Soil carbon dynamics and aquatic metabolism of a wet–dry tropics wetland system

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Abstract Freshwater wetlands are a key component of the global carbon cycle. Wet–dry tropics wetlands function as wet-season carbon sinks and dry-season carbon sources with low aquatic metabolism controlled by predictably seasonal, yet magnitude-variable flow regimes and inundation patterns. However, these dynamics have not been adequately quantified in Australia’s relatively unmodified wet–dry tropics freshwater wetlands. A baseline understanding is required before analysis of land-use or climate change impacts on these aquatic ecosystems can occur. This study characterises geomorphology and sedimentology within a seasonally connected wet–dry tropics freshwater wetland system at Kings Plains, Queensland, Australia, and quantifies soil carbon stocks and wet- and dry-season aquatic metabolism. Soil carbon stocks derived from loss-on-ignition on samples to 1 m depth were 51.5 ± 7.8 kg C m⁻², higher than other wet–dry tropics wetlands globally, with potential for long-term retention at greater depths. Gross primary productivity of phytoplankton (GPP) and planktonic respiration (PR) measured through biological oxygen demand bottle experiments in the water column of sediment inundated under laboratory conditions show overall low GPP and PR in both wet- and dry-season samples (all wetland samples were heterotrophic with GPP/PR < 1). Despite the short-term dominance of aquatic respiration processes leading to net release of carbon in the water column under these conditions, there is appreciable long-term storage of carbon in sediment in the Kings Plains wetlands. This demonstrates the importance of wet–dry-tropics wetland systems as hotspots of carbon sequestration, locally, regionally and globally, and consideration should be given to their conservation and management in this context.

Keywords Seasonal freshwater wetland · Wetland conservation · Carbon sequestration · Soil organic carbon · Ecosystem productivity · Geomorphology

Introduction

Wetlands perform key ecological functions that support biodiversity, mitigate flood and coastal erosion impacts, enhance water quality, and store carbon
In many parts of the world, resource development and population pressure has led to a loss of ecosystem services and environmental degradation, including sediment loss, changes to hydrology, soil oxidation, and carbon loss (Junk et al. 2013). The river systems of Australia’s wet–dry tropics, and their associated permanent and ephemeral wetland complexes remain relatively undisturbed and unmodified due to low population density and minimal economic development (Warfe et al. 2011). Establishing a baseline understanding of soil carbon dynamics and aquatic metabolism is critical for determining potential land-use or climate change impacts on the conservation status of these systems.

Soil carbon in wetlands

Carbon dynamics in the sediments and aquatic ecosystems of wetlands are shaped by geology and climate setting, geomorphology, hydrology, vegetation structure and residence time (Renschler et al. 2007; Kayranli et al. 2010; Marín-Muñiz et al. 2014; Sutfin et al. 2016). Globally, the extensive areal extent of freshwater wetlands results in substantial total stores of soil organic and inorganic carbon, that are well documented for temperate and boreal wetlands, but less so for tropical freshwater wetlands (Nahlik and Fennessy 2016; Pettit et al. 2017a; Pearse et al. 2018). To date there are no accurate global estimates of the tropical freshwater wetland soil carbon pool (Villa and Bernal 2018). Within this wetland category, research has focused on humid tropical wetlands and less on wet–dry tropics wetlands (Peel et al. 2007; Warfe et al. 2011).

Wetland soil carbon storage is in part determined by its decomposition characteristics, that is, the balance between anaerobic and aerobic conditions (Sutfin et al. 2016). Globally, tropical wetlands have moderate soil organic carbon (SOC) density. This is due to the balance between elevated primary productivity and decomposition rates resulting from high temperatures and rainfall in the tropical regions (Ontl and Schulte 2012). Total carbon stocks are also dependent on the sediment bulk density. The high SOC stocks of tropical peat soils are due to high SOC concentrations, which are rich in organic matter yet moderated by their low bulk densities (Köchy et al. 2015). Carbon stores in deeper soils (below 1 m) can be stable for centuries if left undisturbed, contingent on local environmental and biological controls (Schmidt et al. 2011), with the residence time of this carbon vulnerable to environmental and anthropogenic disturbance (Bernal et al. 2016). Estimates of SOC concentration (SOC_{conc}), dry bulk density (DBD) and SOC stocks (SOC_{stock}) in global wetland classes are highly variable (Craft and Casey 2000; Köchy et al. 2015; Villa and Bernal 2018) (Table 1).

Within wet–dry tropics wetlands there is significant variation in soil carbon concentration and retention, dependent on wetland type and sediment distribution, composition and density. For example, during the inundation phase, carbon may have longer residence time in lentic (standing water) wetlands compared to more rapid export from lotic (running water) wetland systems (Marín-Muñiz et al. 2014). Vertisols, or ‘cracking clays’, characterised by wet season swelling and dry season shrinkage, facilitate carbon cycling down through the soil profile during the dry season as surface organic matter falls into the cracks (Cook et al. 2010; DES 2013). Australian wet–dry tropics soils are predominantly infertile sandy to sandy clay loams (Woinarski et al. 2005; Isbell 2016), although some are dominated by dark-coloured vertisols, occurring in alluvium filled valleys (Hutley et al. 2011). Faster aerobic decomposition in wet–dry tropics wetlands results in lower SOC levels and carbon sequestration (CS) rates than in humid tropical wetlands, causing these wetlands to function variously as carbon sources or sinks (Page and Dalal 2011; Bernal and Mitsch 2013; Adame and Fry 2016). Australian wet–dry tropics wetlands can be dry season carbon sources or wet season sinks under predictable seasonal flows (Page and Dalal 2011). Potentially significant carbon releases may occur through disturbance, temperature-induced evapotranspiration increases, or wetland desiccation under changed hydrology patterns (Bernal and Mitsch 2013). For example, drainage of Australian wet–dry tropics wetlands would convert them from carbon sink to source, with SOC losses of ~ 25% (Page and Dalal 2011). The impacts of land clearing, overgrazing, conversion to cropping, and burning, on soil structure breakdown, erosion and altered vegetation community, all contribute to SOC loss (Cook et al. 2010; Page and Dalal 2011). Within Australia, research on the carbon dynamics of ephemeral freshwater wetlands has focused on semi-arid wetlands (Boon and Sorrell 1991; Kobayashi et al. 2013, 2015; Villa and Bernal 2018).
Table 1  SOC\textsubscript{conc} and SOC\textsubscript{stock}, and DBD for (a) global wetland classes and (b) selected freshwater wetlands

| Climate zone wetland type | Wetland system | SOC\textsuperscript{a} (%) | SOC concentration\textsuperscript{2} (g C kg\textsuperscript{-1}) | DBD\textsuperscript{4} (g cm\textsuperscript{-3}) | SOC stock\textsuperscript{a} (kg C m\textsuperscript{-2}) | Depth (m) | Reference |
|---------------------------|----------------|-----------------------------|---------------------------------|---------------------------------|---------------------------------|--------|----------|
| (a) Global wetland classes |                |                            |                                 |                                 |                                 |        |          |
| Wet–dry tropics, intermittent | Global average e.g. northern Australia, southern Africa | .. | .. | .. | 4.1 | 1.0 | Köchy et al. (2015) |
| Wet–dry tropics, permanently inundated | Global average e.g. northern Australia, southern Africa | .. | .. | .. | 9.2 | 1.0 | Köchy et al. (2015) |
| Tropical, swamp forest | Global average e.g. Brazil | .. | .. | .. | 11.0 | 1.0 | Köchy et al. (2015) |
| Tropical, floodplain | Global average e.g. central Africa, Brazil | .. | .. | .. | 9.5 | 1.0 | Köchy et al. (2015) |
| All temperate and tropical | Global average | .. | .. | .. | 75 | 1.0 | Villa and Bernal (2018) |
| (b) Selected freshwater wetlands |                |                            |                                 |                                 |                                 |        |          |
| Wet–dry tropics, seasonal | Palo Verde NP, Costa Rica | 25.4–65.1 | 0.66 | Avg 8.2 (1.36 per 5 cm) | 0.3 | Bernal and Mitsch (2013) |
| Wet–dry tropics, seasonal | Okavango Delta, Botswana | 4.1–152.7 | 0.96–1.02 | 4.8–9.0 (0.8–1.5 per 5 cm) | 0.3 | Bernal and Mitsch (2013) |
| Wet–dry tropics, swamp | Veracruz, Mexico | 20.0 ± 2.91 | 50–225 | 0.31 ± 0.08 | 34.96 ± 1.3 | 0.8 | Marín-Muñiz et al. (2014) |
| Wet–dry tropics, marsh | Veracruz, Mexico | 13.73 ± 3.38 | 50–150 | 0.28 ± 0.05 | 25.85 ± 1.19 | 0.8 | Marín-Muñiz et al. (2014) |
| Sub-tropical, forested floodplain | Georgia, USA | 5.2 ± 1.3 | .. | 1.02 ± 0.11 | 5.3 | 0.30 | Craft and Casey (2000) |
| Temperate, seasonally inundated | Cobboboonee NP, Victoria, Australia | 29–62 | 196.3 ± 13.9 | .. | 68.3 ± 18.0 | 1.0 | Pearse et al. (2018) |
| Temperate, upland peat swamp | Blue Mountains, NSW, Australia | .. | 31–170 | 0.49–1.74 | 55.4–70 | 2.0 | Cowley et al. (2016), Cowley et al. (2018) |
| Temperate, wetland\textsuperscript{b} | Ohio, USA | .. | 146 ± 4.2 | 0.55 ± 0.01 | 4.2 | 0.35 | Bernal and Mitsch (2012) |
| Temperate, wetland\textsuperscript{c} | Ohio, USA | 1.0–10.4 | 50.1 ± 6.9 | 0.74 ± 0.06 | 1.5 ± 7.8 | 0.35 | Bernal and Mitsch (2012) |

Wet–dry tropics wetlands highlighted in bold
NP National Park
\textsuperscript{a}Range plus mean ± std error where available
\textsuperscript{b}Depressional
\textsuperscript{c}Flow-through
Woodhouse et al. 2015). While research on aquatic metabolism in Australia’s wet–dry tropics has been undertaken (Jardine et al. 2013; Ward et al. 2013; Pettit et al. 2017b), less is known of carbon stored in sediments in wet–dry tropics ephemeral wetlands (Finlayson et al. 2013).

Aquatic metabolism

In the water column, carbon is derived from autochthonous inputs from aquatic primary production, and allochthonous inputs from the littoral zone, benthic biofilms, and aquatic macrophytes (Sutfin et al. 2016, Wagner et al. 2017). Inorganic carbon is converted to organic carbon through photosynthesis (Kayranli et al. 2010) with the balance between gross primary productivity of phytoplankton (GPP) and planktonic respiration (PR) determining part of the carbon turnover in wetlands. Wetland inundation patterns vary according to their climate, hydrological regimes and geomorphology, which impacts their aquatic metabolism (Hoellein et al. 2013; Bortolotti et al. 2016). Semi-arid inland wetlands have highly intermittent inundation regimes and ‘booms’ of GPP and PR related to flood conditions (Kobayashi et al. 2011, 2013). In contrast, the Australian wet–dry tropics wetland inundation pattern drives a highly seasonal aquatic metabolism response, determining whether a wetland system is autotrophic or heterotrophic, or alternates between the two metabolism states (Webster et al. 2005; Ward et al. 2013; Bortolotti et al. 2016; Pettit et al. 2017b). Seasonal hydrology responses are the key driver in aquatic metabolism of wet–dry tropics wetlands, with the balance in aquatic metabolism dependent on the balance of processes occurring at that time (Pettit et al. 2017a).

Importantly, GPP and PR are fuelled by carbon, nitrogen, phosphorous and other nutrients, so the balance of GPP/PR can have some impact on SOC over time (Kobayashi et al. 2013). Critical to regulation of carbon storage is the seasonal hydrological regime, and whether the wetland is permanent or ephemeral (Page and Dalal 2011; Beringer et al. 2013). Permanent wetlands tend to remain carbon sinks under seasonal hydrology, though not in all cases. For ephemeral wetlands, the predictable wet season flooding may change carbon stores, moving wetlands from sink to source (Page and Dalal 2011; Beringer et al. 2013). The Australian wet–dry tropics is considered a low nutrient environment, partly due to its ancient and weathered geology (Pettit et al. 2017a). Planktonic metabolism enables carbon transformation in wetland aquatic ecosystems, with the balance between GPP and PR determining its contribution to wetland carbon storage (Kobayashi et al. 2013). Aquatic metabolism rates vary widely in freshwater wetland systems. Whilst some values for Australian wet–dry tropics river systems are available, values for wetlands are rare in the literature (Table 2).

Aims

This study examines carbon dynamics in sediment and the water column of a hydrologically variable wet–dry tropics wetland system in far north Queensland, Australia. We quantify soil organic and inorganic carbon in sediment to assess long-term carbon storage, and quantify aquatic metabolism to assess carbon transformation and short-term carbon cycling. Measurements of aquatic metabolism in this study were undertaken under controlled laboratory conditions and did not include metabolism due to epiphytic algae on macrophytes and biofilms. The specific aims are threefold. Firstly, quantify soil carbon concentrations and stock levels of permanent and ephemeral wetlands, across different geomorphic units and at various sediment depths. Secondly, quantify the response of aquatic microbial communities following inundation of wetland sediments by measuring the rates of carbon transformation through planktonic metabolism during dry and wet seasons, and thirdly, examine and synthesise these findings in the context of other wet–dry tropics wetland systems.

Regional setting

The Kings Plains Nature Refuge in the upper catchment of the Normanby River, ~ 50 km southwest of Cooktown, Queensland, Australia, contains a series of palustrine wetlands that cover ~ 31 km² (Fig. 1). Kings Lake (KL; ~ 10 km²) is a permanent wetland confined by bedrock on its northern perimeter, that contracts during the dry season. Downstream from KL, Top Plain (TP; ~ 6 km²) and Bottom Plain (BP; ~ 15 km²) are shallow ephemeral wetlands situated in a broader alluvial valley, inundated during
the wet season, and progressively drying out in the dry season except for their central channels, which retain water in pools (personal communication Hughes, 2017). The system has a wet–dry tropical climate, with mean monthly wet season rainfall of 258 mm and mean monthly dry season rainfall of 31 mm (mean annual rainfall 1485 mm) (Bureau of Meteorology 2018).

The regional geology is Devonian/Lower Carboniferous Hodgkinson Formations slates and greywacke, forming prominent hills that bound the valleys (Lucas 1962). Resistant chert strike-ridges project into the valley at the Kings Plains Nature Refuge, confining it to several partly closed basins where the connected, westward-draining wetlands of KL, TP and BP lie (Fig. 1). The valley follows the ancestral bed of the Annan River when it formed part of the Normanby headwaters (Heidecker 1973). However, the Annan River no longer flows into the Normanby catchment due to stream capture from a Pleistocene-era easterly regional geological tilt, reducing hydrological input to the valley (Best and Dallwitz 1963; Bik and Lucas 1963). As a consequence, the ~ 50 m deep valley has aggraded with fine clay and sand alluvium from low energy flows, forming the Kings Plains wetlands (Best and Dallwitz 1963). In the contemporary Annan River, there is evidence of carbon concentrated at > 50 cm depth in vertically accreted dark silty sediments, reflecting slow sediment deposition. There may be parallels with the post-stream capture low energy sediment deposition of the study area.

### Methods

**Topography and sediment sampling**

Wetland topography and geomorphology was assessed using a high-resolution digital elevation model derived from light detection and ranging (LiDAR) data, a digital elevation surface model (Japan Aerospace Exploration Agency 2018), aerial photographs, and previous mineral exploration studies reports. From this, the distribution of geomorphic units (landforms) was mapped and six valley-wide cross-sections (Transects A–F) and channel bed and wetland

| Wetland system                        | Wetland type                                      | GPP (mg C m\(^{-3}\) h\(^{-1}\)) | PR (mg C m\(^{-3}\) h\(^{-1}\)) | GPP/PR | References             |
|---------------------------------------|---------------------------------------------------|-----------------------------------|----------------------------------|--------|------------------------|
| Daly River, NT Australia              | Wet–dry tropics, low flow river                   | 0.00–0.03                         | 0.03–0.07                        | 0.0–0.5| Webster et al. (2005)  |
| Pantanal, Brazil                      | Wet–dry tropics, seasonal wetland                 | –                                 | –                                | 0.5    | Hamilton et al. (1995)  |
| Okavango River, Botswana              | Wet–dry tropics, seasonal floodplain              | 0.0–33.0 (mean 5.2)               | –                                | –      | Lindholm et al. (2007)  |
| Macquarie Marshes, NSW Australia      | Semi-arid, channel and non-channeled floodplain   | 3.7–405.5                         | 1.5–251                          | 0.2–15.6| Kobayashi et al. (2013) |
| Macquarie Marshes, NSW Australia      | Semi-arid, in-channel floodplain                  | 89.4 ± 9.2                        | 43.2 ± 5.6                       | 3.0 ± 0.3| Kobayashi et al. (2011) |
| Ryan’s Billabong, Murray River, NSW Australia | Semi-arid, floodplain wetland                    | 0.3–3.1                           | –                                | –      | Boon and Sorrell (1991) |
| Everglades, Florida USA               | Sub-tropical, seasonal wetland                    | 25.1–166.5 (mean 95.81)           | 131.2–278.1 (mean 204.7)         | 0.5    | Hagerthey et al. (2010) |

Wet–dry tropics wetlands in bold

*Range plus mean ± std error where available*
longitudinal profiles were created. Along the transects, bank exposures and sediment cores were used to analyse sedimentology. In 2016, five bank exposures were excavated at selected locations to characterise the sedimentology and stratigraphy of the upper ~2 m of the wetland. Sampling locations within each wetland were identified according to their different hydrological and geomorphological characteristics, and a twofold sediment sampling plan devised: (a) sediment cores for sedimentology and soil carbon analysis; and (b) surface sediment samples for an aquatic metabolism experiment to determine dissolved organic carbon concentration through ecosystem metabolism. Where possible, cores and surface

Fig. 1 Study location and map showing a state of Queensland, b study area within Normanby catchment, c Kings Plains study area relative to East Normanby and Annan Rivers, d satellite imagery of study area’s three interconnected wetlands, Kings Lake, Top Plain and Bottom Plain including image locations (ESRI 2018), e Kings Lake in dry season, view to SW, f Bottom Plain in wet season, view to SW, g Bottom Plain in wet season, view to NW. Images: d Agnew (e, h), T. Hughes (f, g)
samples were taken within ~ 5 m proximity of each other (Fig. 2). Sediment logs derived from mineral exploration studies in the 1960s were also used to assess sediment to depths of ~ 50 m (Best and Dallwitz 1963).

For sedimentology and carbon analysis, 20 sediment cores, each of depth 100 cm, were collected at 10 different sampling locations (2 cores per location) at each wetland during the 2017 dry season. For BP and TP, cores were taken on the floodplain, not in the channels. At KL, cores were taken as close to the water as possible. The replicate cores were used for sedimentology and soil carbon analysis, and for bulk density analysis. Additionally, 3 sediment cores, each of depth 300 cm, were taken, one at each wetland. Sediment cores were taken using a Christie Soil Sampler, a 4WD utility truck-mounted hydraulic hammer-powered 50 mm push tube, providing a 38 mm diameter sample. Each undisturbed 100 cm sample was extracted from the push tube, placed in a semicircular PVC channel, divided into 10 cm sections and sealed in double ziplock bags to prevent moisture loss. The 300 cm cores were divided into 3 × 100 cm sections and sealed to prevent moisture loss. Discrete sedimentary facies discerned in the cores were logged and bagged separately. There was minimal compression of the cores.

Due to the study site’s remoteness and logistical constraints, in situ aquatic metabolism experiments were not conducted, rather, at each wetland 10 sampling locations were identified. In both the wet-season and dry-season, 10 surface sediment samples, each of depth 10 cm (totalling 1000 cm³), were taken at random within a 10 × 10 m area at each sampling location. The 10 replicate samples from each location were combined, resulting in 10 × ~ 1000 cm³ samples from each of the three wetlands. Samples were refrigerated to avoid microcosms that could affect major biological change and were transported to the laboratory within 2 days of sampling. Inundation of sediment samples with water was commenced in the laboratory within 7 days of collection. Dry-season samples were collected in September 2017, and wet-season sampling took place in May 2018, immediately after site access was possible. Wet-season sampling occurred as close as possible to the dry-season locations, although in some cases high water levels meant some sample locations could not be accessed, so sampling occurred in nearby locations.

Sedimentology and carbon content

Characterisation and stratigraphy of the core samples was analysed in the laboratory using standard sediment analysis (Miall 1999; Munsell Color 2000). The samples and their stratigraphy were compared to drill hole data (Best and Dallwitz 1963) and bank exposures from previous investigations. Two BP bank exposure samples were analysed by qualitative x-ray diffraction (XRD) analysis to determine mineralogy using PANalytical X’Pert Pro Multi-purpose Diffractometer and CSIRO XPLOT and PANalytical HighScore Plus search/match software (Raven 2016).

Dry bulk density (DBD; g cm⁻³) was determined by standard methods (Blake and Hartge 1986). Sub-samples of known volume were weighed, then oven dried at 105 °C for 2 h and reweighed to determine dry mass and soil moisture content (Raymond and Lyons 2011). A temperature of 105 °C is commonly used for drying wetland soils, enabling comparison with other studies (Bernal and Mitsch 2008). A batch of 30 replicate samples was dried for a further 2 h at 105 °C; there was no further weight loss, therefore constant weight had been reached after the initial 2 h drying. DBD was calculated using the formula:

\[
DBD = \frac{M_{105}}{V}
\]

where \(M_{105}\) is the mass after drying at 105 °C, and \(V\) is the volume.

For soil carbon analysis, soil organic matter (SOM) content (%) was determined for sub-samples at 10 cm intervals in each core by loss-on-ignition at 550 °C (LOI550) (Raymond and Lyons 2011). Sampling from the centre of each of core was undertaken to avoid contaminated sediment from the core exterior. Homogenized 4–7 g samples were oven dried at 105 °C for 24 h, weighed, then combusted in a Lindberg Blue furnace at 550 °C for 5 h and reweighed. The same sub-samples then underwent loss-on-ignition at 950 °C for 1 h in the furnace to estimate soil inorganic matter (SIM) content (LOI950) (Raymond and Lyons 2011). LOI550 and LOI950 were calculated from the formulas:

\[
SOM\% = \frac{LOI_{550} \times 100}{M_{105} - M_{550}}
\]

where \(M_{105}\) is the mass after drying at 105 °C, and \(M_{550}\) is the mass after combustion at 550 °C.
where $M_{105}$ is the mass after drying at 105 °C, $M_{550}$ is the mass after combustion at 550 °C, and $M_{950}$ is the mass after combustion at 950 °C.

Given the large number of samples, LOI was considered the most appropriate and efficient method of determining organic and inorganic carbon content. In general, the conventional SOM to SOC conversion factor of 0.58, i.e. SOM = 58% carbon, is not supported by empirical evidence and considered too high (Pribyl 2010). A more conservative conversion factor of 0.50 (Pribyl 2010) was utilised. This avoids overestimating SOC, given potential problematic accuracy issues of LOI due to ignition temperature and duration, and structural water loss in clay rich soils (> 35% clay) (McKenzie et al. 2004). Structural water loss in clay-rich soils heated to high temperatures can lead to overestimation of SOM. Hoogsteen et al. (2015) recommends a clay correction factor of 0.09 for samples dependent on furnace temperature and duration, and was considered relevant for samples ignited from 550 to 950 °C. As the majority of samples in this study contained > 35% clay content, LOI$_{950}$ was adjusted with the clay correction factor of 0.09 (Hoogsteen et al. 2015).

Fig. 2 Sampling locations for sediment cores and wet and dry season aquatic metabolism surface sediment samples of a Top Plain and Bottom Plain and b Kings Lake (ESRI 2018)
SOC density (SOCd) is the density of carbon within a given sample analysed (Pearse et al. 2018), determined by the formula:

\[ \text{SOCd} = \frac{\text{DBD} \times \text{SOC}\%}{100} \]

where SOCd is SOC density in g C cm\(^{-3}\).

SOCconc is the concentration of carbon within a given sample analysed (Bernal and Mitsch 2008), determined by the formula:

\[ \text{SOCconc} = \frac{\text{SOC}\%}{10} \]

where SOCconc is SOC concentration in g C kg\(^{-1}\).

SOCstock is the conversion of SOC density to a volumetric measure, i.e. mass of carbon contained in a given sample (Pearse et al. 2018), determined by the formula:

\[ \text{SOCstock} = \text{SOCd} \times T \]

where SOCstock is SOC stock in g C m\(^{-2}\), and T is sample tube length (sample thickness) in cm of a given sample. To enable comparison with other studies, SOCstock was multiplied by 0.001 to convert g C m\(^{-2}\) to kg C m\(^{-2}\). Total SOCstock in each core was calculated by summation of incremental samples.

Aquatic metabolism

Dry surface sediment samples collected from the field were inundated to a depth of ~ 18 cm in plastic containers (dimensions 19 cm diameter and 19 cm deep) to allow a standardised biological oxygen demand (BOD) experiment under controlled laboratory conditions. Each 1000 cm\(^3\) sediment sample was incubated in 4 L of de-ionised (DI) water for 5 days to activate metabolism prior to the BOD experiments. A five-day incubation period has been shown to approach relatively stable initial inundation responses in sediment samples from other Australian wetlands (e.g. see Fig. 5 in Kobayashi et al. 2009, p. 852). The use of DI water standardised the quality of water added and minimised the risk of introducing microbial organisms such as bacteria and algae in the containers at the beginning of the incubation experiment (Kobayashi et al. 2009; Knowles et al. 2012). Following the 5 days of inundation, light (transparent) and dark (non-transparent) BOD bottles (300-mL volume) were filled with unfiltered water subsampled from each plastic container (i.e. one pair of BOD bottles per each 4 L inundated sediment sample) and then the BOD bottles were re-introduced to the containers for a 24-h BOD experiment to assess GPP and PR (Wetzel and Likens 2000). The experiment had an imposed diurnal ~ 4000 LUX light–dark cycle of 12:12 h at 25 °C. LUX was measured at the water surface. The BOD experiment was performed twice, first using 30 dry season sediment samples, and a second time using 30 wet season samples, and each included three control samples of 4 L of DI water that were also incubated. The DO concentration of each sample was measured at the beginning and end of the BOD incubation period using a DO meter (YSI Model 5100 DO/Temperature Meter, YSI Inc., Ohio) (YSI Incorporated 2002). From these measurements, GPP and PR for each sample was calculated using the formulas in Wetzel and Likens (2000):

\[
\text{GPP} = \frac{(\text{LB} - \text{DB}) \times 1000 \times 0.375}{\text{PQ} \times t}
\]

\[
\text{PR} = \frac{(\text{IB} - \text{DB}) \times 1000 \times \text{RQ} \times 0.375}{t}
\]

where IB is DO concentration at beginning (mg L\(^{-1}\)), LB is DO concentration in light bottle at end (mg L\(^{-1}\)), DB is DO concentration in dark bottle at end (mg L\(^{-1}\)), 0.375 factor is the ratio of moles of carbon to moles of oxygen (12 mg C/32 mg O\(_2\) = 0.375), PQ of 1.2 is photosynthetic quotient, RQ of 1.0 is respiratory quotient, and t is time (hours).

Statistical analysis

Comparison of soil carbon and aquatic metabolism were made among the wetlands using one-way analysis of variance (ANOVA), with the significance level of \(p = 0.05\). When one-way ANOVA showed significant results, post hoc Tukey’s pairwise comparisons were used to compare each pair of means. Where appropriate to compare two or more independent samples of different or equal size, the Kruskal–Wallis test by ranks was performed. Where appropriate, data values were log\(_{10}\)-transformed to stabilize the variance (Zar 2013). Differences in soil carbon and soil moisture between site means for the entire depth, and also differences in depth and the interaction between site and depth were tested using a repeated measures ANOVA, based on the \(F\)-test with the significance level of \(p = 0.05\). This method was used
as depth groups were related, and not independent of each other. All statistical analyses were performed using Minitab 18 (Minitab Inc 2017), except for repeated measures ANOVA, which was performed using SAS PROC GLM statistical software (SAS Institute Inc 2017).

Results

Geomorphology

The Kings Plains wetlands are situated in broad alluvium-filled basins up to ~ 4100 m in width, separated by narrow confined sections to ~ 450 m width at steep protruding chert ridges, with an overall very low valley slope of 0.0004 m m⁻¹ (Fig. 3). The upstream wetland, KL, contains a permanent lake covering ~ 1/3 of the 2700 m wide valley basin, and several backswamps, fed by ephemeral tributaries from surrounding hillslopes. During the wet season, the KL valley basin is inundated and the main channel contains continuous flow. Downstream of the lake outlet, the valley constricts to 450 m in width and the main channel has overall low sinuosity of 1.09, before it enters TP. Both downstream wetlands, TP and BP, contain a seasonally disconnected main channel. TP is situated in a 2000 m wide relatively flat basin, with a meandering channel (average sinuosity 1.55), floodplains, backswamps, and ephemeral tributaries fed from surrounding hillslopes. Sinuosity increases from 1.13 to 2.60 as the channel approaches TP’s downstream end, where the valley is ~ 600 m wide. The channel flows through this confined zone into BP, a broad flat valley basin up to 4100 m wide. Here the main channel divides and narrows, dispersing into distributary channels and a large floodout area across the floodplain. A palaeochannel is evident downstream of the left branch of the main channel. At the downstream end of BP, small return channels re-form into single channel. The change in elevation from KL to BP is ~ 9 m over ~ 22 km.

Sedimentology

The sedimentary structure of each wetland is relatively uniform, with little variation between the three wetlands. An overall fining of sediment occurs downstream through the three wetlands from silty/sandy clays found at KL (Transects A, B, C), light medium/silty clays at TP (Transect E), to very fine heavy clays at BP (Transect F) (Figs. 4, S1, S2). The exception to this was in the steeper channel zone immediately downstream of KL, where medium and coarse sands were found (Transect D) (Figs. 4, S1, S2). At the top of the system, KL had some stratigraphic variation (up to four sediment classes) while downstream at BP organic-rich clays sat atop uniform massive heavy clays. Surface sediments generally comprised dark brown or yellowish-brown coloured clays or clay loams with decaying organics that were most pronounced at KL. These overlaid massive clays, except in the channel zone which comprised interbedded clays and sands. Around KL, the dark organic rich clays transitioned into orange or black mottled grey clays, indicative of the saturated environment. On TP and BP, massive clays remained darker in colour with less orange mottling and increased black mottling (Figs. S1, S2). Generally, few roots were found below 30 cm depth, and in the case of TP and BP were absent altogether by ~ 70 cm depth. Ferruginous-manganese nodules, indicative of periodically saturated soils, were present in most sediment samples of TP and BP. The clays of TP and BP also exhibited the characteristics of vertisols (soils with clay content > 35%, shrink swell properties, and slickensides) (Isbell 2016). Bedrock is situated at a depth of 45 m in one of the previous exploration drill holes on Transect A, and there was evidence of saprolite in proximity to the northern and western margins of KL (Best and Dallwitz 1963). Bedrock was not reached in the channel zone, or on TP or BP.

Moisture content (wet:dry 105 °C to 100 cm depth) ranged from 10.5 to 75.8%, with a mean of 25.6% (Fig. 5; Table 3). Moisture content of surface sediments declined downstream through the three wetland areas, with mean 44.0% KL moisture levels transitioning to a uniformly low 16% at BP. At 100 cm depth, moisture content ranged from 20 (KL) to 26% (BP). DBD to 30 cm ranged from 0.8 to 1.9 g cm⁻³ with a mean of 1.3 g cm⁻³ (Fig. 5, Table 3). DBD for each sample gradually increased with depth, with a study area mean of 1.5 g cm⁻³ (to 100 cm depth) (Fig. 5; Table 3).
Soil carbon

Mean SOM (LOI$_{550}$) across the three wetlands was 7.1%, with TP having the highest, and KL the lowest, 7.6% and 6.6% respectively. Across all samples, KL had both lowest and highest LOI$_{550}$, 1.7% and 18.0% respectively (Table 3). Mean SIM (LOI$_{950adj}$) across the three wetlands was 2.7%, with TP the highest, and KL the lowest, 3.1% and 2.0% respectively. Across all samples, LOI$_{950adj}$ was lowest for KL and highest for TP, 1.0% and 5.0% respectively (Table 3). Overall, mean soil carbon for all samples was comprised of 97.3% organic matter, with 2.7% inorganic matter (Table 3).
Mean $SOC_{stock}$ to 100 cm depth across the three wetlands was 51.5 kg C m$^{-2}$, with BP having the highest and KL the lowest, at 54.0 and 48.7 kg C m$^{-2}$, respectively (Table 3). Variability of KL $SOC_{stock}$ was highest, compared to TP and BP (Fig. 5). Mean $SOC_{stock}$ to 30 cm depth across the three wetlands was 16.6 kg C m$^{-2}$, with KL highest and BP lowest, at 18.3 and 15.7 kg C m$^{-2}$, respectively (Table 3). $SOC_{stock}$ in the 3 m cores was 84.0, 87.6, and 83.9 kg C m$^{-2}$ for BP, TP and KL, respectively (Fig. 6, Table 3). $SOC_{stock}$ in these cores declined with depth (Figs. 5, 6). $SOC_{stock}$ for 0–20 cm compared to the deepest 20 cm of the core declined by 64.5, 56.0 and 87.6% for BP, TP and KL, respectively.

Fig. 4 Correlated cross-sections (Transects a–f) with sediment columns (where available). Transect A represents valley fill to ~ 50 m depth with a vertical exaggeration (VE) of 40x. Transects b–f show surface elevation to 6 m depth, to clearly display texture classes in sediment columns, and therefore the surface topography looks highly exaggerated (VE 435x). In reality, topography of transects b–f resemble Transect A. # Best and Dallwitz (1963). Refer to Fig. S1 in Online Resource 1 for full description of sediment columns included in transects.
Table 3  Descriptive statistics for (a) soil organic carbon (SOC): loss on ignition (LOI550, LOI950adj), moisture content, SOCconc and SOCstock, and (b) aquatic metabolism: dry and wet season GPP, PR, and GPP/PR ratio, for total wetland area, Bottom Plain, Top Plain, and Kings Lake

| (a) SOC | Totala | Bottom plain | Top plain | Kings lake |
|--------|--------|--------------|-----------|------------|
| LOI550 i.e. SOM % | 7.1 ± 0.13 (1.7–18.0, 32) | 7.1 ± 0.05 (5.4–8.9, 7) | 7.6 ± 0.17 (4.6–13.0, 22) | 6.6 ± 0.35 (1.7–18.0, 53) |
| LOI950adj (adj by 0.09)c | 2.7 ± 0.04 (1.0–5.0, 24) | 3.1 ± 0.03 (2.6–4.1, 9) | 3.1 ± 0.05 (1.7–5.0, 16) | 2.0 ± 0.05 (1.0–3.1, 24) |
| DBD to 100 cm depth (g cm⁻³) | 1.5 ± 0.01 (0.8–2.2, 16) | 1.5 ± 0.01 (1.1–1.7, 8) | 1.4 ± 0.02 (0.8–1.8, 15) | 1.6 ± 0.03 (0.9–2.2, 19) |
| DBD to 30 cm depth (g cm⁻³) | 1.3 ± 0.02 (0.8–1.9, 16) | 1.4 ± 0.03 (1.1–1.7, 11) | 1.2 ± 0.02 (0.8–1.4, 12) | 1.3 ± 0.04 (0.9–1.9, 18) |
| SOC stock to 100 cm depth (kg C m⁻²) | 51.5 ± 0.63 (50.6–57.5, 4) | 51.6 ± 1.15 (46.0–58.5, 13) | 48.7 ± 4.05 (30.4–64.3, 34) | 47.3 ± 1.35 (35.4–64.8, 16) |
| SOC stock to 30 cm depth (kg C m⁻²) | 16.6 ± 0.61 (10.4–26.5, 20) | 15.7 ± 0.28 (14.3–17.2, 6) | 15.9 ± 0.90 (12.3–21.4, 18) | 18.3 ± 1.48 (10.4–26.5, 25) |
| SOC stock to 3 m depth (kg C m⁻²) | 85.2 | 84.0 | 84.0 | 87.6 |
| SOC stock 3 m cores (kg C m⁻²) | 8.9 (0–20 cm), 3.2 (280–300 cm) | 10.9 (0–20 cm), 4.8 (280–300 cm) | 19.2 (0–20 cm), 2.4 (260–280 cm) | 29.3 (0–20 cm), 0.6 (280–300 cm) |
| % change (decline) | 64.5% | 56.0% | 87.6% | 83.9% |
| SOC conc to 100 cm depth (g C kg⁻¹) | 35.4 ± 0.66 (8.7–90.0, 32) | 35.5 ± 0.25 (27.2–44.4, 7) | 37.8 ± 0.83 (23.0–64.8, 22) | 32.8 ± 1.74 (8.7–90.0, 53) |
| SOC conc to 30 cm depth (g C kg⁻¹) | 44.9 ± 1.32 (16.4–90, 28) | 37.5 ± 0.43 (34.6–44.4, 6) | 47.3 ± 1.35 (35.4–64.8, 16) | 50.0 ± 3.34 (16.4–90.0, 37) |
| Wet season extent (km²) | 30.77b | 14.74 | 5.59 | 28.9 |
| Carbon pool to 100 cm depth (million tonnes ha⁻¹) | 1.583 ± 0.04 (1.343–1.823) | 0.796 ± 0.03 (0.766–0.825) | 0.289 ± 0.02 (0.268–0.309) | 0.509 ± 0.13 (0.375–0.643) |
| Moisture content wet:dry105°C (%) | 25.6 ± 0.62 (10.5–75.8, 42) | 21.1 ± 0.48 (11.3–31.1, 23) | 26.4 ± 0.51 (10.5–35.9, 19) | 29.3 ± 1.61 (12.5–75.8, 55) |

(b) Aquatic metabolism

| Dry season | (n = 26) | (n = 9) | (n = 7) | (n = 10) |
|------------|----------|--------|--------|--------|
| GPP (mg C m⁻³ h⁻¹) | 2.1 ± 0.40 (0.2–9.3, 95) | 1.5 ± 0.24 (0.4–2.7, 48) | 1.9 ± 0.96 (0.2–7.5, 135) | 2.9 ± 0.75 (1.2–9.3, 81) |
| FR (mg C m⁻³ h⁻¹) | 19.1 ± 1.77 (10.8–55.0, 51) | 16.0 ± 1.27 (11.3–23.8, 25) | 20.4 ± 4.17 (11.3–55.0, 66) | 20.6 ± 3.14 (10.8–37.8, 48) |
| GPP/PR | 0.1 ± 0.11 (0.0–0.3, 58) | 0.1 ± 0.09 (0.0–0.2, 50) | 0.1 ± 0.07 (0.0–0.1, 62) | 0.1 ± 0.14 (0.1–0.3, 47) |

| Wet season | (n = 29) | (n = 9) | (n = 10) | (n = 10) |
|------------|---------|--------|---------|--------|
| GPP (mg C m⁻³ h⁻¹) | 5.1 ± 0.62 (0.3–15.0, 66) | 3.4 ± 0.56 (1.0–5.7, 51) | 5.7 ± 1.06 (0.3–9.1, 59) | 6.1 ± 1.34 (1.4–15.0, 69) |
| FR (mg C m⁻³ h⁻¹) | 26.0 ± 1.96 (14.0–51.1, 41) | 19.4 ± 0.87 (15.2–22.5, 14) | 28.9 ± 3.98 (14.1–49.5, 43) | 29.5 ± 3.65 (18.6–51.1, 39) |
| GPP/PR | 0.2 ± 0.19 (0.0–0.5, 50) | 0.2 ± 0.02 (0.1–0.3, 43) | 0.2 ± 0.04 (0.0–0.5, 64) | 0.2 ± 0.02 (0.1–0.3, 37) |

Mean ± standard error, range and coefficient of variation (%) in parentheses
aAverage of three wetlands unless indicated
bSum of sites
cHoogsteen et al. (2015)
Comparison of SOC stock, soil moisture and DBD of 100 cm and 300 cm sediment cores across Transects B, C, E, and F are shown in Fig. 6. Overall, SOC conc declined with depth across all locations, most notably in the 0–50 cm range. Mean SOC conc for each 10 cm increment from 0–50 cm (0–10, 10–20, 20–30, 30–40, and 40–50 cm) differed significantly from the 90–100 cm increment (p < 0.0001, p < 0.0001, p < 0.0001, p = 0.008 and p = 0.0352), respectively. There was a statistically significant decline in SOC linearly rather than incrementally. All 100 cm sediment cores, including those forming part of the transects, were used in SOC analysis. Cores also used for sedimentology analysis of transects include one of the following suffixes (B, C, E, F) on their identifying code. Refer to Figs. S1 and S2 in Online Resource 1 for sediment columns and associated descriptions for all cores.
significant difference among wetlands, among depths, and interaction between wetland and depth, for log$_{10}$SOC$_{conc}$ as determined by repeated measures (GLM procedure) ANOVA ($F_{2,27} = 4.62$, $p = 0.0188$), ($F_{9,243} = 74.72$, $p < 0.0001$), and ($F_{18,243} = 17.65$, and $p < 0.0001$) respectively (Table 4).

Total C pool to 100 cm depth across Kings Plains was estimated at $1.58 \pm 0.04$ million tonnes based on wet season areal extent (Table 3) and extrapolated to $2.60 \pm 0.04$ million tonnes based on the 3 m cores.

Aquatic metabolism

For dry season sediment samples inundated under controlled conditions, GPP in the water column varied 46-fold (0.2–9.3 mg C m$^{-3}$ h$^{-1}$), and PR varied fivefold (10.8–55.0 mg C m$^{-3}$ h$^{-1}$), but there were no significant differences over the study area (Tables 3, 4). GPP/PR ratio varied 16-fold (0.02–0.31 mg C m$^{-3}$ h$^{-1}$), and was < 1 for all samples, representing a range restricted to the heterotrophic spectrum (Figs. 7, 8). There was a statistically significant difference between wetlands for GPP/PR as determined by one-way ANOVA ($F_{2,23} = 3.93$, $p = 0.0341$) (Table 4). Post-hoc Tukey’s test showed that KL was significantly higher than TP ($p = 0.04$). Overall, there was a significant positive relationship between log$_{10}$GPP and log$_{10}$PR ($r = 0.62$, $p = 0.0007$, n = 26).

For the wet season sediment samples inundated under controlled conditions, GPP in the water column varied 48-fold (0.3–15.0 mg C m$^{-3}$ h$^{-1}$) and PR varied fourfold (14.1–51.1 mg C m$^{-3}$ h$^{-1}$), but there were no significant differences over the study area (Tables 3, 4). GPP/PR varied 22-fold (0.02–0.47 mg C m$^{-3}$ h$^{-1}$) and was < 1 for all samples (i.e. heterotrophic conditions; Figs. 7, 8). There was a statistically significant difference in PR between wetlands as determined by one-way ANOVA ($F_{2,27} = 3.41$, $p = 0.0477$ for log$_{10}$PR) (Table 4). Post-hoc Fisher LSD test showed that KL was significantly higher than both BP and TP ($p = 0.02$, and $p = 0.04$, respectively). Overall, there was a significant positive relationship between log$_{10}$GPP and log$_{10}$PR ($r = 0.74$, $p = 0.0001$, n = 29).
Table 4  Statistical analysis of (a) SOC (SOCconc) and (b) aquatic metabolism (GPP, PR, and GPP/PR); significant results in bold

| Season       | Responses                                      | Test                  | P value |
|--------------|------------------------------------------------|-----------------------|---------|
| (a) SOC      |                                                 |                       |         |
| n/a          | log10SOCconc versus wetland                    | Repeated measures ANOVA | 0.0188  |
| n/a          | log10SOCconc versus depth                      | Repeated measures ANOVA | < 0.0001 |
| n/a          | log10SOCconc versus wetland by depth interaction| Repeated measures ANOVA | < 0.0001 |
| (b) Aquatic metabolism |                                  |                       |         |
| Dry          | log10GPP dry versus wetland                    | ANOVA                 | 0.0720  |
| Dry          | log10PR dry versus wetland                     | ANOVA                 | 0.7030  |
| Dry          | GPP/PR dry versus wetland                      | ANOVA + Tukey         | 0.0341  |
| Wet          | log10GPP wet versus wetland                    | ANOVA                 | 0.1206  |
| Wet          | log10PR wet versus wetland                     | ANOVA + Fisher LSD    | 0.0477  |
| Wet          | GPP/PR wet versus wetland                      | ANOVA                 | 0.8752  |
| Dry vs wet   | log10GPP dry versus log10GPP wet               | ANOVA + Tukey         | < 0.0001|
| Dry vs wet   | log10PR dry versus log10PR wet                 | ANOVA + Tukey         | 0.0024  |
| Dry vs wet   | GPP/PR dry versus GPP/PR wet                   | ANOVA + Tukey         | 0.0004  |
| Dry vs wet   | GPP BP dry vs wet                              | Kruskal–Wallis        | 0.0114  |
| Dry vs wet   | GPP TP dry vs wet                              | Kruskal–Wallis        | 0.0112  |
| Dry vs wet   | GPP KL dry vs wet                              | Kruskal–Wallis        | 0.0257  |
| Dry vs wet   | PR BP dry vs wet                               | Kruskal–Wallis        | 0.0792  |
| Dry vs wet   | PR TP dry vs wet                               | Kruskal–Wallis        | 0.0637  |
| Dry vs wet   | PR KL dry vs wet                               | Kruskal–Wallis        | 0.0696  |
| Dry vs wet   | GPP/PR BP dry vs wet                           | Kruskal–Wallis        | 0.0275  |
| Dry vs wet   | GPP/PR TP dry vs wet                           | Kruskal–Wallis        | 0.0147  |
| Dry vs wet   | GPP/PR KL dry vs wet                           | Kruskal–Wallis        | 0.1509  |

Fig. 7  Relationship between GPP and PR of study area in dry and wet seasons, showing (a) individual samples and (b) wetland means. GPP/PR < 1 for all samples (below red line), indicating a heterotrophic system for all samples, in both seasons. Bottom

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Several samples (dry = 4, wet = 1) with negative GPP values were excluded from data analysis (after Pace and Cole 2000). Negative GPP values occurred in samples when the post-inundation dark bottle respiration measurement was higher than the corresponding light bottle reading, possibly due to differences in particulate organic matter content between the two bottles. For both dry and wet season data, GPP and PR values were log-transformed to enable comparison with results from other Australian wetlands studies. When log-transformed, several log10GPP values were negative, and thus excluded from further analysis.

Across the wetland system, GPP, PR and GPP/PR from wet season sediment samples were significantly higher than for the dry season samples as determined by one-way ANOVA \((F_{1,53} = 24.44, p < 0.0001\) for log10GPP), \((F_{1,54} = 10.14, p = 0.0024\) for log10PR), and \((F_{1,54} = 14.28, p = 0.0004\) for GPP/PR) (Table 4). Post-hoc Tukey’s test showed that GPP, PR and GPP/PR for wet season samples were significantly higher than that for dry season samples \((p < 0.0001, p = 0.0002, \) and \(p = 0.0004, \) respectively). Five samples with negative GPP values and four samples with negative PR values were excluded from data analysis (Pace and Cole 2000).

GPP was significantly higher in all three wetlands for wet season samples than for dry season samples, as determined by Kruskal–Wallis \((H = 6.4, df = 1, p = 0.0114\) for BP), \((H = 6.4, df = 1, p = 0.0112\) for TP), and \((H = 4.97, df = 1, p = 0.0257\) for KL) (Figs. 7, 8; Table 4). GPP/PR was significantly higher for wet season samples from BP and TP than dry season samples as determined by Kruskal–Wallis \((H = 4.86, df = 1, p = 0.0275\) for BP) and \((H = 5.95, df = 1, p = 0.0147\) for TP) (Figs. 7, 8; Table 4).

**Discussion**

**Controls on wetland character**

Wetlands have formed in the Kings Plains region due to coincident geological and climatic changes over time. Cessation of source headwater flow from the ancestral Annan River through river capture (Heidecker 1973), has produced the basins in which a low
flow, depositional, wetland system now occurs (Best and Dallwitz 1963). Wetland processes dominate in this low flow environment due to the seasonality of the modern climate, with wet–dry tropics rainfall, resulting in seasonally (dis)connected channels and recurrent sediment deposition. The geomorphic units and sediment composition of the three wetlands at Kings Plains reflect varied hydrogeomorphic characteristics (Tooth et al. 2002), with sediments fining downstream to the low relief TP and BP, reflecting an overall decline in slope. Following the cessation of rainfall post wet season, suspended load deposition contributes to the heavy clay soils of the low relief plains, and declining energy (stream power) produces distributary channels and a large floodout, where water spread out across the alluvial plains, as well as a highly sinuous palaeochannel on BP (Tooth et al. 2002; Brierley and Fryirs 2005). The valley fill of the Kings Plains setting is representative of other zones in the wet–dry tropics of northern Australia that are dominated by black cracking clays (Cook et al. 2010; Hutley et al. 2011). The dominant clay mineral montmorillonite found in BE1_F infers an elevated water-holding capacity due to its high cation-exchange characteristics (Ahmad 1983). The lack of stratigraphy on TP and BP demonstrates the reworking, or self-mulching, of cracking clays common in periodically wet environments (McKenzie et al. 2004). Downstream of BP, water flows into a seasonally (dis)connected channel via a series of return channels which have potential for disturbance through knickpoint retreat. Resultant changes in the geomorphic structure of BP from floodout to continuous channel would lead to wetland drainage and loss and convert BP from a sediment accumulating soil carbon sink to a carbon source through the fluvial export of carbon (Sutfin et al. 2016; Cowley et al. 2018; Villa and Bernal 2018).

Soil organic carbon concentration, stock and residence time

There is a paucity of research available on soil carbon storage in Australian wet–dry tropics freshwater wetlands. Comparison to the few studies on similar wetlands globally needs to be approached cautiously due to diversity of wetland type. At Kings Plains the lower energy environment of TP and BP supports retention of carbon, and hence a slower decline in SOC$_{conc}$ through the soil profile than in KL. Kings Plains’ mean SOC$_{conc}$ of 35 g C kg$^{-1}$ (to 100 cm depth) aligns with wet–dry topics wetlands in Costa Rica and Botswana (Bernal and Mitsch 2013), but is lower than wetlands in the Mexican wet–dry tropics (Marín-Muñiz et al. 2014). This may be due to differences in geomorphic structure, hydroperiodicity, and vegetation structure between these wetlands (Marín-Muñiz et al. 2014). Kings Plains SOC$_{conc}$ are low when compared to wetland studies from other climate zones, such as NSW temperate highland peat swamps (Cowley et al. 2018), humid tropics forested wetlands of Costa Rica (Bernal and Mitsch 2013), and Victorian temperate zone depressional wetlands (Pearse et al. 2018) (Table 1).

In comparison, the Kings Plains wetland system has considerable SOC$_{stock}$ when compared to the few available wet–dry tropics wetland studies undertaken (Table 1). Total SOC$_{stock}$ to 1 m depth across the three wetlands is 1.58 ± 0.24 million tonnes. However, SOC$_{stock}$ could be greater if carbon is also being stored deeper in the profile, especially for BP and TP. Kings Plains SOC$_{stock}$ are either similar in magnitude to the Mexican wetlands (Marín-Muñiz et al. 2014) or considerably higher than Costa Rican and Botswanan wetlands (Bernal and Mitsch 2013), when adjusted for sampling depth. The SOC$_{stock}$ of Kings Plains are comparable to those of temperate Australian wetlands (Cowley et al. 2018; Pearse et al. 2018) (Table 1). SOC$_{stock}$ variability across KP’s three wetlands may be due to greater wet–dry cycling at shallower soil depths compared to sub-surface soils (Clarkson et al. 2014) and differences in vegetation structure among the wetlands (Pearse et al. 2018).

The usual pattern of SOC$_{stock}$ decline in non-peat soils from 0 to 100 cm depth occurs at Kings Plains (Jobbágy and Jackson 2000). However, surprisingly there is only a gradual decline from 100 to 250 cm in the 3 m cores from TP and BP, suggesting that these soils retain their carbon levels at depth. However, caution is advised due to a small number (n = 3) of 3 m cores taken. For cores to 75 cm, Pearse et al. (2018) found that the decrease in SOC$_{stock}$ through the profile is lower in wetland soils, compared to terrestrial soils, due to slow decomposition under saturated conditions. Cracking clays allow direct organic matter input to deeper soil layers during the dry season, which decompose under saturated conditions once swollen (Department of Environment and Science 2013). The
extent to which this decomposed organic matter adds to the SOC\textsubscript{conc} at depth is not well documented.

It is acknowledged that soil carbon measurement can be problematic due to spatial variability of carbon (Allen et al. 2010; Pallassser et al. 2013), non-standardised analytical methods (Allen et al. 2010), inclusion of SOM in SOC analysis (Conyers et al. 2011; Rayment and Lyons 2011), the use of SOM:-SOC conversion factors (Pribyl 2010), and LOI accuracy issues (Hoogsteen et al. 2015).

DBD has a strong effect on the levels of SOC\textsubscript{stock} derived from SOC\textsubscript{conc} (Köchy et al. 2015). High SOC\textsubscript{stock} values of peat-rich soils are characterised by their organic matter rich concentrations and low bulk densities (Köchy et al. 2015). In contrast, Kings Plains’ high SOC\textsubscript{stock} compared to other wet–dry tropics wetlands is largely driven by its elevated DBD (mean 1.5 g cm\textsuperscript{-3}) in its cohesive clay-rich wetland sediment, despite similar SOC\textsubscript{conc} (Table 1). Kings Plains’ mean DBD is between 1.5 and 5 times higher than the average DBDs of wet–dry tropics wetlands (Marín-Muñiz et al. 2014) (Table 1). Kings Plains SOC\textsubscript{stock} is comparable to other Australian temperate wetlands, but again this is due to their higher SOC\textsubscript{conc} offset by generally lower DBDs (Cowley et al. 2016, 2018; Pearse et al. 2018). For wet–dry tropics wetlands, detrital SOC storage (small particles) is critically important, as seen at Kings Plains, rather than macro carbon (plant matter) as found in peatlands. Generally in soils where DBD is > 1.6 g cm\textsuperscript{-3}, and specifically for clay soils > 1.4 g cm\textsuperscript{-3}, poor aeration and physical resistance inhibits root growth (McKenzie et al. 2004; Weil 2016), as evidenced by lack of roots from ~ 70 cm depth. The influence of DBD on SOC\textsubscript{conc} in determining SOC\textsubscript{stock} underscores the importance of accurate bulk density calculations when estimating larger scale carbon pools (Köchy et al. 2015).

Despite having the lowest SOC\textsubscript{conc}, the highest mean SOC\textsubscript{stock} to 1 m is found on BP. This wetland has the highest mean DBD for uniform, cohesive, very fine, cracking clay sediments. The physicochemical structure of the sediment allows the soil to remain saturated for extended periods, potentially resulting in higher SOC\textsubscript{conc} at depth. Despite the relatively dry surface layer, BP holds more moisture than KL in the 70 -100 cm depth range. Both SOC\textsubscript{stock} and SOC\textsubscript{conc} within KL is more variable, due to greater geomorphological complexity compared to BP and TP (Sutfin et al. 2016). The relationship between sedimentology and SOC is clear. SOC\textsubscript{conc} variation is a function of the different geomorphological drivers affecting each wetland (Aufdenkampe et al. 2011; Wohl et al. 2017). In the slow vertically accreting, uniform heavy clays across BP, SOC values show little variability between sampling locations. In contrast, at KL SOC\textsubscript{conc} is more variable across sampling locations and through the profile due to a complex arrangement of backswamps, proximity to input from the northern hillslope, and an extensive gradual drainage area on the southern lake edge. The sediments vary, with a higher proportion of sandy clays, which store less carbon than the fine clays of TP and BP. High moisture content delays vegetation decay, preserving carbon longer (Bernal and Mitsch 2012; Sutfin et al. 2016), with the highest moisture content found in the northern edge locations.

Little is known about the composition and structure of the deeper strata of the Kings Plains alluvial fill, apart from records of ~ 50 m depth at the study area’s eastern perimeter (Best and Dallwitz 1963; Bik and Lucas 1963) that show the basins have been in place since at least the late Pleistocene when the ancestral Annan River changed course (Heidecker 1973). This raises interesting questions about the extent and residence time of soil carbon at depth. The processes by which carbon resides in soils at depth is not fully understood (Bernal et al. 2016). A range of biophysicochemical interactions are implicated, including limitations of microbial activity on organic matter (Kuzyakov 2010), rising temperature (Hagerty et al. 2014), and physicochemical interactions with clays (Schmidt et al. 2011). Disturbance of deeper (to 3 m) stores of carbon in a sub-tropical sandy soil can be activated by the response of microorganisms to ‘priming’ by inputs, such as organic nitrogen (Bernal et al. 2016). Whether this priming would occur in BP and TP where carbon is strongly bonded to clay is not understood. The estimate of mean 1.58 ± 0.04 million tonnes of carbon stock at Kings Plains could therefore be considered a minimum.

Aquatic metabolism and ecosystem function

Wetlands can display significant spatial and temporal variation in the balance between autotrophy and heterotrophy, even when they have similar hydrological, geomorphological and ecological characteristics.
Despite the variations in GPP, PR and GPP/PR found within and between samples from the wetlands in the Kings Plains system, both dry and wet season samples from all three wetlands inundated under controlled conditions were heterotrophic, with GPP/PR in the mesocosm water column consistently < 1. There is the possibility of significant spatial heterogeneity in aquatic metabolism in wetlands due to varying inundation regimes, with variation in phytoplankton abundance and carbon dynamics (Cardoso et al. 2012). This is likely in the Kings Plains wetlands, as, during the dry season, the wetlands become hydrologically disconnected systems and KL remains inundated while TP and BP completely dry out. This is due to their position in the valley, and their constituent geomorphic units, including the presence and/or absence of major channels. Based on our findings, KL has slightly higher GPP and PR than at TP and BP, but if KL were to become channelised leading to less inundation, then the balance of aquatic metabolism in this part of the system may not change significantly (i.e. GPP/PR would stay around 0.2). It is also clear that there is less change in GPP and PR at BP between the wet- and dry-seasons, probably due to the fact that BP has the least inundation during the wet season. Therefore, if KL and TP were to receive less inundation, akin to BP, then a suppression of GPP and PR is likely, perhaps leading to a change in GPP/PR ratio.

While Kings Plains’ wet season GPP and PR were greater than the dry season, overall levels of GPP/PR were still relatively low, and remained heterotrophic under controlled conditions. These results are at the low end of the productivity range of other wet–dry tropics wetland systems within northern Australia (Butler 2008), and globally (Hamilton et al. 1995; Lindholm et al. 2007) (Table 2). In northern Australian wet–dry tropics wetlands, low overall GPP and PR levels may be due to several factors, including system-wide turbidity from suspended clay particles, as evidenced at Kings Plains, in a phytoplankton dominated system (Butler 2008; Ward et al. 2013) and from feral animal foraging induced turbidity (Doupé et al. 2010). Additionally, possible nutrient deficiency in these waters can also limit productivity levels (Butler 2008; Pettit et al. 2017b). Sub-tropical wetlands are also characterised by seasonal wet–dry periods (Peel et al. 2007), and can display higher levels of productivity, but still with a dominance of heterotrophy (Hagerthemy et al. 2010). However, the drivers in sub-tropical wetlands differ; primary productivity can be suppressed through shading induced by the presence of dense floating aquatic plants (Hagerthemy et al. 2010) rather than turbidity in the water column.

For aquatic metabolism in this study, only part of the carbon production was measured in BOD bottles using unfiltered water samples from the water column of inundated sediment samples, which does not include, for example, primary production and respiration due to epiphytic algae on macrophytes (Pettit et al. 2016), or biofilms consisting of benthic algae and heterotrophic microorganisms (Bunn et al. 2006). Although the use of DI water and imposing a diurnal ~ 4000 LUX light–dark cycle in the laboratory ensured that water quality, light intensity, length of daylight hours, and temperature were standardised for all incubation experiments, they may have led to lower levels of GPP and PR than under ‘natural’ conditions. Although limitations of controlled laboratory experiments exist, whereby the whole ecosystem metabolism has not been measured due to the exclusion of epiphytic algae and biofilm primary production and respiration measurements, and potential lower light intensity than under natural conditions, our findings demonstrate that antecedent environmental conditions leading to inherent sediment and biological characteristics in the Kings Plains wetlands drive...
similar aquatic metabolism responses to inundation across the system.

Furthermore, the strongly seasonal hydrological pulse of wet–dry tropics wetlands such as Kings Plains contrasts markedly with the highly variable and intermittent hydrological regimes of semi-arid inland floodplain wetland systems (Bureau of Meteorology 2018). Carbon cycling and transformation has been found to be highly variable in channel and non-channel floodplain environments in semi-arid inland systems, although usually these systems are predominantly autotrophic (Kobayashi et al. 2013, 2015; Woodhouse et al. 2015). Wet–dry tropics wetlands such as Kings Plains possibly have a naturally low productivity baseline compared to other wetland types, perhaps due to the muted response of phytoplankton, zooplankton and other organisms that are adapted to seasonal inundation, and also due to turbidity from suspended clays. Regular seasonal inundation of Kings Plains possibly elicits a lower productivity response compared to the ‘boom-bust’ productivity pattern of semi-arid inland wetlands systems (Sheldon et al. 2010; Arthington and Balcombe 2011). Based on our and other studies, we present a conceptual model that shows how these systems vary in terms of GPP and PR (Fig. 9).

### Implications for wetland conservation

Australia has some of the last relatively undisturbed wet–dry tropics wetlands in the world (Pettit et al. 2017a). Despite recognition of their importance, significant knowledge gaps of this extensive, complex and variable wetland class exist (Warfe et al. 2011; Beringer et al. 2013; Pettit et al. 2017a). At the global scale, estimates of the soil carbon pool of tropical freshwater wetlands are considered inaccurate (Villa and Bernal 2018). Understanding the drivers of ecosystem function (Warfe et al. 2011) and soil carbon storage in these relatively unmodified systems is an important step toward redressing this knowledge gap, and also provides essential baseline information for their future conservation and management. This is needed for both national and global wetland conservation efforts, providing insight for assessment and management of changes associated with future economic development and climate impacts in a changing world.

Specific threats to wet–dry tropic wetlands in Queensland include the renewed interest in the promotion of irrigated agricultural development in northern Australia, for example in the Flinders and Gilbert catchments (Ash et al. 2017). Water extraction for economic development is highly likely to impact the complex wetland systems associated with Australia’s northern rivers (Ward et al. 2013). Agricultural development would potentially release carbon through irrigation-induced changes to hydrological regimes (Finlayson et al. 2013). Wetland drainage and carbon release will change the distinctive ecological character of these rivers. Page and Dalal (2011) estimate that ~25% of SOC in the top 1 m of wetland soils drained for economic development will be lost within the first 50 years of drainage. In Australia’s wet–dry tropics, the most productive areas for economic development, especially grazing, include regions with cracking clay soils (Cook et al. 2010). The conversion of freshwater wetlands to grasslands for cattle grazing in a Mexican wet–dry tropics zone was found to cause SOC loss within 20 years of conversion (Hernandez et al. 2015). SOC losses occur as a result of soil structure degradation and erosion, and modification of vegetation cover from cattle grazing and animal foraging (Baker et al. 2000).

Further, climate change impacts on Australia’s wet–dry tropics zone are expected to significantly change hydrological regimes, particularly floodplain and wetland inundation. Increased rainfall predicted under various future climate scenarios for northern Australia (IPCC 2014) may be offset by increased evapotranspiration rates under warmer temperatures (Hamilton 2010). Soil moisture content was found to be the primary environmental factor controlling GHG emissions from a wet–dry tropics wetland in northern Australia (Beringer et al. 2013). Increasing temperatures and longer dry periods, albeit with potentially less frequent but more intense rainfall and cyclone activity, may lead to wetland desiccation and erosion, causing a change from carbon sink to source (Finlayson et al. 2013; Larkin et al. 2016). For the persistence of SOC within a wetland, environmental and biological controls dominate over the molecular structure of soils (Schmidt et al. 2011). Having a baseline scientific understanding of the carbon and metabolism dynamics of these aquatic ecosystems is critical for their protection and persistence into the future.
Conclusion

The wet–dry tropics freshwater wetlands of Kings Plains are diverse and display variability in their geomorphic, sedimentological and hydrological characteristics. These factors contribute to the considerable, but spatially variable, soil carbon stores and low aquatic metabolism responses measured in this study. Hydrogeomorphic conditions drive sediment composition and distribution, resulting in a considerable long-term carbon pool in the low energy, clay-rich sediment deposits of the wetlands. Relatively undisturbed alluvial fill wet–dry tropics wetlands like Kings Plains hold 51.5 kg C m⁻² of carbon stock with the possibility of large carbon pools at depth. Further study of soil carbon stores is needed to accurately quantify the total carbon pool, for this and other equivalent wetland systems. Aquatic productivity was low in both the wet and dry season and all three wetlands were heterotrophic. Naturally, the inclusion of other carbon cycle components is critical for understanding carbon dynamics of wet–dry tropics wetlands and requires further work. Both the short-term dominance of carbon release by aquatic metabolism, and the long-term storage of carbon in sediments, demonstrate the importance of prevention of wetland deterioration and preservation for their biodiversity and significant carbon storage potential as part of environmental conservation efforts in northern Australia.

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