidS	0.211	Taraxerol	0.187

Proposed precursor: [L], Lignin; [F], Fatty Acid Methylated; [S], Carbohydrate; [C], Chlorophyll; [P], Phenol

Appendix C: Sampling and monitoring dates of *in situ* GHG emissions

Table C: Sampling and monitoring dates

Site	Block 1	Block 2	Block 3	Block 4	Block 5	Block 6
Chiriquí Grande	12/16/2010	03/24/2011	05/17/2011	07/06/2011	08/11/2011	09/15/2011
Cricamola River	12/10/2010	03/19/2011	05/28/2011	07/14/2011	08/10/2011	09/14/2011
San San Pond Sak 1a	12/07/2010	03/06/2011	05/16/2011	07/17/2011	08/12/2011	09/16/2011
San San Pond Sak 2b	12/21/2010	01/16/2011	04/27/2011	07/11/2011	08/14/2011	09/11/2011
Damani-Guariviara	12/08/2010	03/17/2011	04/07/2011	07/13/2011	08/09/2011	09/12/2011
Almirante Bay	12/05/2010	03/25/2011	04/06/2011	07/15/2011	08/13/2011	09/13/2011

[a,b] San San Pond Sak sites 1 and 2 correspond to Sites 1 and 2 respectively from Sjögersten *et al*., 2010

[c] Gas samples were collected between 9 am and 4 pm

Appendix D: Carbon Pool Calculations

The estimation of carbon pools in tropical peatlands requires information about: i) peatlands extent, ii) peat thickness, iii) peat bulk density and iv) peat carbon content. The uncertainty of any estimate can be traced back to the level of uncertainty in each of these factors.

The simplest approach to obtain a carbon pool estimate involves:

a) Measure the extent of a peatland (m^2)

b) Measure an average peat thickness (m)

c) Calculate the volume of peat in certain area (m^3)

d) Multiply the volume of peat by the bulk density ($m^3 \times g_{dw}\ m^{-3}$)

e) Multiply the total mass of peat by its carbon content ($g_{dw} \times gC\ g_{dw}^{-1}$)

$$Carbon\ pool = Peat\ volume\ \times Peat\ bulk\ density\ \times Carbon\ content$$

However, measuring the extent and thickness of a peatland requires significant amounts of field work, which is time consuming and expensive. Therefore, the average peat thickness, bulk density and carbon content has been use to estimate the carbon pools of large areas of peatlands in SEA (Page et al. 2011) and South America (Lähteenoja et al. 2009). Furthermore, the identification of phasic communities through the analysis of satellite imagery has been widely used to estimate the extent of peatlands. By adding up these assumptions, the current estimates of the carbon pool in tropical peatlands are highly uncertain.

The carbon pool estimates presented in this thesis were calculated as follows:

a) The area of the peatlands was estimated from the analysis of aerial imagery and existing maps of wetlands vegetation of Panama. It was assumed that *R. taedigera* palm swamps and mixed forests in the coastal region were likely to contain peat. This assumption was based on the exploratory campaign carried out in 2010, where the presence of peat was corroborated by manual coring in different locations (Fig. 2.1).

b) The peat thickness was estimated from available isopachous maps from San San Pond Sak and by manual coring (Fig. D; Table D). High and low estimates were to exemplifying how uncertain the carbon pool calculations can result if the peat thickness is under or overestimated.

c) The bulk density was measured in one core at each of the six sites selected for this study (Chapter 2, App. A). Measurements were made in 0.05 m intervals through the peat cores.

d) The carbon content was measured in 3 cores at each of the six sites selected for this study (Chapter 2, App. A). Measurements were made in 0.1 m intervals through the peat cores.

The carbon pool was calculated for each peat column by adding the carbon content (gC) of peat layers with a thickness of 0.1 m and 1 m^2 area; reducing the uncertainty of using an average bulk density and carbon content.

a)

$$\text{Peat Layer}_{\text{Dry Weight}} = \text{Peat Bulk Density } (\frac{g_{dw}}{m^3}) \times (0.1 \times 1 \times 1 \text{ m}) \text{ peat layer}_{fw}(m^3)$$

b)

$$\text{Peat Carbon Content} = \text{Peat Layer}_{\text{Dry weight}} (g_{dw}) \times \text{Carbon in sample } (\frac{gC}{g_{dw}})$$

c)

$$\text{Carbon content in peat colum} = \sum_{0.1\text{ m}}^{\text{Column depth (m)}} \text{Carbon content (gC)}$$

d)

$$\text{Carbon pool} = \text{Carbon content } (gC\ m^2) \times \text{Peatland extent } (m^2)$$

The carbon pool estimates presented here (Table D) show that the calculations are extremely sensitive to variations in the peat depth. For instance, the carbon pool at Damani – Guariviara was *ca*. 13 times higher when the average peat depth was used. Addressing these uncertainties are important if peatlands are to be included in conservation programs under the global carbon market scheme.

Table D- Estimates of the Potential Belowground Carbon Store at BDT. Lower estimate considers 1 m depth; the high estimate considers the average depth from the cores manually taken. For the CPD Cohen et al. (1989) was the depth reference.

Site	Peat depth range (m)*	Average depth (m)	Area (ha)	Carbon pool (MtC)
CPD	0.9 - 9.45	NA	9,230	20.44
Bahia Almirante	1.2 – 1.8	1.65 ± 0.15	3,189	0.79 – 1.84
Chiriquí Grande	0.8 – 1.0	0.96 ± 0.07	1,693	0.27 - 0.37
Cricamola	2.5 – 3.8	3.16 ± 0.37	697	0.25 – 0.97
Damani-Guariviara	1.9 – 5.8	4.83 ± 0.98	24,089	3.18 – 41.03
Total			38,898	25.02 – 64.54

* Peat definition: 30 % of dry weight organic matter (Joosten & Clarke, 2002).

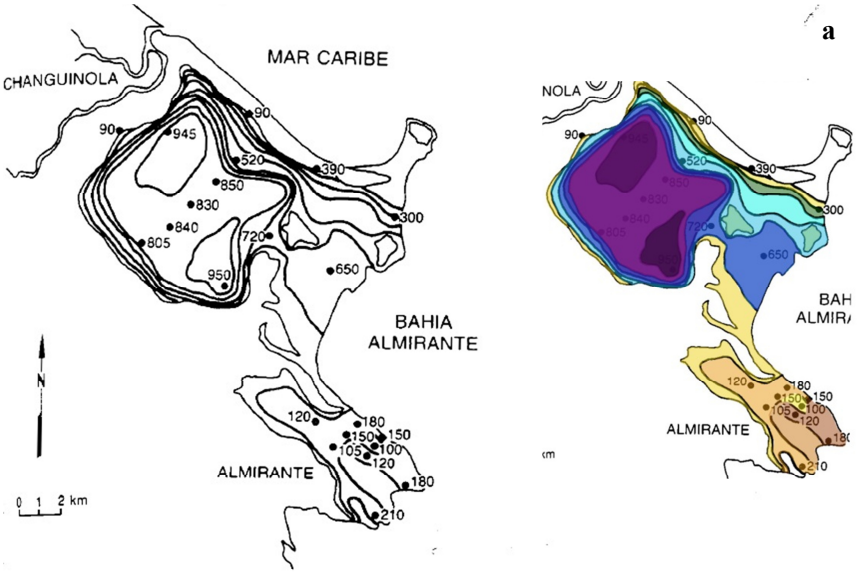

Fig. 3. Isopachous map of the peat deposit at Changuinola, Panama. Peat thickness (cm).

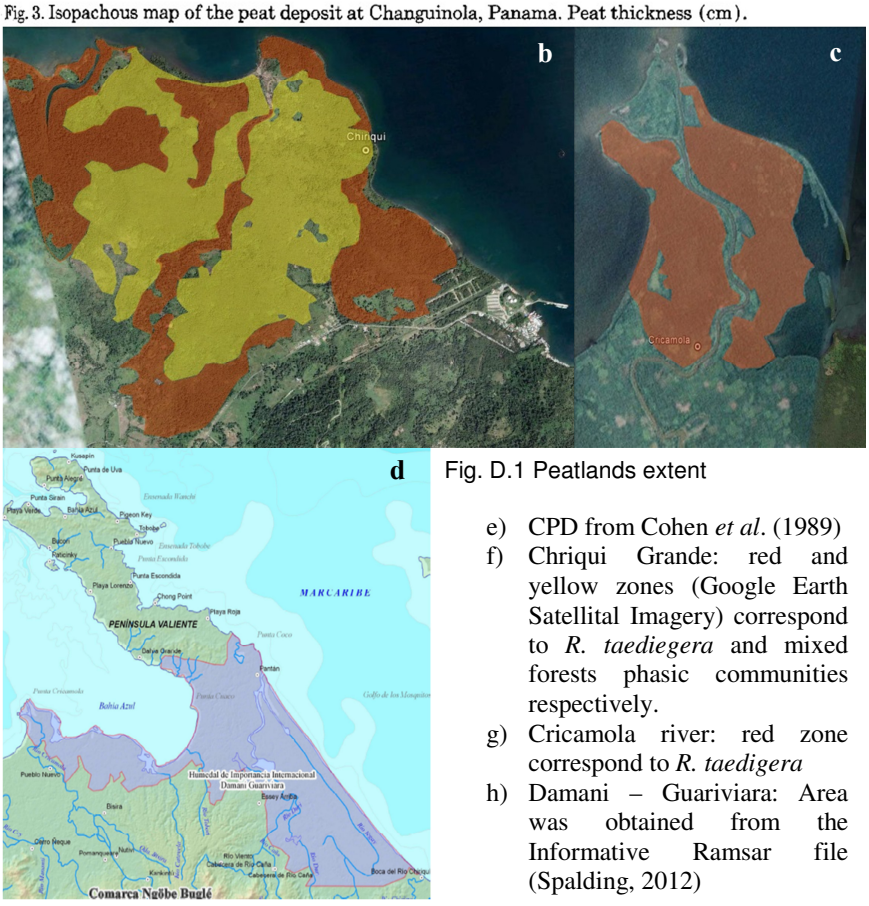

Fig. D.1 Peatlands extent

e) CPD from Cohen *et al*. (1989)
f) Chriqui Grande: red and yellow zones (Google Earth Satellital Imagery) correspond to *R. taediegera* and mixed forests phasic communities respectively.
g) Cricamola river: red zone correspond to *R. taedigera*
h) Damani – Guariviara: Area was obtained from the Informative Ramsar file (Spalding, 2012)