Ecosystem productivity of a wet-dry tropics wetland system: Establishing a baseline understanding for conservation

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Key Points

- Measurement of ecosystem productivity across three connected ephemeral and permanent wet-dry tropics freshwater wetlands
- Ecosystem productivity as measured by biological oxygen demand indicates dry season low productivity
- Understanding ecosystem productivity is important as baseline for conservation

Abstract

Terrestrial environments, including freshwater wetlands, play a key role in global carbon dynamics. Australian wet-dry tropics savannah wetlands function as wet season carbon sinks or dry season carbon sources under seasonal, yet variable, flow regimes. Land-use and climate change potentially affect carbon dynamics by altering these hydrological regimes and associated ecosystem processes, however these factors are inadequately quantified in Australia. Inundation patterns in these wetlands are hypothesised to drive a characteristic response in aquatic gross primary productivity and respiration. This response, as a significant component of wetland carbon cycling, would inform whether a wetland system is autotrophic or heterotrophic. This study assessed variation in aquatic ecosystem productivity in a wet-dry tropics wetland system at Kings Plains, Queensland. Ecosystem productivity was measured from samples obtained during the dry season in ephemeral and permanently inundated wetland areas. A biological oxygen demand experiment was undertaken using sediment inundated under laboratory conditions. Results indicated a dominance of respiration. This signal differs from semi-arid inland floodplain environments, where strongly intermittent hydrological regimes drive autotrophic aquatic productivity. Do the results indicate a seasonal low, or do wet-dry tropics wetlands have a naturally low productivity baseline? To assess for seasonal differences, samples will again be collected and analysed, immediately following the wet season, to determine wet season aquatic ecosystem productivity.

Keywords

Aquatic metabolism, carbon dynamics, gross primary productivity, respiration, seasonal tropical wetland

Introduction

Australian wet-dry tropics savannah wetlands function as wet season carbon sinks or dry season carbon sources under predictably seasonal, yet magnitude-variable flow regimes (Page and Dalal 2011). These wetlands can be permanently inundated or seasonally ephemeral. Globally, wet-dry tropics savannah wetlands have large differences in wet season length and intensity, and dry season rainfall (Mitsch, Nahlik et al. 2010). In Australia, the hydrological flux is characterised by a short intense wet season, and a long dry season with minimal rainfall, albeit with year-to-year magnitude differences (Ward, Hamilton et al. 2013). Understanding tropical wetland carbon dynamics is important, as under a changing climate, potentially significant increases in carbon releases may occur through wetland disturbance, evapotranspiration increases, or wetland desiccation from altered hydrological regimes (Bernal and Mitsch 2013). Land use changes through economic exploitation of northern

Australian savannah wetlands for agricultural development would potentially release carbon through irrigation-induced altered hydrological regimes (Finlayson, Davis et al. 2013). Additionally, the extent of savannah wetland ephemerality determines their overall carbon dynamics; this is inadequately quantified in the Australian context. More detailed knowledge of wet-dry savannah wetland carbon dynamics would be useful for both carbon and climate change modelling.

Carbon in wetlands can be found in both sediments, as soil carbon, and in the water column (Mitsch and Gosselink 2000). Aquatic productivity in the water column, as part of carbon cycling and transformation of wetlands, can be analysed by measuring phytoplanktonic photosynthetic oxygen production (gross primary productivity) (GPP) less oxygen consumption over a specified length of time (Hoellein, Bruesewitz et al. 2013). Planktonic metabolism enables carbon transformation in wetland aquatic ecosystems, with the balance between GPP and planktonic respiration (PR) determining its contribution to the wetland carbon storage (Kobayashi, Ralph et al. 2013).

Wetland inundation patterns vary according to their climate, hydrological regimes and geomorphology, impacting their ecosystem productivity (Hoellein, Bruesewitz et al. 2013, Bortolotti, Louis et al. 2016). Semi-arid inland wetlands have highly intermittent inundation regimes, and explosions of productivity (Kobayashi, Ralph et al. 2013). The Australian wet-dry tropics wetland inundation pattern drives a highly seasonal elevated aquatic productivity response (Ward, Hamilton et al. 2013). This response is a significant component of wetland carbon cycling and transformation and aids in understanding whether a wetland system is autotrophic or heterotrophic (Bortolotti, Louis et al. 2016). Autotrophic phytoplankton can store energy through photosynthesis alone, whereas heterotrophic zooplankton consume organic matter produced by other organisms (Kirschbaum, Eamus et al. 2001) (Figure 1).

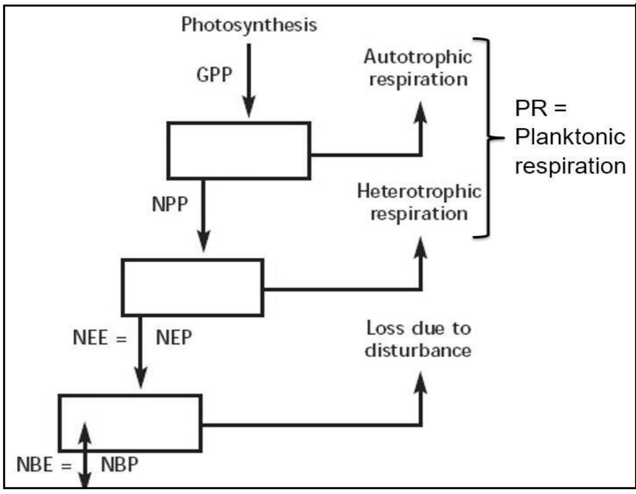


Figure 1. Diagrammatic representation of main carbon fluxes in aquatic ecosystems. The carbon loss by autotrophic respiration represents ~50% of carbon fixed by phytoplankton. GPP = gross primary productivity, NPP = net primary productivity i.e. GPP less autotrophic respiration by phytoplankton, NEP = net ecosystem productivity i.e. NPP minus heterotrophic respiration by plankton, NBP=carbon stock change after natural or anthropogenic disturbance. Adapted from Kirschbaum, Eamus et al. (2001).

Wet-dry tropics wetlands become increasingly disconnected as the dry season progresses. Australia palustrine wetland waterbody area is estimated to shrink by >90% from March (peak of wet season extent) to end October (Ward, Hamilton et al. 2013). This study broadly aims to understand ecosystem productivity of the Kings Plains wet-dry tropics savannah wetland system, comprised of a series of permanently inundated and ephemeral wetlands. Specifically, this paper aims to evaluate the:

1. Level of carbon transformation as measured by wetland aquatic ecosystem productivity; and
2. Impact geological and geomorphological controls have on wetland aquatic ecosystem productivity.

Regional Setting

The study area is situated in the Kings Plains Conservation Reserve, ~30 km southwest of Cooktown, Queensland, ~130 m above sea level, in the Normanby River upper catchment. The study area is a series of palustrine wetlands totaling ~31 km^2 (DEHP 2016) located in an alluvium-filled deeply incised valley lying between the East Normanby and Annan Rivers (Best and Dallwitz 1963). The geology is Devonian/Lower Carboniferous Hodgkinson Formation slates and greywacke, forming prominent hills on both sides of the valley (Lucas 1962). Resistant chert strike-ridges project into the valley, confining it to several partly closed basins, and forming three connected westward-draining wetlands that make up the Kings Plain system, namely Kings Lake (KL), Top Plain (TP) and Bottom Plain (BP) (Figure 2).

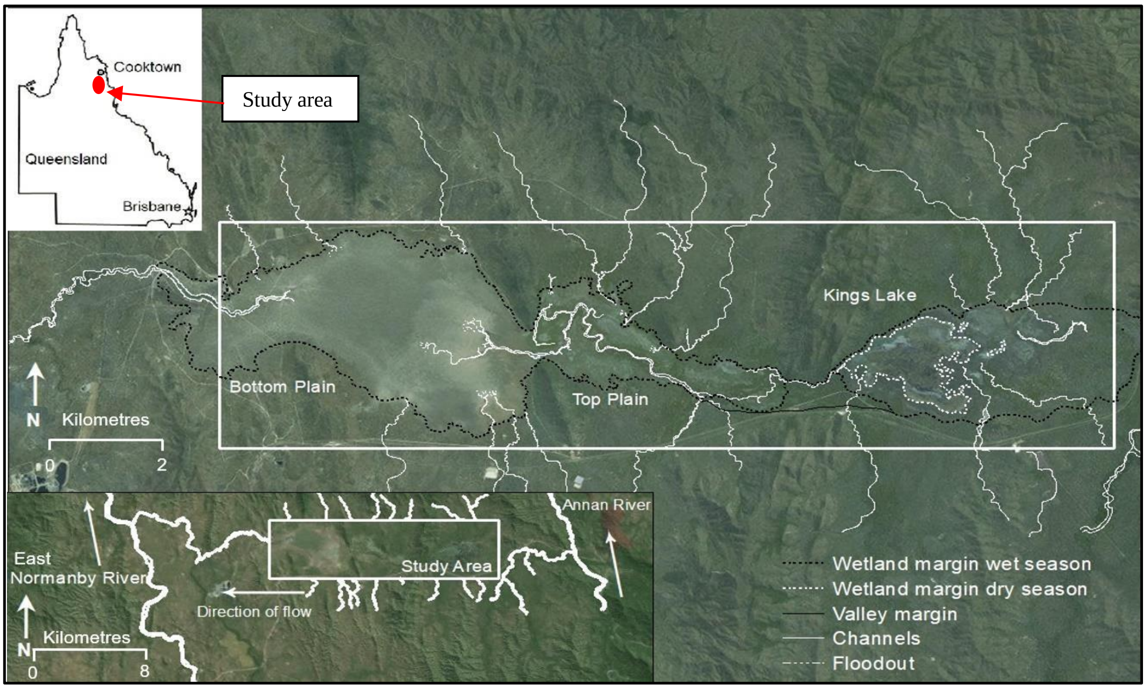


Figure 2. Location and geomorphic structure of three interconnected wetlands of the study area in the upper catchment of the East Normanby River, Queensland. The inset shows the location of the study area relative to the East Normanby and Annan Rivers.

The valley follows the ancestral bed of the Annan River when it formed part of the Normanby headwaters. However, due to stream 'capture' from an easterly regional geological tilt, the Annan River no longer flows into the Normanby catchment and now flows eastwards, and hydrological input to the valley has reduced. As a consequence, the valley has aggraded with fine clay alluvium from low energy flows, and the wetlands have formed (Best and Dallwitz 1963).

With a tropical savannah climate, average rainfall is 1680 mm yr^{-1}, and heaviest during the wet season from December to April when the average is 1414 mm yr^{-1}. Dry season (May – November) average rainfall is 261 mm yr^{-1} (BOM 2017). Biodiversity is very high in this region, and the Normanby catchment provides a major north-south biodiversity corridor between the Cape York and Wet Tropics bioregions (DEE 2017).

Field sites

King's Lake (KL) is an ~11 km^2 permanent wetland, bedrock-confined on its northern perimeter, and which contracts during the dry season. KL is dominated by a lower stratum of persistent emergent species including lotus lily (*Nymphaea nucifera*), giant water lily (*N. gigantea*), and widespread reed beds, with the wetland fringed by an upper stratum of broadleaved paperbark (*Melaleuca viridiflora*). Top Plain (TP) is a ~7 km^2 shallow ephemeral wetland, inundated during the wet season, which progressively dries out, in the dry season except for the central channel, which stops flowing (Hughes, 2017). Bottom Plain (BP) is a ~13 km^2 shallow ephemeral wetland, inundated in the wet season, which progressively dries out in the dry season except for the central channel's western section (Hughes, 2017). Both TP and BP have dominant upper stratum species including *M. viridiflora*, wet season lower stratum small aquatic species (*Nymphoides spp.*, *Caldesiaoligococca*) and dry season native and exotic grasses (Queensland Herbarium 2016). BP also has strong recruitment of *M. viridiflora* seedlings, possibly a function of restricted stream flow during the high tides and heavy rainfall of 2014's Cyclone Yasi.

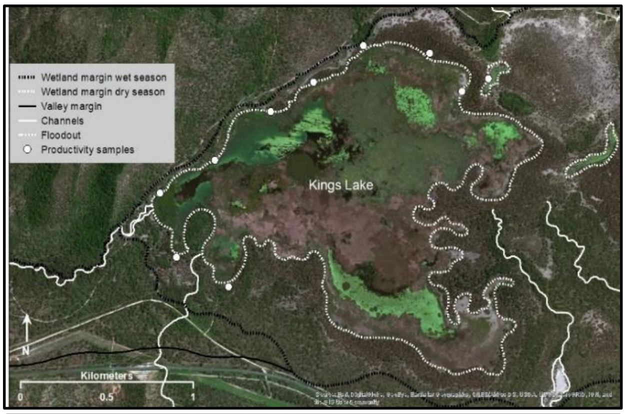
Methods

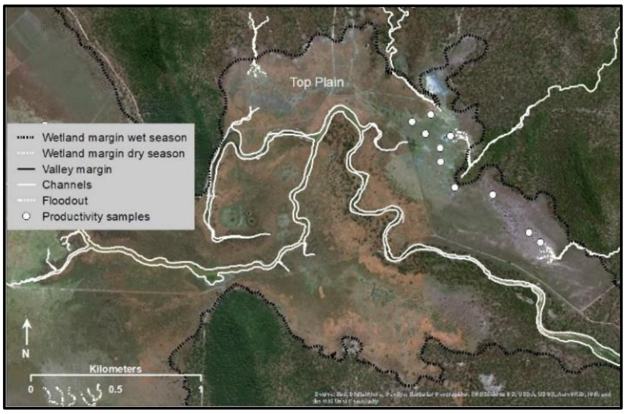
Desktop survey

A geomorphology survey was undertaken using light detection and ranging (LiDAR) digital elevation model data, Google Earth satellite imagery, aerial photographs, and previous mineral exploration studies reports to determine the landscape components and geomorphic units in the study area. This established the valley setting and margins, channel bed longitudinal profile, and the type and arrangement of channels, paleochannels, wetlands and floodouts in the system. From this, sampling locations within KL, TP and BP were identified due to their different hydrological and geomorphological characteristics.

Field sampling

The study area's remoteness presented logistical issues for GPP analysis. Instead of *in situ* water column analysis, an alternative method was utilised whereby surface sediment samples collected from the field and inundated under laboratory conditions to determine a snapshot of carbon transformation through ecosystem productivity. Surface sediment sampling was carried out across representative areas of the three wetland areas, however at KL, we were constrained by inaccessibility to the wetland's eastern and south-eastern perimeter. Sampling locations for each wetland are shown in Figure 3a, b and c. In each of the three parts of the wetland system, 10 sampling sites were identified, and 10 x 150 g surface sediment samples were taken at random within a 10x10 m grid cell at each site. The 10 replicate samples were collated, resulting in 10 x ~1.5 kg samples from each of the three wetland areas. Samples were refrigerated to avoid microcosms that could affect major biological change and were transported to the laboratory within two days of sampling. All sediment samples were analysed within ~7 days of collection, during September 2017.





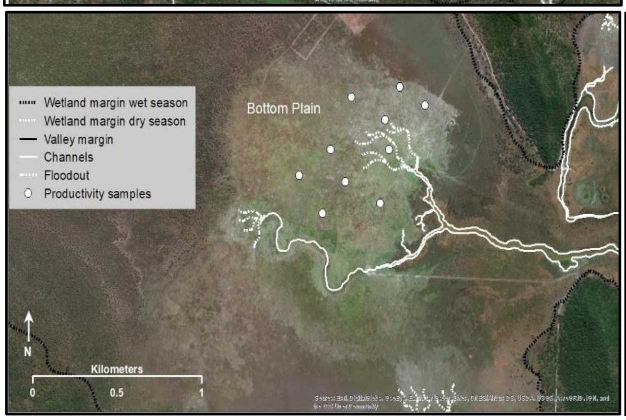


Figure 3

a) (top left). Geomorphic structure at Kings Lake site, and productivity sampling locations.

b) (top right). Geomorphic structure at Top Plain site, and productivity sampling locations.

c) (opposite). Geomorphic structure at Bottom Plain site, and productivity sampling locations.

Laboratory analysis

For GPP analysis, a variation of the biological oxygen demand (BOD) method (Wetzel and Likens 2000), was undertaken in the laboratory, using surface sediment samples collected in the field. ~1.5 kg of each sample was inundated with 4 litres of de-ionised water, and incubated for 5 days, with an imposed diurnal light cycle (12 hours day/night) and constant 25°C ambient temperature, to activate metabolism. Three control samples of 4 litres of de-ionised water were also included. At the end of five days, the 24-hour BOD procedure was undertaken. For each sample, clear and dark 300 ml bottles were filled with sample water, without air bubbles, sealed, placed on the laboratory bench and incubated for 24 hours, under the same light and temperature conditions as the 5-day inundation. Salinity (electrical conductivity) and pH were measured at completion of the 24-hour BOD incubation using standard instruments. Dissolved oxygen (DO) concentration of each sample was measured at the beginning and end of incubation using a DO meter (YSI Model 5100 Dissolved Oxygen/Temperature Meter, YSI Inc., Ohio, USA). From these measurements, carbon production for each sample can be calculated using the following formulas (Wetzel and Likens 2000):

GPP = [(LB – DB) x 1000 x 0.375]/(PQ x t), and
PR = [(IB – DB) x 1000 x RQ x 0.375]/t
where:
IB = DO concentration at beginning (mg L-1)
LB = DO concentration in light bottle at end (mg L-1)
DB = DO concentration in dark bottle at end (mg L-1)
Factor 0.375 = ratio moles carbon: moles oxygen, converts mass of oxygen to mass of carbon
PQ = 1.2 = photosynthetic quotient i.e. relative amounts of oxygen and carbon in photosynthesis
RQ = 1.0 = respiratory quotient i.e. relative amounts of oxygen and carbon in respiration

Statistical analysis

Comparison of GPP, RP and GPP/PR were made among the sites 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. Prior to analysis, all data values except for GPP/PR were $\log_{10}$-transformed to stabilize the variance and meet the assumption of normality.

Results

GPP of phytoplankton varied 46-fold (0.2 - 9.3 mg C m^{-3} h^{-1}), and PR varied 5-fold (10.8 - 55.0 mg C m^{-3} h^{-1}), over the whole study area. There was no statistically significant difference among the sites for $\log_{10}$GPP and $\log_{10}$PR as determined by one-way ANOVA (F(2,23) = 2.95, p = 0.07 for GPP) and (F(2,23) = 0.36, p = 0.70 for PR) (Table 1). GPP/PR ratio varied 16-fold (0.01-0.31), and was <1 for all samples, representing a range restricted to the heterotrophic spectrum. There was a statistically significant difference between sites for GPP/PR as determined by one- way ANOVA (F(2,23) = 3.93, p = 0.03). Post-hoc Tukey test showed that KL and TP differed significantly (p= 0.03), however BP was not significantly different from TP or KL. Four samples with negative GPP values were excluded from data analysis (Pace and Cole 2000). Negative GPP values occurred where a sample's post-inundation dark bottle respiration reading was higher than its corresponding light bottle reading and was possibly due to organic content differences between the two bottles. Overall, there was a significant positive relationship between $\log_{10}$ GPP and $\log_{10}$ PR ($r = 0.62$, p = 0.0007, n=26) and GPP/PR were log transformed to enable comparison with results from other Australian wetlands studies. When log transformed, several log10GPP values were negative, and excluded from further analysis, hence the low number of samples for BP and TP. The GPP/PR ratio was <1 for all samples, indicating all samples were highly heterotrophic (Table 1, Figure 4).

Table 1. Gross Primary Productivity (GPP, mg C m^{-3} h^{-1}) of phytoplankton, planktonic respiration (PR, mg C m^{-3} h^{-1}), and GPP/PR ratio of study area, Bottom Plain, Top Plain and Kings Lake. Mean ± standard error, range and coefficient of variation (%) in parentheses based on untransformed data. Negative GPP values excluded.

	Total (n=26)	Bottom Plain (n=9)	Top Plain (n=7)	Kings Lake(n=10)
GPP	2.1 ± 0.4 (0.2-9.3, 95)	1.5 ± 0.2 (0.4-2.7,48)	1.9 ± 1.0 (0.2-7.5,135)	2.9 ± 0.8 (1.2-9.3,81)
PR	19.1 ± 2.0 (10.8-55.0,53)	16.3 ± 1.4 (11.3-23.8,25)	20.4 ± 5.8 (11.3-55.0,76)	20.6 ± 3.1 (10.8-37.8,48)
GPP/PR	0.11 ± 0.01 (0.02-0.31, 58)	0.09 ± 0.02 (0.05-0.16,50)	0.07 ± 0.02 (0.02-0.14,61)	0.14 ± 0.02 (0.05-0.31,47)

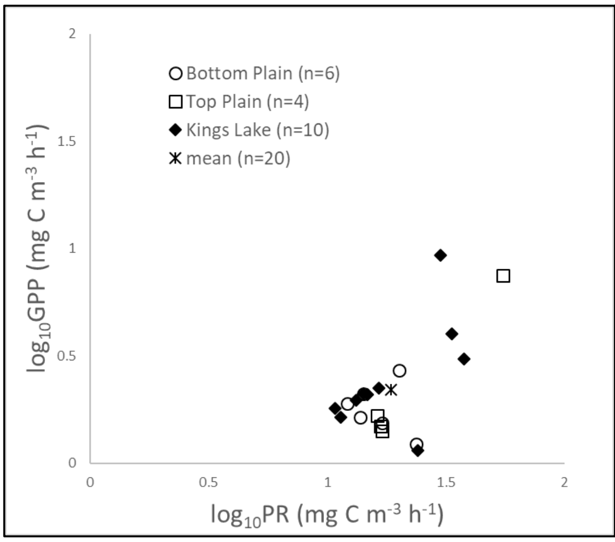


Figure 4. Relationship between gross primary productivity (GPP) of phytoplankton and planktonic respiration (PR) of Kings Plains wetlands. GPP/PR <1 for all samples, indicating a heterotrophic system. Bottom Plain (open circles), Top Plain (open squares), Kings Lake (closed diamonds), mean value of study area (∗ cross).

Discussion

Ecosystem productivity of wetlands varies temporally due to seasonal hydrology differences, depending on the balance of processes occurring at that time. Wetlands can display significant spatial and temporal variation in the balance between autotrophy and heterotrophy, even in wetlands with similar characteristics (Hoellein, Bruesewitz et al. 2013, Bortolotti, Louis et al. 2016). Taking one set of measurements only provides a snapshot. Nevertheless, if GPP is greater than PR, i.e. GPP/PR >1, the system is currently autotrophic, and the wetland aquatic ecosystem functions as a carbon sink. Where GPP/PR ratio is <1, the system is heterotrophic and functions as a carbon source (Kayranli, Scholz et al. 2010). Despite the variations in GPP, PR and GPP/PR within and between wetlands in the Kings Plain wetland system, all three sites were determined to be heterotrophic when inundated under controlled conditions based on samples taken during the dry season.

There is the possibility of significant spatial heterogeneity in ecosystem productivity, and carbon dynamics, between the three sites (BP, TP and KL) as during the dry season, their wetlands become separate disconnected systems, as they are no longer connected hydrologically (Cardoso, Roland et al. 2012). Post-wet season, as water recedes, wetlands can reform as diverse individual systems. Connectivity differences between water bodies can highlight variances in phytoplankton abundance (Cardoso, Roland et al. 2012). Differences in GPP/PR may relate to the inundation duration variance each year, which is in part determined by each site's geomorphology. Due to its geomorphic setting, KL is inundated for more months each year compared to BP and TP. The significant difference between GPP/PR of KL and TP may be explained by anecdotal evidence that TP dries out earlier than BP (Hughes 2017).

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

(BOM 2017). Previous research has shown that intermittent hydrological regimes impact the timing of planktonic metabolism, an important component of aquatic carbon cycling and transformation (Kobayashi, Ralph et al. 2013). 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 have a dominance of autotrophic conditions (Kobayashi, Ralph et al. 2013). A conceptual model in Figure 5 shows how these systems seem to vary in terms of GPP and PR.

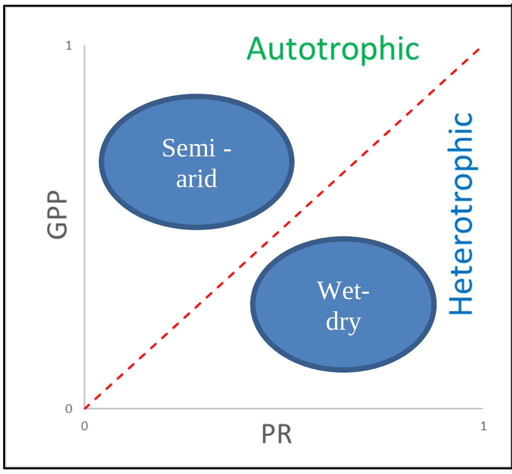


Figure 5. Conceptual model of variations in GPP and PR for seasonal wet-dry wetlands and semi-arid inland wetlands.

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 used to seasonal inundation. Regular seasonal inundation of Kings Plain possibly elicits a lower productivity response compared to the 'boom-bust' productivity pattern of semi-arid inland wetlands systems (Sheldon, Bunn et al. 2010, Arthington and Balcombe 2011), where inundation may only occur decadally. Animal activity (e.g. kangaroo and cattle grazing) also affect GPP and PR (Kobayashi, Ryder et al. 2009) while a suite of anthropogenic activities, including potential land-use change, and desiccation through climate change, also affects water quality and volume, and wetland conditions leading to changes in ecosystem productivity.

Conclusion

The wetlands of Kings Plains are diverse and display variations in geomorphology, hydrology and vegetation communities. As a result, it is likely that these factors contribute to the varied ecosystem productivity responses measured in this study. Based on the findings, all the wetlands were heterotrophic, but the aquatic ecosystem productivity of KL and TP were significantly different. To establish more robustly whether carbon cycling and transformation are unevenly distributed both spatially and temporally in the Kings Plains wetland system, a more comprehensive study of ecosystem processes over time would need to be undertaken and coupled with analyses of carbon burial and storage in sediment. Nevertheless, the importance of planktonic metabolism in the aquatic ecosystems of wetlands in providing carbon storage is established and our findings contribute to this growing body of research.

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