LRH: Adame *et al.*

RRH: Epiphyton primary production

The contribution of epiphyton to the primary production of tropical floodplain wetlands

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Abstract

Tropical floodplains are one of the most productive ecosystems on earth. Studies on floodplain productivity have primarily focused on trees and macrophytes, rather than algae, due to their greater biomass. However, epiphyton –algae and bacteria attached to the submerged portion of aquatic macrophytes- is a major source of energy in many tropical floodplains. Epiphyton productivity rates are unknown for most tropical floodplain wetlands, and spatial variability is not well understood. In this study, we measured primary productivity of epiphyton in Kakadu National Park in northern Australia. We estimated the relative contribution of epiphyton to aquatic production (epiphyton, + phytoplankton + macrophytes). We sampled sites dominated by different macrophyte structural types: vertical emerging grasses, horizontal emerging grasses, submerged macrophytes, and macrophytes with floating leaves. Epiphyton productivity was highly influenced by the structural type of the macrophyte. Highest potential productivity per weight was measured from epiphyton growing on macrophytes with floating leaves and horizontal grasses (1.52 ± 0.53 and 1.82 ± 0.61 mgC/dw g epiphyton/h, respectively) and lowest in submerged macrophytes and vertical grasses (0.57 ± 0.26 and 0.66 ± 0.47 mgC/dw g epiphyton/h, respectively). When considering the areal biomass of the macrophyte and the amount of epiphyton attached, epiphyton on horizontal grasses and submerged macrophytes had productivity values approximately ten times higher ($45\text{--}219$ mgC/m²/d) compared to those on vertical grasses and macrophytes with floating leaves ($2\text{--}18$ mgC/m²/d). Epiphyton contributed between 2 to 13 percent to the aquatic production of these tropical floodplain wetlands.

Keywords: Australia; epiphyton; Kakadu; macrophyte; paragrass; phytoplankton; productivity; wetland.

TROPICAL FLOODPLAINS ARE AMONGST THE MOST PRODUCTIVE ECOSYSTEMS ON EARTH, ONLY RIVALED BY INTENSIVELY MANAGED AGRO-ECOSYSTEMS (Davies *et al.* 2008). The high productivity within floodplains supports various ecosystem services such as flood regulation, water depuration, and provision of habitat for many commercially important species (Costanza *et al.* 1997). The productivity of floodplains has long been associated with trees and fast-growing aquatic macrophytes, which by far have the highest biomass contribution of all primary producers (Finlayson *et al.* 1993, Junk & Piedade 1997, Silva *et al.* 2009). However, epiphyton – algae and bacteria attached to the submerged portion of aquatic macrophytes- is highly nutritious, with low carbon to nitrogen molar ratios (C:N) and high protein content (Becker 2007), making it an important food source for primary consumers. In many tropical floodplains, epiphyton drives most secondary production (Bunn *et al.* 2003, Douglas *et al.* 2005, Lewis *et al.* 2001). For example, in northern Australia, epiphyton from floodplains significantly contribute to the production of barramundi (*Lates calcarifer*), an iconic species of high commercial value (Jardine *et al.* 2012). The productivity of epiphyton is key for determining accurate C budgets of primary and secondary production, which are required when establishing baselines for wetland restoration and conservation (Davies *et al.* 2008, Lewis *et al.* 2000). The productivity of epiphyton of most tropical floodplains is unknown (Davies *et al.* 2008).

Contrary to epiphyton productivity, epiphyton biomass has been widely studied (e.g. Engle & Melack 1990, McCormick *et al.* 1998), especially in temperate ecosystems (e.g. Squires *et al.* 2009, Turner *et al.* 1991). Epiphyton biomass in floodplain wetlands is associated with the structure of the macrophyte, with highest epiphytic biomass per unit area found on wetlands covered by macrophytes of large surface blade area (Pettit *et al.* 2016). For instance, submerged macrophytes with a complex branching structure have ten times more

epiphyton than grasses with a simple vertical structure (Pettit *et al.* 2016). In turn, environmental parameters such as depth of inundation, light, nutrients, inorganic C, and physical substrate determine the structural type of the dominant macrophyte (Sand-Jensen & Borum 1991, Mosisch *et al.* 2001). Thus, highest epiphyton biomass is likely to be found on patches of vegetation that contain suitable conditions for both macrophyte and epiphyton to grow. In tropical Australia, depth of inundation and light appear to be the overriding factors controlling macrophyte and epiphyton biomass and production (Mosisch *et al.* 2001, Pettit *et al.* 2016).

Primary productivity of epiphyton can be measured as change of biomass over time (e.g. Robertson *et al.* 2001). However, turnover time for epiphyton, as for most single-celled algae, is typically very short due to fast growth (Aloi 1990) and high grazing rates, causing variations on epiphyton biomass irrespective of productivity (Cattaneo 1983). Changes in O₂ concentrations in incubations have also been used to measure epiphyton production; however, this methodology has some drawbacks, such as the overestimation of productivity due to the formation of bubbles during incubations (Aloi 1990). Other methods such as incubations with ¹⁴C are much more sensitive than the O₂ method, however they are expensive and generally cannot be done in the field (Aloi 1990). Bottle incubations may also influence C and nutrient limitation due to the lack of water flow (Turner *et al.* 1991). The lack of a standard cost-effective methodology to measure epiphyton productivity might have contributed to the scarcity of data in tropical floodplain wetlands.

In this study, we assessed epiphyton production and its contribution to the aquatic primary production of tropical floodplain wetlands in tropical Australia. We used multiple techniques to measure productivity: ¹³C uptake experiments, an adaptation of a methodology

previously used for phytoplankton (Burford *et al.* 2012), variations of dissolved oxygen (DO) in dark/light bottles, and field deployment of DO loggers. We measured epiphyton productivity within different macrophyte structural types: vertical emerging grasses, horizontal grasses, submerged macrophytes, and macrophytes with floating leaves (Fig. 4). We measured diel DO variations to calculate areal productivity and the relative contribution of epiphyton to floodplain aquatic productivity. We also compared aquatic productivity with published values of litterfall NPP (net primary production) of *Melaleuca* forests -probably the second most important source of decomposable carbon in wetlands of tropical Australia (Finlayson 1993). Our predictions were that epiphyton would contribute significantly to floodplain production and that the potential productivity per biomass of epiphyton would be similar among macrophyte structures. We also predicted that total areal epiphyton productivity would be highest where attachment surface area and light penetration are high, mirroring the distribution of epiphyton biomass (Pettit *et al.* 2016), resulting in greater productivity on submerged macrophytes and lower productivity on vertical grasses. Therefore, we expected that macrophyte structure would greatly influence the contribution of epiphyton to the productivity of this tropical floodplain wetlands.

METHODS

STUDY SITE.-The sampling was conducted in three floodplains in Kakadu National Park, northern Australia: South Alligator, East Alligator and its tributary, Magela Creek, all of which have largely undisturbed flooding regimes (Fig. 1). The floodplains are bounded by the Van Dieman Gulf to the north and the Kakadu escarpment to the south. The region is characterized by a monsoonal climate with two distinct seasons, wet and dry. The wet season usually starts in November and lasts for about three months. During this period, the region

receives between 1,300-1,500 mm of rain (Australian Bureau of Meteorology), which results in the inundation of the floodplain. During periods of inundation, which can last from six to eight months, shallow water provides habitat for rapidly growing macrophytes and large populations of vertebrates and invertebrates (Pettit *et al.* 2011, Ward *et al.* 2014).

The floodplains comprise small patches of *Melaleuca* forests and macrophyte-dominated wetlands. Common species include *Oryza spp* (wild rice), *Eleocharis spp* (“spike rush”), *Hymenachne acutigluma* (“native hymenachne”), *Pseudoraphis spinescens* (“spiny mud grass”), and aquatic plants with floating leaves such as water lilies (*Nymphaea spp* and *Nymphoides spp*; Finlayson 2005). However, in recent years, invasive macrophyte species such as *Urochloa mutica* (“para grass”) and *Hymenachne amplexicaulis* (“olive hymenachne), have become widely distributed (Setterfield *et al.* 2013).

SAMPLING STRATEGY.- Sampling was conducted at the end of the wet season in May 2012, May 2013, and April 2014, while the floodplains were still largely inundated and when macrophyte biomass reaches its highest annual peak (Ward *et al.* 2016). Locations were selected on the basis of representativeness of the wetland communities of the floodplain and accessibility. Within each location, we categorized sampling sites according to the dominant macrophyte structure following categories established for the region by Pettit *et al.* 2016 (Fig. 4, based on Den Hartog and van der Velde 1988):

- (1) Helophytes- Vertical emerging graminoids with a submerged and an emergent section, such as wild rice, native hymenachne, and *Leersia*, hereafter called “vertical”
- (2) Horizontal helophytes- helophytes with horizontal stems growing just below the water surface, with inflorescence and leaves emerging above the surface, such as the spiny mud grass, hereafter called “horizontal”

- (3) Ceratophyllids- submerged plants with whorls of leaves at each node such as *Ceratophyllum* (“hornwort”), *Najas* (najas), and *Utricularia* (“bladderwort”), hereafter called “submerged”.
- (4) Nymphaeids- plants attached to the soil with floating leaves such as water lilies, hereafter called “floating”

To assess the characteristics of the water within each vegetation type, we obtained field measurements of water depth, pH, temperature, and conductivity using a multi-parameter meter (Hydrolab, QUANTA, Econ Environmental, WA, Australia). A light sensor was used to measure the photic zone depth (LI-1400 datalogger, Spherical Sensor LI 193, Li-Cor Biosciences, NE, USA). At each sampling location, six to eight points were selected across the range of macrophyte structural types. We measured dissolved inorganic phosphorus (DIP) as Filterable Reactive Phosphorus, and dissolved inorganic nitrogen (DIN) as nitrous oxides (N-NO_x^-), and ammonium (NH_4^+). Water samples were taken with a bucket, filtered in the field (Whatman GFF filters), and stored frozen. Thawed samples were analysed using standard colorimetric analyses (EPA 353.2 for NO_x , EPA 350.1 for NH_4^+ , and OP5A for P [SM-4500], Griffith University, Australia).

To estimate aquatic primary productivity we used three complementary methods: (1) Experiments of ^{13}C - bicarbonate uptake; (2) measurements of DO variations in light/dark bottles; and (3) estimations of ecosystem productivity from diel variations of DO measured with *in-situ* loggers. Experiments of ^{13}C -bicarbonate uptake were conducted in Jabiluka, Yellow Waters and Cannon Hill during May 2013; experiments in dark/light bottles were conducted in Jabiluka during May 2012; and diel DO variations were obtained from the Magela Creek floodplain during May 2013 (Fig. 1). Finally, measurements of biomass were

conducted in April 2014 from 72 locations throughout the three floodplains (Fig. 1). The detailed methodology is explained below.

¹³C-BICARBONATE UPTAKE.- Within each sampling location, we collected macrophytes of different structural types (see above) with their attached epiphyton. Each macrophyte sample included stems and leaves. The macrophytes were collected so as not to disturb the attached epiphyton, placed in buckets full of water from the site, and kept with aerators until the experiments were conducted (< 24 h from collection).

Primary productivity was measured as ¹³C-bicarbonate uptake adapting a protocol initially developed by Burford et al. (2012) to measure phytoplankton productivity. We placed a known weight of macrophyte and the epiphyton attached to it in polycarbonate bottles (250 ml) filled with water from each sampling location. The bottles were placed inside large containers with running water to maintain a constant temperature. To simulate light conditions along the water column, we selected three light treatments that captured the range of light levels that macrophytes are exposed in the field (Pettit *et al.* 2016). One of the containers was fully covered with shade cloth (“dark” treatment); the other was fully exposed to sunlight (“light” treatment), and a third one was covered with shade cloth that reduced 70% percent of the light (“30 percent light” treatment). In every experiment, a blank sample of distilled water and a ‘control’ sample, which consisted of surface water from a nearby waterhole connected to the floodplain (Jabiru), were also incubated ($n = 45$). The “control” sample allowed us to verify that experimental conditions were maintained relatively constant between runs, which were done throughout a week. We also investigated the effect of two methodological approaches: measuring productivity from the epiphyton while attached to the macrophyte versus the productivity from epiphyton scrubbed off the plant, as the effect is

unknown (Aloi 1990). The incubations were run during the day at full sunlight (between 1100 and 1500 h).

At the beginning of the experiment, ^{13}C -bicarbonate (^{13}C 99 percent, Cambridge Isotope Laboratories, MA, USA) was added to each bottle to obtain a $130.6\ \mu\text{M}$ solution. The exact time of addition was recorded; the bottles were incubated for two to three hours. Light intensity and temperature in the ambient and in the water were recorded throughout the experiment (range from 29.9 to 32.2°C and from 836 to $2277\ \mu\text{mol photons/m}^2/\text{s}^1$; LI-1400 data logger, Spherical Sensor LI 193, Li-Cor Biosciences, NE, USA). To stop the incubation, the bottles were placed in the dark at 4°C . The epiphyton and the phytoplankton were filtered onto pre-weighed, pre-combusted filters (Whatman GF/F) that were kept frozen in the dark until returned to the laboratory.

In the laboratory, macrophytes and filters were dried at 60°C and weighed to measure dry weight (dw). Phytoplankton biomass was measured as chlorophyll *a* (Chl *a*), which was extracted with 90% acetone using a sonicator (Jeffrey & Humphrey 1975, Lorenzen 1967). A separate set of samples was analyzed for $^{13}\text{C}/^{12}\text{C}$ in an elemental-analyser isotope ratio mass spectrometer (EA-IRMS, Sercon System, Griffith University). A water sample was taken within each sampling location to calculate alkalinity (Denny *et al.* 1983), which combined with the conductivity, temperature and pH, was used to estimate bicarbonate concentration. The bicarbonate concentrations within our study sites ranged between 100 - $150\ \mu\text{M}$ resulting in atom enrichment between 47 - 57 percent compared to background levels. Productivity is expressed as mgC dw g/h from the amount of ^{13}C -bicarbonate uptake during incubation, which was estimated by the following equations:

Equation 1

$$\text{Atom excess (\%)} = {}^{13}\text{C}_{(\text{light treatment})} - {}^{13}\text{C}_{(\text{standard})} 1.111$$

Equation 2

$$\text{C uptake (h)} = \frac{\text{Atom excess (\%)}}{\text{Atom enrichment in experiment (\%)} * \text{Incubation time (h)}}$$

Equation 3

$$\text{Productivity (mgC dw g/h)} = \frac{\text{C in epiphyton (mg)} * \text{C uptake rate (h)}}{\text{epiphyton biomass (dw g)}}$$

DARK/LIGHT BOTTLES EXPERIMENT.- Experiments were undertaken following the technique outlined by Odum (1955). Three replicate pairs of 250 ml Schott glass bottles were filled either with water, macrophytes and water, or macrophyte with associated epiphyton and water. The sampling sites were chosen to include representatives of the different structural categories (see above): para grass, *Leersia hexandra*, *Eleocharis dulcis* (vertical), *Pseudoraphis spiniscens* (horizontal), *Ceratophyllum demersum* (submerged), and *Nymphaea violacea* (floating). To measure respiration, one of each pair of bottles was covered in aluminum foil to exclude light ($n = 18$ bottles per experiment).

The bottles were placed in the littoral zone of the floodplain just below the water surface and left to incubate for approximately two hours. Measurements were taken between 1000 and 1400 h in open areas at full sunlight. There was minimal cloud cover on the days of measurement that could potentially limit photosynthesis. Light, DO concentration, and water temperature (YSI PRO, YSI Incorporated, OH, USA; LI-1400 datalogger, Spherical Sensor LI 193, Li-Cor Biosciences, NE, USA) were recorded at the start and end of the incubation.

At the completion of the experiment, samples were placed in zip lock bags, immediately frozen, and then dried and weighed in the laboratory.

Oxygen production and consumption were calculated as $\text{mg O}_2/\text{L/h}$ from the linear regression of DO as function of incubation time. Areal productivity and respiration were estimated from water volume and epiphyte/phytoplankton biomass. Oxygen was converted to C assuming a molar conversion of 1:1. Net ecosystem productivity (NEP) was calculated as gross productivity (GPP; light treatment) minus respiration (R; dark treatment). The productivity of phytoplankton was estimated as the productivity of the bottle with only water. Productivity of epiphyton was estimated as productivity of the bottles with macrophytes and epiphyton minus the productivity of the bottles with only macrophytes.

DISSOLVED OXYGEN DIEL VARIATIONS.- Dissolved oxygen loggers (TPS Pty Ltd, QLD, Australia, and YSI 6920; YSI 600XLM sensors, YSI Incorporated, OH, USA) were used to measure ecosystem productivity in selected locations. The loggers were placed approximately 1m below the surface and were fixed inside a steel cage to protect them from being damaged by crocodiles. The loggers were deployed for at least 24 h at four different vegetation communities: (1) dominated by the invasive para grass (vertical structural type, see categories above), (2) dominated by hymenachne (vertical), (3) combination of water lilies (floating) and najas (submerged), and (4) combination of water lilies (floating) and hornwort (submerged). On the basis of DO variations, we calculated productivity accounting for respiration and re-aeration rates across the water-air interface following the Delta Method described by Chapra (1997). First, we estimated the reaeration rate (k) from the time lag between solar noon and maximum DO concentrations. The k value for our sampling sites was low ($k=0.1$), which is reasonable, as turbulence in the wetlands is minimal. We used k and the range of DO deficit

(mg/L) or delta (Δ) to estimate productivity (mg L/d) from the graphic relationship between Δ/P , k and photoperiod (Chapra 1997). Respiration rates were estimated as follows:

Equation 4.

$$\text{Respiration (mg/L/d)} = \text{Productivity (mg/L/d)} + k * \text{daily DO deficit (mg/L)}$$

AREAL PRODUCTIVITY.- To calculate productivity per unit area of wetland, we estimated phytoplankton, epiphyton, and macrophyte biomass for each wetland community.

Phytoplankton biomass was measured as Chl *a* concentrations for each site. The Chl *a* from our sampling sites was 1 ± 0.1 percent of the total C, and about 24 percent of the phytoplankton biomass (Platt & Irwin 1973). Macrophyte biomass was measured by harvesting the plant material below the water surface within the photic zone for each species. Harvesting was done in triplicate (0.5 x 0.5 m quadrats) at each site and in three locations per macrophyte species ($n = 72$). The harvested material was weighed in the field and a subsample was taken to the laboratory where it was dried at 60°C and weighed. Epiphyton biomass was measured by scrubbing the macrophyte with a soft brush to remove all attached material, suspending it in distilled water, then filtering it onto a pre-weighed filter (Whatman, GF/F; $n = 45$). The samples were immediately frozen, then dried and weighed in the laboratory. Epiphyton biomass is likely to be overestimated as some detritus could be attached to the algal material. The amount of epiphyton was extrapolated to the amount of macrophyte within the photic zone for each plant species.

The biomass of each primary producer was used to estimate their contribution to total productivity measured as ecosystem DO variations (Chapra 1997). There is likely additional primary productivity by microalgal mats from the sediment, however, due to light limitations,

it is likely to be minor (Pettit *et al.* 2016). Additionally, we compared our aquatic productivity estimates with published values of *Melaleuca* forest litterfall NPP, which included leaves, twigs, bark, fruit, floral bracts, flower parts and woody material < 2.5 cm diameter (Finlayson *et al.*, 1993). We used the litterfall production of *Melaleuca* forests at the end of the wet season (April to July), coincident with the highest productivity of the year (Finlayson *et al.* 1993). The aim was to compare aquatic autochthonous productivity with the likely most important fraction of allochthonous decomposable carbon in these floodplain wetlands (Finlayson *et al.* 1993). Throughout the manuscript, productivity is reported as mgC/d/m²

FLOODPLAIN PRODUCTIVITY.- We estimated the productivity of the sampled floodplains during the month of May by extrapolating our productivity estimates to the extent of wetland area during this time of the year (Ward *et al.* 2014). For comparison, we also included an estimation of litterfall NPP of *Melaleuca* forests within the floodplain during May (Finlayson *et al.* 1991; Bowman *et al.* 2010).

STATISTICAL ANALYSES.- We used Analysis of Variance (ANOVA) to test for differences in nutrient concentrations and primary productivity of epiphyton among macrophyte structures and treatments. The model was run with “structural type” (horizontal, vertical, submerged and floating) as the fixed effect and “site” (Jabiluka, Cannon Hill, Yellowwaters) and “light treatment” (full light vs 30 percent of light) as the random effect of the model. Conversely, the difference among light treatments were tested using “treatment” as the fixed effect and “structural type” and “site” as the random effect. The difference between the productivity of epiphyton while attached or separated from the macrophyte was tested with “treatment” (attached or separated) as the fixed effect, and “light treatment” as the random effect of the model.

Normality was assessed using Shapiro-Wilk tests; data that were not normally distributed were $\log_{10}$ transformed. When significant differences were found, pair-wise comparisons were explored using Scheffé post-hoc tests. Data that did not comply with normality despite transformations (macrophyte and epiphyton biomass) were analyzed using Kruskal-Wallis non-parametric tests with “macrophyte structure” as the predicting factor and epiphyton (n= 45) or macrophyte biomass (n=72) as the random factor of the model. Analyses were performed with SPSS Statistics (version 22, IBM, New York, USA). Throughout the manuscript, data are reported as mean $\pm$ standard error.

RESULTS

ENVIRONMENTAL CHARACTERISTICS.- The floodplain wetlands studied were characterized by interconnected patches of vegetation with relatively shallow water (< 260 cm; Table 1). During sampling, mean water temperature ranged between 29 and 30°C. Mean nutrient concentrations in the water across sampling points were $1.17 \pm 0.19 \mu\text{mol/L}$ for N-NH_4^+ , $0.64 \pm 0.12 \mu\text{mol/L}$ for N-NO_x^- , and $0.17 \pm 0.03 \mu\text{mol/L}$ for DIP. Concentrations of N-NH_4^+ were highest in water sampled from vertical grasses ($1.93 \pm 0.79 \mu\text{mol/L}$) compared to water from horizontal and submerged vegetation ($0.71 \pm 0.09 \mu\text{mol/L}$ and $0.79 \pm 0.14 \mu\text{mol/L}$, respectively; $F_{3, 27} = 5.11$ $p = 0.007$). Similarly, N-NO_x concentrations in water from vertical grasses ($1.19 \pm 0.23 \mu\text{mol/L}$) were twice as high as water from any other vegetation type ($F_{3, 27} = 5.47$ $p = 0.006$; $F_{3, 27} = 6.38$ $p = 0.003$). Molar DIN:DIP ranged from 9.5 in wetland dominated by submerged macrophytes to 18.8 in wetlands dominated by floating macrophytes (Table 1).

BIOMASS OF PRIMARY PRODUCERS.- Macrophyte biomass was 304.0 ± 147.9 dw (dry weight) g m^{-2} and was lowest for floating macrophytes (22.6 ± 4.0 dw g m^{-2}), followed by submerged macrophytes (75.7 ± 3.8 dw g m^{-2}), vertical grasses (533.8 ± 28.9 dw g m^{-2}) and finally, horizontal grasses (584.1 ± 51.1 ; $Z = 54.47$, $p < 0.001$). Epiphyton biomass was about 3 percent of that of macrophytes with a mean of 11.7 ± 4.1 g m^{-2} . Epiphyton was most abundant on submerged (20.8 ± 0.2 g m^{-2}), and least abundant on floating macrophytes (0.9 ± 0.0 g m^{-2} , $Z = 26.75$ $p < 0.001$). Phytoplankton mean biomass was 22.6 ± 2.7 $\mu\text{g Chl } a/\text{L}^1$ or 0.004 ± 0.017 g m^{-2} , which was 0.001 percent of the macrophyte biomass.

EPIPHYTON POTENTIAL PRIMARY PRODUCTIVITY.- Mean primary productivity of epiphyton was 1.14 ± 0.31 $\text{mgC/dw g epiphyton/h}$ measured as ^{13}C -bicarbonate uptake, and 0.23 ± 0.07 $\text{mgC/dw g epiphyton/h}$ measured as DO variations in dark/light bottle incubations. Both methods gave similar patterns of variation across macrophyte structures, but productivity rates estimated from DO variations were lower than those measured from ^{13}C -bicarbonate uptake (Fig. 2A, B). Respiration rates estimated from DO variations were 0.03 ± 0.03 mgC/g/h .

Epiphyton productivity estimated by ^{13}C -bicarbonate uptake was significantly different among structures from different sites (structure*site $F_{4,11.1} = 83.69$; $p < 0.001$), with highest values for epiphyton on floating and horizontal macrophytes (1.52 ± 0.53 $\text{mgC/dw g epiphyton/h}$ and 1.82 ± 0.61 $\text{mgC/dw g epiphyton/h}$, respectively) and lowest in epiphyton on submerged and vertical macrophytes (0.57 ± 0.26 $\text{mgC/dw g epiphyton/h}$ and 0.66 ± 0.47 $\text{mgC/dw g epiphyton/h}$, respectively; Fig. 2A).

Epiphyton productivity estimated by ^{13}C -bicarbonate was higher at full light compared

to 30% light in floating and horizontal macrophytes, but not on submerged and vertical macrophytes. Epiphyton productivity decreased when it was artificially scrubbed off the macrophyte in all species except in para grass (1.07 ± 0.48 mgC/dw g epiphyton/h versus < 0.5 mgC/dw g epiphyton/h; $F_{1,11} = 8.27$, $p = 0.018$).

EPIPHYTON PRIMARY PRODUCTIVITY PER AREA OF MACROPHYTE.- Primary productivity and DO variation experiments were extrapolated to a square meter of macrophyte. On this areal basis, productivity (estimated from ^{13}C - bicarbonate uptake) was ten times higher on epiphyton on submerged and horizontal macrophytes (165.5 and 218.6 mgC/m²/d¹) compared to epiphyton on floating and vertical macrophytes (12.9 - 18.2 mgC/m²/d¹; Fig. 2C). Thus, even though potential productivity was lowest in submerged macrophytes and highest in floating and horizontal macrophytes, when the biomass of the epiphyton was considered, the most productive patches for epiphyton were those dominated by horizontal and submerged macrophytes (Fig. 2C, D).

CONTRIBUTION OF EPIPHYTON TO THE AQUATIC PRIMARY PRODUCTIVITY OF THE FLOODPLAIN.- Ecosystem productivity was estimated from diel DO variations in four sites, two dominated by vertical macrophytes, and two dominated by submerged and floating macrophytes (Fig. 1, 3). The DO concentrations in the water (1m deep) ranged from 0.1 to 6.2 mg/L across the 24 h period. Lowest DO concentrations were measured during the early hours of the morning and increasing towards late afternoon (15:00-16:00) with some differences in patterns for each vegetation structure. The site dominated by vertical macrophytes had consistently low DO values (< 3 mg/L), with a short peak of about 1.5 mg/L in the afternoon, which rapidly decreased after dawn. In comparison, the wetland dominated by submerged and floating macrophytes had a peak of up to 6 mg/L in the afternoon that decreased only until midnight.

Ecosystem GPP mean rates were $1,775 \pm 15 \text{ mgC/m}^2/\text{d}$ for wetlands dominated by vertical grass and $3,620 \pm 40 \text{ mgC/m}^2/\text{d}$ for wetlands dominated by floating and submerged macrophytes (Table 2). Ecosystem respiration (R) was higher than production with $2,085 \pm 65 \text{ mgC/m}^2/\text{d}$ for wetlands dominated by vertical grass and $3,900 \pm 180 \text{ mgC/m}^2/\text{d}$ for wetlands dominated by submerged and floating macrophytes. Thus, GPP:R were 0.9 ± 0.0 for all wetlands sampled.

Considering the biomass for each primary producer and the ecosystem GPP estimated from diel DO variations, we calculated the contribution of each primary producer to the aquatic productivity of the wetland (macrophytes + epiphyton + phytoplankton). Macrophytes contributed between 88 to 98 percent to the total productivity with 1550 to 3290 $\text{mgC m}^{-2} \text{ d}^{-1}$, epiphyton contributed between 2 to 13 percent with 38 to 465 $\text{mgC/m}^2/\text{d}$ and phytoplankton contributed 0.02 percent with 0.3 to 0.6 $\text{mgC/m}^2/\text{d}$ (Table 2).

Overall, the epiphyton productivity ranged between 2.2 to 460 $\text{mgC/m}^2/\text{d}$ (Table 3). Phytoplankton productivity was within a similar range, between 0.3 to 300 $\text{mgC/m}^2/\text{d}$; macrophyte productivity was orders of magnitude higher, with a range between 1750 to 3290 $\text{mgC/m}^2/\text{d}$ (GPP estimated by diel DO variations). In comparison, the litterfall NPP of the nearby *Melaleuca* forests is approximately between 600 and 1800 $\text{mgC/m}^2/\text{d}$ (Finlayson *et al.* 1993; Fig. 4).

FLOODPLAIN C PRODUCTION DURING MAY.- During May, around the time flooding peaks, the production of phytoplankton in flooded areas without aquatic vegetation (776.5 ha) was about 2 tonC/d In comparison, the production on 52,054 ha of vegetated wetlands was about 180

tonC/d, half of which was produced by vertical grasses. For comparison, the litterfall NPP of the *Melaleuca* forests (2948 ha) was about 35 tonC/d. The overall decomposable fraction of C produced by the floodplains wetlands during May was about 217 tonC/d; from which 4 tonC/d were produced by epiphyton.

DISCUSSION

The primary production of epiphyton constituted between 2 and 13% of the total production of the floodplain wetlands. Previous studies in tropical floodplains predicted that phytoplankton would contribute 2 percent of the total production, followed by epiphyton with 5 percent, floodplain forests with 28 percent, and macrophytes with 65 percent (Melack and Forsber 2001 in Davies *et al.* 2008). Our results corroborate this prediction; we found lowest contributions for phytoplankton and epiphyton ($< 500 \text{ mgC/m}^2/\text{d}$), and highest for macrophytes ($> 1500 \text{ mgC/m}^2/\text{d}$). Additionally, our results fill an important gap in the Flood Pulse Concept (Junk *et al.* 1989), which did not include periphyton production rates, but predicted they would be substantial, with values within the range of phytoplankton. Thus, epiphyton is not only one of the most important food sources in these tropical floodplain wetlands, but also an important component of their aquatic productivity.

The ecosystem GPP estimates (derived from DO variations) in Kakadu's wetlands ranged from 1760 to 3660 $\text{mgC/m}^2/\text{d}$, values similar to the those of nearby floodplain waterholes in the Flinders River (2200- 2800 $\text{mgC/m}^2/\text{d}$; Faggotter *et al.* 2013). These values are high compared to other aquatic systems such as lakes and ponds (GPP $< 2000 \text{ mgC/m}^2/\text{d}$, Hoellein *et al.* 2013), rivers and streams (GPP $< 1000 \text{ mgC/m}^2/\text{d}$, Davies *et al.* 2008).

However, our productivity measurements were within the lower range of other tropical floodplains, which range between 2000 and 12,000 mgC/m²/d (Davies *et al.* 2008). The moderately low productivity of the wetlands in our study site might reflect the relatively low concentration of nutrients associated with minor levels of anthropogenic impacts. Thus, these productivity values might reflect “natural” levels, at least for similar wetlands during the flooding season. This information could be used to guide restoration and conservation efforts.

Despite the relatively high productivity of Kakadu’s wetlands compared to other aquatic and terrestrial ecosystems, the wetlands were heterotrophic. Heterotrophy is a common characteristic of wetlands with high inputs of organic matter (Hoellein *et al.* 2013, Lewis *et al.* 2000). During the dry season, dead macrophytes, detritus, and fish carcasses accumulate on the floodplain floor; during the following flooding season, the accumulated organic material rapidly decomposes causing strong anoxic conditions in the water (Lewis *et al.* 2000; Burford *et al.* 2008). Low DO concentrations and high levels of NH₄⁺ were especially evident in wetlands dominated by macrophytes with a vertical structural type. This result supports the idea that the invasion of macrophytes with vertical structural types changes not only the habitat structure but also physicochemical characteristics of wetlands (Bunn *et al.* 1998, Setterfield *et al.* 2013), in this case, by increasing heterotrophy. However, because we know so little about the function of most tropical floodplain wetlands, caution needs to be used if extrapolating these results to other regions or times of the year.

Epiphyton productivity was spatially variable among macrophyte structural types. Contrary to our prediction, potential epiphyton productivity (productivity per weight of epiphyton) was different among macrophyte structural types. The species composition of epiphyton varies among macrophytes species (Blindow 1987, Fernandes *et al.* 2016). Innate

differences in the physiological characteristics of algal species could explain differences in productivity, for instance their response to light availability (Falkowski & LaRoche 1991). In our study, epiphyton of horizontal and floating macrophytes responded to an increase in light by increasing their productivity. In contrast, the productivity of epiphyton of most submerged and vertical macrophytes did not increase when light was augmented, suggesting that their photosynthetic capacity reached saturation level. Epiphyton biomass is also variable among macrophyte structures, with highest biomass in submerged and horizontal macrophytes and lowest in floating and vertical macrophytes (Pettit *et al.* 2016). Overall, differences in the spatial distribution of epiphyton productivity are likely to be due to variability in epiphyton species and epiphyton biomass.

The changes in the structural composition of macrophytes, either natural or human-induced, could have cascading effects down to the microalgal level up to secondary consumers, affecting the overall diversity and productivity of the wetland. Our results suggest that wetlands dominated by submerged and horizontal macrophytes could provide important food sources for fish and other animals. Contrarily, wetlands dominated by the invasive para grass and hymenachne, which have a vertical structure, have less epiphyton, low concentrations of DO and high concentrations of NH_4^+ , conditions that are adverse for most fish species (Perna *et al.* 2011).

In conclusion, the productivity rates measured in the tropical floodplain wetlands of Kakadu, northern Australia were high compared to other aquatic systems, but low compared to floodplain wetlands with higher anthropogenic impacts. The productivity of the epiphyton contributed between 2 and 13 percent to the total primary production. Epiphyton productivity differed among macrophyte structural types. On an aerial basis, the most productive wetlands

were those dominated by submerged and horizontal macrophytes, while the least productive were those dominated by vertical macrophytes, including those invaded by hymenachne and para grass.

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TABLES

TABLE 1. Environmental characteristics of water (depth, temperature, conductivity, DO, pH and dissolved nutrients) of macrophyte communities of different structural types: horizontal grasses, vertical grasses, submerged macrophytes and macrophyte with floating leaves. DIP = dissolved inorganic phosphorus as Filterable Reactive Phosphorus, DIN = dissolved inorganic nitrogen. Data are mean $\pm$ standard error

	Horizontal	Vertical	Submerged	Floating
Water depth (cm)	72.7 $\pm$ 11.0	28.0 $\pm$ 7.9	253.8 $\pm$ 29.1	119.1 $\pm$ 29.1
Temperature (C°)	30.1 $\pm$ 0.7	30.3	28.9 $\pm$ 0.9	28.9
Conductivity (mS cm ⁻¹)	0.08 $\pm$ 0.02	0.02	0.08 $\pm$ 0.03	0.03
pH	6.8 $\pm$ 0.1	7.0	6.7 $\pm$ 0.2	6.4
N-NH ₄ ⁺ (μmol/L)	0.71 $\pm$ 0.09	1.93 $\pm$ 0.79	0.79 $\pm$ 0.14	1.13 $\pm$ 0.15
N-NO _x ⁻ (μmol/L)	0.61 $\pm$ 0.13	1.19 $\pm$ 0.23	0.54 $\pm$ 0.07	0.51 $\pm$ 0.09
DIP (μmol/L)	0.12 $\pm$ 0.02	0.27 $\pm$ 0.05	0.18 $\pm$ 0.06	0.09 $\pm$ 0.01
DIN:DIP (molar)	15.3	10.8	9.5	18.8

TABLE 2. Respiration (R) and gross primary productivity estimated from ecosystem DO variations (GPP; mgC/m²/d) of floodplain wetlands dominated by macrophytes with different structure: vertical, submerged and with floating leaves; and contribution of macrophytes, epiphyton and phytoplankton to total productivity, assuming no other major primary producer. *Cer* = Ceratophyllum.

	(mgC/m ² /d)		Relative contribution (%)		
	R	GPP	Macrophyte	Epiphyton	Phytoplankton
Vertical-					
<i>Para grass</i>	2020	1790	98.0	2.1	0.02
<i>Hymenanche</i>	2150	1760	88.1	2.1	0.02
Submerged/ Floating					
<i>Najas/ waterlillies</i>	4080	3660	89.9	12.7	0.02
<i>Cer /waterlillies</i>	3720	3580	89.7	12.7	0.02

TABLE 3. Comparison of methods for estimating primary productivity of epiphyton on different macrophyte structures: Experiments with ^{13}C enrichment to estimate C uptake; 2) measurements of DO variations in light/dark bottles to estimate NEP; and 3) estimations of GPP from diel variations of DO measured with *in-situ* loggers scaled to biomass. Values are mean and standard errors of replicates of structural type.

Macrophyte structure	^{13}C uptake ($\text{mgC}/\text{m}^2/\text{d}$)	NEP from DO variations in light/dark bottles ($\text{mgC}/\text{m}^2/\text{d}$)	GPP from diel DO variations and biomass ($\text{mgC}/\text{m}^2/\text{d}$)
Vertical	18.2 ± 11.1	3.7 ± 1.6	37.8 ± 0.3
Horizontal	219	61.1	-
Submerged	166 ± 84.5	44.7	$460 \pm 5.1^*$
Floating	12.9 ± 2.7	2.2	-

*The site was dominated by submerged macrophytes, but had some floating macrophytes.

FIGURES

FIGURE 1. Sampling sites within floodplain wetlands of Kakadu National Park, Australia.

Crosses indicate the locations where biomass was sampled; triangles indicate the locations where primary productivity was sampled; heptagons indicate locations for DO loggers.

Photograph by M. Douglas

FIGURE 2. Primary productivity of epiphyton ($\text{mgC/dw g epiphyton/h}$ and $\text{mgC/m}^2/\text{d}$) attached to different macrophyte structures measured as ^{13}C -bicarbonate uptake (A,C), and as net ecosystem productivity (NEP) from the variations of dissolved oxygen (DO) in dark/light bottle experiments (B,D).

FIGURE 3. Dissolved oxygen (DO) concentrations during a dial cycle within two wetland communities: one dominated by water lilies and hornwort (*Nymphaeae* sp. and *Ceratophyllum*; floating and submerged structural types), and one dominated by hymenanche (vertical structural type) in Kakadu National Park, Australia

FIGURE 4. Schematic representation of the primary productivity within wetlands of Kakadu National Park ($\text{mgC}/\text{m}^2/\text{d}$) during the flooding season (April-May) and the relative contribution of each component (M = macrophytes, P = phytoplankton, and E = epiphyton). Primary productivity for epiphyton and phytoplankton was estimated as ^{13}C uptake (see Methods); productivity of horizontal grasses and *Melaleuca* forests was obtained from published data (Finlayson 1991 macrophyte productivity measured as biomass accumulation, and Finlayson et al. 1993, *Melaleuca* litterfall NPP) and for vertical and submerged macrophytes from diel DO variations as: $\text{GPP macrophytes} = \text{GPP total} - (\text{GPP epiphyton} + \text{GPP phytoplankton})$.

***Melaleuca* forest**
Trees = 970*