Seasonal contrasts in carbon resources and ecological processes on a tropical floodplain

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SUMMARY

1. Globally, tropical floodplains are highly productive ecosystems. This is largely because of predictable seasonal rains providing replenishing floodwaters that stimulate nutrient turnover which, in turn, substantially boosts both primary and secondary productivity. This is associated with concomitant shifts in the types of primary producers and associated food webs.
2. The Magela Creek floodplain on Kakadu National Park in northern Australia is one of the most studied tropical freshwater ecosystems in Australia and provides an opportunity to collate and examine information on organic carbon sources and pathways through food webs to gain a fundamental understanding of how these systems may function.
3. We reviewed biophysical information published since the early 1980s to construct an assessment of the carbon resources for the channel and floodplain.
4. We conclude that macrophytes, largely in the form of grasses and aquatic plants, produce the greatest above-ground biomass on the Magela Creek floodplain. Although macrophytes provide suitable substrata for the attachment of epiphytes, they do not appear to be an important carbon source for aquatic consumers themselves. Nevertheless, macrophytes do provide critical seasonal food and habitat structure for other producers and consumers on the floodplain, such as the abundant magpie geese.
5. We developed a generalised conceptual food web and carbon budget contrasting the 'wet' and 'dry' seasons for the Magela Creek system, as a representative of tropical seasonal floodplain systems.
6. Our conceptual model of tropical floodplains indicates that knowledge of the seasonal and spatial links and exchanges between the floodplain and the river is critical in understanding ecosystem function.

Keywords: aquatic food webs, connectivity, consumers, productivity, sources, wet–dry tropics

Introduction

Tropical floodplains are highly productive ecosystems of global importance to both wildlife and people. They are dominated by seasonal flooding that results in the recurrent deposition of nutrient-rich sediment (McClain & Richey, 1996; Junk & Wantzen, 2004) and the replenishment of water supplies that, together, substantially boost primary productivity (Winemiller, 2004; Davies, Bunn & Hamilton, 2008). According to the Flood-Pulse Concept (Junk, Bayley & Sparks, 1989; Tockner, Malard & Ward, 2000), seasonal inundation and subsequent drainage are the primary drivers of ecological processes in large floodplain rivers,

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particularly when the flood pulse is of relatively long duration (Junk & Welcomme, 1990). In floodplain rivers, a large proportion of the primary productivity that subsequently supports consumers occurs outside the main channel (Junk *et al.*, 1989; Tockner *et al.*, 2000). This typifies many floodplain rivers in the tropics, where seasonal changes in water levels are associated with a dramatic increase in aquatic primary productivity and a corresponding shift in the nature of the dominant primary producers, from algae largely confined to the river channel and isolated water bodies in the dry season, to emergent aquatic macrophytes during floodplain inundation in the wet season (Finlayson, Cowie & Bailey, 1990a; Finlayson, Cowie & Bailey, 1993; Douglas, Bunn & Davies, 2005).

In northern Australia, tropical floodplain rivers are characterised by extreme contrasts between the wet and dry seasons. The pattern of flooding in the wet season is the main driver of productivity on the floodplain, and rates of primary production typically show high levels of spatial and temporal heterogeneity (Davies *et al.*, 2008). Flood conditions are usually associated with increased nutrient availability and higher aquatic primary production (Junk & Piedade, 1997) and secondary production including fish (Winemiller, 1996, 2004). Flooding can also lead to an increase in allochthonous carbon inputs, the importance of which to floodplain food webs has been a subject of debate (Zeug & Winemiller, 2008). How much allochthonous carbon is transferred into the main channel from the floodplain during or following floods is not well understood (Hamilton, Lewis & Sippel, 1992).

Primary production provides the energy that fuels aquatic food webs but, unlike lentic systems, rivers are generally open systems where carbon and nutrients are 'imported', often from the riparian zone (Bunn, Davies & Mosisch, 1999). The quality of the autotrophic food source is important in aquatic systems and many studies have pointed to the dominant role of algae in river food webs over other sources of carbon such as C_4 macrophytes (Hamilton *et al.*, 1992; Thorp & Delong, 1994; Bunn, Davies & Kellaway, 1997; Martinelli *et al.*, 1999; Bunn *et al.*, 2005). Although macrophyte production can be very high during the period of floodplain inundation (Junk *et al.*, 1989; Finlayson, 1991; Piedade, Junk & Long, 1991), only a small fraction of this can be actually consumed, as the coarse particulate matter derived from macrophytes is evidently of poor nutri-

tional value compared to algal organic matter (Hamilton *et al.*, 1992; Bunn *et al.*, 1997; Lewis *et al.*, 2001). Plant detritus on the floodplain will also be broken down via the photochemical effects of solar radiation (Anesio, Tranvik & Graneli, 1999; Austin & Vivanco, 2006). This is likely to be particularly important in tropical savanna regions. Fire can also be an important 'consumer' of macrophyte biomass on the floodplain (Edwards *et al.*, 2003), as are termites (Salick, Herrera & Jordan, 1983). However, the fate of this large source of carbon produced by macrophytes on tropical floodplains during the wet season remains largely unknown.

Tropical floodplains are found throughout the northern third of the Australian continent, which is predominantly savanna terrain. Although many areas have been modified by feral animals such as pigs (*Sus scrofa*), domestic cattle (*Bos taurus*, *Bos indicus*) and water buffalo (*Bubalus bubalis*), as well as alien plants such as mimosa (*Mimosa pigra*) and para grass (*Urochloa mutica*), they retain their natural hydrological regimes and have seen little large-scale alteration (Stein, Stein & Nix, 2002; Douglas *et al.*, 2005). In Kakadu National Park, 250 km east of Darwin, Australia, there have been numerous environmental studies related to monitoring the impacts of uranium mining on the Magela Creek system within the Park (Gardner, Finlayson & Pidgeon, 2002). The majority of these studies have focussed on describing the environment and biota, with less attention paid to understanding fundamental ecological processes (Finlayson, 2005) or the cultural and livelihood values for indigenous communities (Jackson, Storrs & Morrison, 2005). This article uses the available information from the Magela Creek system as a case study and combines it with data on similar systems from other tropical regions to present a generalised account of carbon resources supporting tropical river/floodplain ecosystems. We address the following questions: what are the ecological functions driving food webs in wet–dry tropical floodplains; and what information is required to improve our knowledge of these ecologically and culturally important tropical ecosystems?

Methods

Study site

This study focuses on information collected in Kakadu National Park in the wet–dry tropics of northern

Australia, and specifically on the floodplain of Magela Creek, a seasonally flowing tributary of the East Alligator River, Northern Territory (Fig. 1). Magela Creek arises from sandstone plateau country in the western part of Arnhem Land before flowing across the lowland plains that cover most of Kakadu. Here, the creek distributes water in an expansive clay-based floodplain system that covers approximately 200 km^2 of the 1600 km^2 catchment (Hart, Ottaway & Noller, 1987a). The floodplain soils of silt and clay have built up through deposition in wet season flooding, and these alluvial soils are mostly relatively shallow and are underlain by gleyed marine sediments (Wasson, 1992). The Alligator Rivers Region (Fig. 1), which encompasses the study area, is characterised by a monsoonal climate with two distinct seasons, 'wet' and 'dry'. The wet season starts November–December and usually lasts for 3–4 months; however, this can vary from year to year (Finlayson *et al.*, 1990a).

Vegetation communities on the lowlands and floodplain are related to micro-topography and therefore to water depth during the wet season (Bowman & Wilson, 1986; Finlayson, Cowie & Bailey, 1990b; Finlayson, 2005). Common vegetation includes paperbark (*Melaleuca* spp.) forests, open perennial and annual swamps, billabongs and grass/sedge herbfields (Williams, 1979). The widespread aquatic grassland communities occupy around 40% of the floodplains (Finlayson *et al.*, 1993), with *Melaleuca* spp. forests or woodlands covering around 30–40% (Finlayson, Bailey & Cowie, 1989).

Data collection

Biomass and productivity values for the different functional groups were sourced from the large number of published and unpublished reports from over 30 years of environmental studies undertaken on the floodplain of Magela Creek and surrounding aquatic systems. The majority of the unpublished reports can be viewed via the website of the Supervising Scientist Division of the Australian Government Department of the Environment, Water, Heritage and the Arts (http://www.environment.gov.au/ssd/index.html). Where there were gaps in these data, estimates were obtained from published studies on tropical floodplain environments from other regions of the world. Data given as biomass per unit area were scaled up for the total floodplain area (200 km^2) to give an estimate of carbon for the entire floodplain, expressed as kilogram per hectare. Similarly, data expressed as biomass per unit time were scaled up for the wet season, the dry season or a combined annual amount. This provided a common 'currency' allowing comparison between the contributions of different functional groups to floodplain carbon resources between seasons. An estimate of total surface area and volume of water in billabongs on the Magela Creek floodplain were calculated from dimensions (length, width, depth) given for each waterhole in Bishop *et al.* (1990).
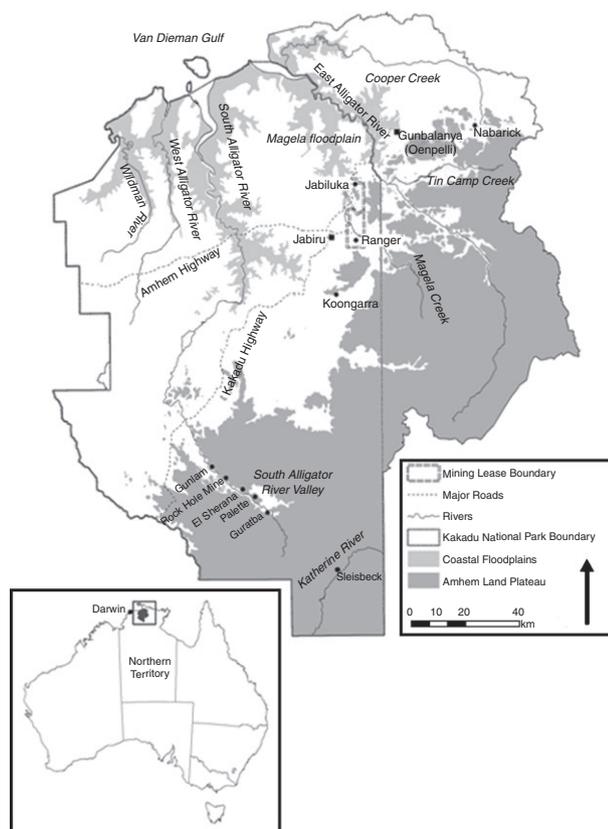
Magela Creek hydrology

Flow data for Magela Creek were from a gauging site (GS-8210009) just before the creek flows out onto the floodplain and rainfall data was from the nearby town site of Jabiru. There is high consistency in wet season rainfall and therefore creek flow, but the timing of the commencement and cessation of flows and in particular the magnitude of flows can be highly variable
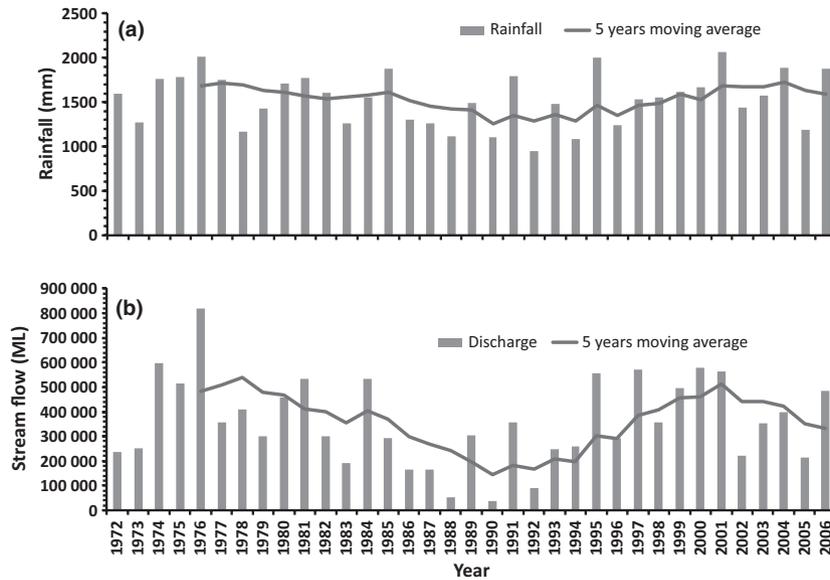

Fig. 1 Location of the Magela Creek floodplain within Kakadu National Park, east of Darwin in the wet/dry tropics of Northern Australia.

Fig. 2 Magela Creek wet season (October to April) (a) rainfall (mm) and (b) stream flow volume (ML) from 1972 to 2006 (5-year moving averages shown).

from year to year (Fig. 2). The long-term mean for total wet season flows in the Magela Creek is 359 000 ML with a coefficient of variation of 0.49.

The start of the wet season in the Alligator Rivers Region commences around early November with intermittent rain storms saturating the soils and, as more consistent rain occurs, water collects in the creeks that then begin to flow (Hart *et al.*, 1987a). Once the creeks and rivers are full, the freshwater moves out across the floodplains and can cover them to a depth of several metres (Finlayson, 2005). Flooding occurs once the catchment is saturated and heavy falls of rain later in the season generate more widespread flooding and discharge than equivalent flows earlier in the season (Finlayson, 2005). An area of about 200 km^2 of floodplain is flooded in most years, and the extensive areas of aquatic grasses and sedges on the floodplain are generally flooded for 3–6 months with some low-lying swamps flooded for more than 6 months of the year (Hart & McGregor, 1980). By early April, rain becomes intermittent and then stops altogether, and freshwater flow in the creeks and rivers ceases within a few months of the end of the rains. From mid-April to mid-September, no rain falls and the creeks dry up and the floodplain slowly dries out, except for a few permanent swamps and billabongs (Finlayson *et al.*, 1990a). Total flow volume for the 1982–3 wet season (192300 ML), when several of the studies reported here were undertaken, was only 53% of the long-term average for Magela Creek (Fig. 2). In addition to this, the commencement

of the wet season was later than usual with initial flows occurring in late December 1982 instead of the usual late November or early December (Hart *et al.*, 1987a).

Water quality and material budget

Data for water quality and material budgets are taken from a study on the Magela Creek in the 1982–3 wet season (Hart, Ottaway & Noller, 1987b; Hart *et al.*, 1987a). Samples were collected from eight locations to collect water flowing in Magela Creek and entering the floodplain, particularly at the rising stage of the hydrograph when material and nutrient concentrations would be greatest. Organic matter in the sediments of seven billabongs on Magela Creek floodplain was measured at the end of the dry season 1977 (Thomas, Davies & Hart, 1981). Total organic carbon concentrations in the waters for billabongs of Magela Creek were sampled in December 1977 (Hart & McGregor, 1980).

Aquatic microorganisms

As there are no data for biomass or productivity of microorganisms in the Magela Creek, figures for microbial production given by Castillo (2000) on the Orinoco floodplain in South America were extrapolated for the area of Magela Creek floodplain (~200 km^2). Castillo (2000) sampled two floodplain lagoons and two main river sites on the Autana River

in Venezuela between 1997 and 1998. Bacterial production was estimated from water samples by the rate of incorporation of tritiated leucine into protein (Kirchman, 1993; cited in Castillo, 2000).

Floodplain grasses

Estimates of the productivity of the major grass species growing on the Magela Creek floodplain were made from biomass samples taken at 4-weekly intervals from October 1983 to February 1985 (Finlayson, 1991) and also from biomass samples of these grasses measured in the dry season 1999 (Douglas & O'Connor, 2004). The proportions of the floodplain occupied by these major grass species are as follows: 15% for *Hymenachne acutigluma*, 14% for *Pseudoraphis spinescens* and 12% for *Oryza meridionalis* (Finlayson *et al.*, 1993).

Woody plants

Tree density and biomass were measured on the floodplain in October 1983 (Finlayson *et al.*, 1993). As an indicator of the short-term productivity, monthly litter fall was measured in the *Melaleuca* forest on the Magela floodplain from September 1983 to September 1985 (Finlayson *et al.*, 1988, 1993).

Plant litter

Using the annual biomass of litter fall from the canopy of *Melaleuca* spp. trees on the Magela Creek floodplain, combined with the dry season biomass of grass (see above), and allowing for 30% removal of detritus in floodplain fires (Edwards *et al.*, 2003), we calculated an estimate of the annual contribution of detrital carbon from vascular plants to the total floodplain.

Algae

Chlorophyll *a* measurements, as an estimate of algae biomass in the water column, were taken in Magela Ck billabongs at the end of dry season 1977 and during the wet season 1978 (Hart & MacGregor). Phytoplankton net productivity was measured using light/dark bottle techniques (*sensu* Odum, 1957) at four sites on the floodplain in the 2000 wet season (P. Davies, unpublished data). Biomass of diatoms attached to aquatic macrophytes was measured using diatom samplers on the floodplain during the wet seasons of 1980–82 (McBride, 1983).

Aquatic macroinvertebrates

Aquatic macroinvertebrates on the Magela Creek floodplain were sampled with sweep nets (epiphytes on aquatic grasses) and suction samplers (benthic habitat), used to quantify abundance across four sites in the mid- to late-wet season of 1998 and 1999 (Douglas & O'Connor, 2003). The abundance and biomass of benthic macroinvertebrates were sampled in 0.25-m² quadrats also at monthly intervals (March 1981 to April 1982) from three sites on four Magela Creek billabongs in littoral and stream riffle areas (Marchant, 1982; Outridge, 1988).

Fish

Comprehensive seasonal sampling of fish in the Magela Creek systems was undertaken from 1978 to 1981 with species collected from all main habitat types (main channel waterbodies; lowland backflow billabongs; lowland sandy creeks, corridor waterbodies; and floodplain billabongs; Bishop, 1987). Two standard netting techniques were used, designed to provide a representative sample from a site: multi-mesh size gill netting and seine netting (Bishop *et al.*, 1990). To estimate fish biomass for the entire area of the floodplain, we assumed that the majority of fish in the system were concentrated at the billabong and creek sites sampled (Bishop *et al.*, 1990) and that sampling years 1978–9 were typical (annual rainfall 1433 mm, long-term average 1400 mm; Fig. 2).

Turtles

The relative abundances and density of freshwater turtles along the Magela Creek and billabongs were estimated from sampling 12 sites surveyed in the early-wet season 1982 (Legler, 1982). Based on these observations and the average size of each species, an estimate of turtle biomass for the Magela Creek floodplain was calculated.

File snakes

File snakes (*Acrochordus arafurae*, Acrochordidae) are an abundant vertebrate predator found in billabongs

on the Magela Creek floodplain (Shine, 1986). The population size of file snakes was estimated in seven billabongs by standard mark and re-capture techniques using fyke nets (Shine, 1986; Houston & Shine, 1994). Estimates of the contribution of files snakes to annual biomass on the floodplain were based on population densities of *A. arafurae* in billabongs and average body size measurements from seven surveys in the late-dry season and two wet season sampling events, from 1985 to 1988 (Houston & Shine, 1993, 1994).

Waterbirds

Estimates of waterbird numbers on the floodplain for the dry and wet seasons were taken from monthly aerial surveys along fixed transects from June 1981 to August 1984 (Morton, Brennan & Armstrong, 1990a,b, 1993a,b) and in August, September and October 1990–92 (Dostine & Skeat, 1993). The wet biomass of waterbirds was estimated from the average adult male and female body weight of each species.

Crocodiles

In the floodplain sections of northern Australian rivers, saltwater crocodiles (*Crocodylus porosus*) tend to greatly outnumber freshwater crocodiles (*Crocodylus johnstoni*) mainly because of competitive exclusion (Webb, Manolis & Sack, 1983), and hence, in this paper we focussed on *C. porosus*. Spotlight surveys were undertaken in June and August 1983 on Magela Creek (Jenkins & Forbes, 1985). In these surveys, marked seasonal variations occurred in the abundance of crocodiles that are attributed to movements between the river and adjacent freshwater swamps. *Crocodylus porosus* males vary in average length between 3 and 5 m and weigh around 400–700 kg, and females vary in average length between 2 and 3.5 m and weigh around 150–300 kg (Webb *et al.*, 1978). We used these measurements to estimate average non-hatchling crocodile biomass on the floodplain.

Results

A summary of the estimated annual carbon contribution for the major sources and consumers on the Magela Creek floodplain is presented in Table 1 and highlights the dominance of macrophytes and leaf litter as carbon sources to floodplain systems. These figures are based on the numerous studies on the Magela Creek and are discussed in more detail in the following sections.

Table 1 Estimates of the contribution of major plant and animal functional groups to carbon resources on the Magela Creek floodplain, based on biomass data synthesised in this article. Estimates are for annual biomass, unless otherwise specified

Source	Carbon (kg ha^{-1})	Reference
Detritus	7938–12826	Finlayson, 1991; Finlayson *et al.*, 1993; Douglas & O'Connor, 2004
Bacteria	0.35–5.4 (production)	Castillo, 2003
Trees[*]	21000–22500	Finlayson *et al.*, 1993
Litterfall	3500–3750	Finlayson *et al.*, 1993
Aquatic grasses[†]	7590–14573 (wet season) 1822–3497 (dry season)	Finlayson, 1991; Douglas & O'Connor, 2004
Algae		
Phytoplankton (billabongs)	180 (dry season) 400 (wet season)	Hart & MacGregor. 1980
Diatoms (epiphytes)	850 (wet season)	McBride, 1983
Macroinvertebrates	6–60	Outridge, 1988
Fish	9–22 (dry season)	Bishop 1987; Bishop *et al.*, 1990
Turtles	1.6	Legler, 1982
File snakes	0.5	Shine, 1986; Houston & Shine, 1994
Water birds	0.55–1.7 (wet season) 3.7–11.8 (dry season)	Dostine & Skeat, 1993; Morton *et al.*, 1990a,b, 1993a,b
Crocodiles	0.4–1.7	Webb *et al.*, 1983; Jenkins & Forbes, 1985

[*]Most carbon in tree biomass is locked up for decades, released as litterfall.
[†]Aquatic grasses include *Hymenachne acutigluma*, *Urochloa mutica*, *Pseudorhaphis spinescens* and *Oryza meridionalis*.

Table 2 Water quality for flood event, first flow and main wet season on Magela Creek 1982–3 wet season (from Hart *et al.*, 1987a)

	Flood event[*]	First flow[†]	Wet season[‡]	Total for catchment
pH	5.2 (5.2–5.3)	5.6 (5.4–5.7)	5.2 (4.8–5.8)	
TSS (mg L^{-1})	12 (6–28)	3 (<0.6–8.4)	13 (3.8–59)	39 kg ha^{-1} $year^{-1}$
TDS (mg L^{-1})				21 kg ha^{-1} $year^{-1}$
EC (μS cm^{-1})§	8.4 (7.3–12)	15 (14–16)	10 (5.4–17)	
Na (mg L^{-1})	0.8 (0.7–0.9)	1.3 (1–1.6)	0.9 (0.6–1.1)	2.5 kg ha^{-1} $year^{-1}$
K (mg L^{-1})	0.3 (0.2–0.5)	0.8 (0.7–1)	0.3 (0.2–0.6)	0.9 kg ha^{-1} $year^{-1}$
Ca (mg L^{-1})	0.2 (0.1–0.3)	0.4 (0.2–0.8)	0.3 (<0.1–1.5)	0.7 kg ha^{-1} $year^{-1}$
Cl (mg L^{-1})	1.4 (0.8–2)	2 (2–3)	1.7 (<1–3)	4.3 kg ha^{-1} $year^{-1}$
Total P (μg L^{-1})	7 (5–13)	15 (<10–30)	6 (<10–30)	16 g ha^{-1} $year^{-1}$
NO_3 (μg N l^{-1})	30 (20–30)	200 (100–2700)	43 (<10–79)	90 g ha^{-1} $year^{-1}$
NH_4 (μg N L^{-1})	<10 (<10)	6 (<10–20)	5 (<10)	

TSS, total suspended sediment.
[*]Mean of five flood events (range).
[†]Mean (range), n = 5–21.
[‡]Mean (range), n = 45.
§At 25 °C

Water quality and material budgets

Water quality for the Magela Creek in the 1982–3 wet season showed high variation depending on climatic and disturbance conditions within the catchment, highlighting the differences between first flows and flood flows (Table 2). First flush flows were quite acidic (pH 4–5), with high conductivity and sulphate concentrations. There were also high concentrations of total P and other nutrients in the first flows of the season while available N was much greater in subsequent wet season flows. The floodplain was generally a net source of the major ions and a net sink for nutrients (N and P) and suspended matter (Table 2). During the 1982–3 wet season on Magela Creek, the input from runoff for the whole catchment was 5400 (±5800) tonnes of total suspended sediment (TSS) and the output was 1700 t (±540), leaving 3700 t (±5900) deposited on the floodplain. Unfortunately, little data on DOM or POM for the Magela Creek floodplain is available. Organic matter in the sediments of the billabongs on Magela Creek varied between 0.1 and 20%, with an average of 9.5%. Total organic carbon concentrations in the waters for billabongs on Magela Creek in December 1977 averaged (±SE) 6.4 ± 2 mg L^{-1}. Water temperature in streams and billabongs varied little between seasons and varied between 28 and 32 °C, with stratification seen only in the deepest billabongs where temperature varied between 30.5 °C at the surface to 25.7 °C on the bottom (Bishop *et al.*, 1990).

Aquatic microorganisms

No studies of aquatic microorganisms (bacteria and fungi) on Magela Creek or nearby floodplains have been published. Bacterial production on the Orinoco River, South America (Castillo, 2000; Castillo, Kling & Allan, 2003) was 0.62–1.03 μg C L^{-1} h^{-1} in floodplain lakes and 0.17–0.19 μg C L^{-1} h^{-1} in the main channel during the period of low water, while during the period of high water, river and lake sites showed similar low levels (0.04 μg C L^{-1} h^{-1}). We used these figures to estimate annual microbial production for the Magela Creek floodplain (Table 1).

Floodplain grasses

The widespread aquatic grasslands that cover the Magela Creek floodplain are highly productive, with standing above-ground dry biomass ranging from 5000–11 000 kg ha $year^{-1}$. Peak above-ground biomass coincides with the end of the wet season, with receding water levels. Peak biomass for major grass species on the floodplain was between 14 100 and 44 300 kg ha^{-1} for *Hymenachne acutigluma*, 5100–11 700 kg ha^{-1} for *Oryza meridionalis*, 16 700 kg ha^{-1} for *Psuedoraphis spinescens* and 41 200 kg ha^{-1} for the introduced para grass (*Urochloa mutica*). The carbon-to-nitrogen ratios for the grasses on the floodplain ranged from 33 to 37 for *Hymenachne acutigluma* and 47–67 for *Urochloa mutica* (Douglas *et al.*, 2002). Higher biomass is generally apparent in grass communities occurring around low-lying channels and billabongs

during the dry season, but varies greatly on the floodplain, both spatially and temporally, depending on climatic conditions and the degree of flooding. Annual biomass of carbon from these grasses is around 45–50% (excluding trees) of the total carbon on the floodplain (Table 1).

Woody plants

Calculated average (±SE) tree biomass for the main tree species on the Magela floodplain was 775 ± 1.6 kg for *Melaleuca viridiflora* and 1009 ± 1.6 kg for *Melaleuca cajaputi*. An average density of 294 trees ha^{-1} with the trees occupying 30% of the floodplain gives a total standing above-ground dry biomass of about 45000 ± 3000 kg ha^{-1}, which is 40–50% of the carbon on the floodplain (Table 1). The majority of this carbon is stored in the woody material of stems and branches of trees and only turned over after long time spans (i.e., decades). However, short time-scale turnover of the productivity from these trees can be measured as litter fall (Table 1). For *Melaleuca* species litter, C:N ratios are likely to be in the order of 25–60 (Greenway, 1994).

Plant litter

The extensive grasslands on the Magela Creek floodplain contribute large amounts of detritus to the aquatic system. Litter from *Melaleuca* trees on the floodplain also contributes detritus to the aquatic system but is likely to decompose at a much slower rate than grass material. The annual biomass of litter fall from the canopy of *Melaleuca* spp. trees on the Magela Creek floodplain was combined with dry season biomass of grass to give an indicative contribution of detrital carbon from vascular plant sources to the total floodplain (Table 1).

Algae

During the wet season, the high flushing rate and subsequent export of phytoplankton resulted in low phytoplankton productivity in the billabongs, while dry season productivity increased but varied substantially according to water-quality conditions including turbidity, light, nutrients and chemistry of individual billabongs. Chlorophyll *a* concentrations in the Magela Creek billabongs showed peak values at the end of the dry season (19 g m^{-3}), which reduced to less

than 8 g m^{-3} after the billabong had become connected during the wet season. For comparison, these figures were converted to kg C per ha of surface water of the floodplain (Table 1). We measured net production rates of 1.1 g C m^{-3} day^{-1} in the 2000 wet season on the Magela Creek floodplain (P. Davies, unpublished data). This measurement of productivity would translate to around 990 kg ha year^{-1}, which is much higher than phytoplankton biomass estimates (Table 1), indicating the high turnover of algal biomass on the floodplain. Diatoms are usually restricted to the littoral areas of billabongs during the dry season but large diatom biomass was found on the floodplain as epiphytes on the abundant macrophytes at the time of highest production during the late-wet season (Table 1). From these figures, annual algal biomass contributes around 4–6% of carbon on the floodplain.

Aquatic macroinvertebrates

Studies of aquatic macroinvertebrates on the Magela Creek system showed the greatest numbers of taxa and individuals were collected during the late-wet season and early dry season in the littoral zones of shallow billabongs (Marchant, 1982). Abundance of aquatic macroinvertebrates on the floodplain in the mid- to late-wet season over 2 years and across four sites averaged 2880–17 287 individuals per sample within the epiphytes and 1952–3210 individuals per sample in the benthic habitat. In the sediments of four Magela Creek billabongs and stream riffles of Magela Creek, annual total standing biomass of invertebrates was dominated by the freshwater mussel *Velesunio angasi* (Hyriidae), representing >98% of the biomass (Outridge, 1988). At all sites, abundance and standing crop were substantially reduced towards the end of the dry season. Total annual standing crop of benthic invertebrates was 119 kg ha^{-1} year^{-1} (1.8 kg ha^{-1} year^{-1} excluding *V. angasi*) in billabongs. Annual contribution to floodplain carbon by macroinvertebrates is only around 0.03% of the total (Table 1).

Fish

Highest interannual variability in community structure, total abundance and biomass across all sites occurred in the late-dry and early-wet seasons. Major contributing factors to interannual variability in fish abundance include the area and depth of water at the

end of the wet and dry seasons, time since initial flow, recent history of inundation and abundance and density of aquatic macrophytes. Many fish migrate to the floodplain from dry season refugia (backflow billabongs) during the early-wet season (Bishop, 1987). Seasonal variation in fish abundance and biomass varied with habitat, and the numbers of fish in backflow billabongs and sandy bed creek channels peaked in the mid-wet season and were lowest at the end of the dry season. If we assume that the majority of fish in the system are concentrated at these sites and that the sampling years 1978–1979 are typical (Fig. 2), then fish biomass (dry weight) in the dry season in backflow billabongs was approximately 18–45 kg ha^{-1}, in corridor billabongs 12–16 kg ha^{-1} and in floodplain billabongs 11–21 kg ha^{-1}, meaning fish contribute 0.04–0.09% of carbon to the floodplain (Table 1).

Freshwater turtles

Average relative density of all turtles along the Magela Creek sites was 0.89 individuals 100 m^{-1}. A total of 51 turtles from five species (Family Chelidae) were observed at eight Magela Creek sites in the early-wet season 1982. This equates to approximately 3.2 kg ha^{-1} of turtle biomass for the billabongs of the Magela Creek floodplain (Table 1). This is potentially an overestimation for the whole of the floodplain because of the concentration of animals in billabongs in the dry season.

File snakes

During the dry season, file snakes (*Acrochordus arafurae*) are restricted to the main billabongs and estimates of 100 snakes ha^{-1} have been recorded. This pattern changes in the wet season, with most snakes migrating onto the shallow, inundated floodplain. File snakes averaged 0.725 kg body mass (based on 4184 snakes, Houston & Shine, 1993), consequently the biomass per hectare at surveyed billabongs was approximately 72.5 kg ha^{-1} so that for the whole floodplain this would translate to a contribution of around 0.5kg C ha^{-1} (Table 1).

Waterbirds

Seasonal variations in waterbird numbers on the Magela floodplain are caused by large numbers of birds moving onto (dry season) and off (wet season) the floodplain. The contrast in numbers between the wet and dry seasons is apparent for most waterbird species with the exception of black-necked storks (*Ephippiorhynchus asiaticus*) and cormorants (*Phalacrocorax* spp.), which have generally low numbers on the floodplain (Table 3). Magpie geese (*Anseranas semipalmata*) are the dominant species on the Magela Creek floodplains and exemplify the dramatic seasonal changes in abundances (Table 3). Magpie geese comprised about 77% of the total waterbird biomass at the dry season peak (Table 3). Wet season waterbird density was much lower with a total observed density of around 0.62–1.82 ha^{-1}, with magpie geese still comprising 76% of the total (Table 3).

Crocodiles

Saltwater (*C. porosus*) are the top predators on the Magela Creek floodplain. Spotlight surveys in June and August 1983 estimated a crocodile density on Magela Creek of between 1.9 and 5.3 km^{-1}. These figures yield an estimate of between 85 and 238 non-hatchling crocodiles along the 45-km section of the Magela Creek in which they would be expected to occur, which would give an approximate total weight of 16 530–465 000 kg of crocodiles on the 200 km^{-2} floodplain or 0.8–2.5 kg ha^{-1} of non-hatchling crocodiles on the Magela Creek floodplain, contributing 0.01% of the total annual carbon on the floodplain (Table 1). These figures are likely to be a substantial underestimate as surveys only identify the crocodiles present in the accessible channels (Bayliss *et al.*, 1986). Saltwater crocodile numbers have increased considerably in northern Australia since hunting was banned in 1971 (Bayliss, 1987; Parks & Wildlife Service NT Government, 2004).

Discussion

Carbon fluxes on the floodplain

Seasonal changes in flow regimes and hydrological connectivity are the principal drivers of tropical aquatic ecosystem function (Douglas *et al.*, 2005; Lewis, 2008). Australian tropical rivers represent an extreme in intra-annual hydrological variability, with flows always strongly seasonal (McMahon *et al.*, 1991;

Petheram, McMahon & Peel, 2008). This is particularly apparent in some regions of tropical Australia where high interannual variability can occur as a consequence of climatic variability and particularly the El Niño-Southern Oscillation (Hamilton & Gehrke, 2005; Bayliss, Bartolo & van Dam, 2008). The marked seasonality between the wet and dry seasons has a great influence on the distribution and productivity of the flora and fauna on the floodplain (Fig. 3; Douglas *et al.*, 2005). The large hydrological changes between the wet and dry seasons require radical changes in diet, behaviour and habitat use of animals using the floodplain (Fig. 3). For example, the change from flooded to dry conditions prompts a characteristic shift in animals between habitats such as dusky rats moving from the floodplain in the dry season to terrestrial habitats when the floodplain is flooded in the wet season (Madsen & Shine, 1996). Similarly, vast populations of magpie geese that congregate on the floodplain in the dry season disperse to other habitats during the wet season (Bayliss, 1989; Bayliss & Yeomans, 1990). Fish experience large changes in habitat conditions between large areas of flooded, highly productive floodplain in the wet season to refugial waterholes with limited space and deteriorating water quality as the dry season proceeds (Fig. 3). Inundation periods on floodplains can bring fish into contact with greater and more varied sources of carbon (Perga, Arfi & Gerdeaux, 2005), and for some fish, inundation provides opportunities for spawning or improving body condition (Winemiller & Jepsen, 1998).

Dry season fires are also a significant 'consumer' of carbon on the floodplains, with ignition of the drying grass from numerous lighting strikes and from indigenous and non-indigenous burning practices (Bayliss *et al.*, 2006; Fig. 3). Increased fire frequency and intensity reported on Kakadu floodplains, including Magela Creek floodplain, in the late 1980s-early 1990s, is related to the eradication of water buffalo and the subsequent increase in above-ground grass biomass (Gill *et al.*, 2000). This will undoubtedly have other ecological effects on the Magela floodplain. For example, several species of frog and freshwater turtle aestivate in the dry sediments on the floodplain during the dry season, and increased fire intensity may increase soil temperatures to levels lethal for these animals.

Table 3 Wet and dry season contrasts of water bird densities (based on aerial surveys) and biomass (based on average bird weights) on Magela Creek floodplain in 1990 and 1980

Species	Dry season abundance (no. km^{-2})		Wet season abundance (no. km^{-2})		Dry season biomass (kg ha^{-1})		Wet season biomass (kg ha^{-1})	
	1990[*]	1980–4[†]	1990	1980–4	1990	1980–4	1990	1980–4
Magpie geese	237 ± 31	691	33 ± 45	106	5.82	17.25	0.85	2.60
Black ducks	7 ± 6	79	0.9 ± 2	10	0.07	0.87	0.09	0.10
Burdekin ducks	4.2 ± 3	42	0.5 ± 0.5	2.6	0.04	0.38	0.002	0.02
Grey teal	2.2 ± 2	58	1 ± 2	2.6	0.02	0.38	0.006	0.02
Whistling ducks[‡]	57 ± 38	159	1.9 ± 2.2	5.3	0.43	1.19	0.014	0.04
Egrets[§]	66.2 ± 12	132	20 ± 17	44	0.26	0.53	0.08	0.18
Herons[¶]	24 ± 14	111	1.7 ± 5	1.3	0.13	0.61	0.009	0.007
Spoonbills[**]	2.5 ± 2	42	0.2 ± 1	0.2	0.02	0.33	0.002	0.002
Jabirus	0.2 ± 0.3	1.5	0.2 ± 0.3	0.6	0.008	0.06	0.008	0.02
Brolgas	7.6 ± 3	9.5	2 ± 2	6.3	0.49	0.62	0.01	0.40
Ibises[††]	47.2 ± 20	297	1.2 ± 3	3.6	0.23	1.48	0.005	0.02
Pelicans	0.2 ± 0.5		0		0.02		0	
Cormorants[‡‡]	0.2 ± 1		0.2 ± 1		0.001		0.001	
Totals	455.5	1622	61.7	182.5	7.53	23.70	1.12	3.40

[*]Dostine & Skeat (1993).
[†]Morton *et al.* (1990a,b).
[‡]Includes plumed and whistling ducks.
[§]Great, intermediate and cattle egrets.
[¶]Greater, pied and pacific herons.
[**]Royal and yellow-billed spoonbills.
[††]Glossy, white, straw-necked ibises.
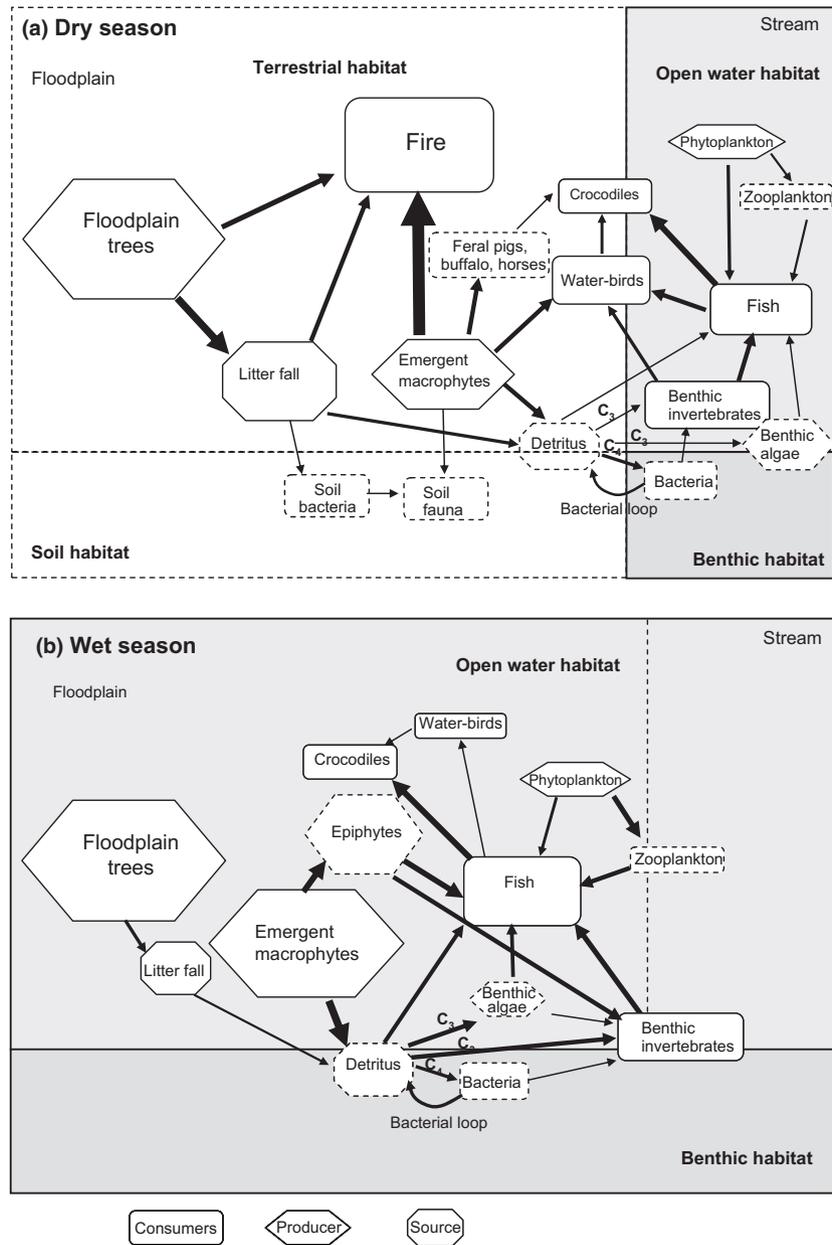[‡‡]Darter, little and pied cormorants.

Fig. 3 (a) Dry season and (b) wet season fluxes of carbon and generalised food web components for the Magela Creek floodplain. Size of boxes give the relative contribution to biomass of each group and relative size of arrow represent dominant pathways. Boxes with broken lines indicate lack of data.

This paper summarises the available information on the abundance and productivity of the predominant producers and consumers that occur on the Magela Creek floodplain as a case study or model of how food webs and carbon fluxes function in tropical Australian floodplain systems (Fig. 3). This highlights the many similarities with other tropical regions such as South America and Africa (Lewis *et al.*, 2001; Winemiller, 2004; Davies *et al.*, 2008) including the nature and relative contributions of primary producers to overall ecosystem productivity and the inferred importance

of algal production to aquatic food webs (Douglas *et al.*, 2005). Although productivity of macrophytes (principally grasses and sedges) on the Magela floodplain was less than the 80 000 kg ha^{-1} measured on the Amazon floodplain for the C$_4$ grass *Echinochloa polystachya* (Piedade *et al.*, 1991), they were similar to the 4000 kg ha^{-1} measured on the Orinoco floodplain (Hamilton & Lewis, 1987) and high in comparison with other tropical savannas (Grace *et al.*, 2006). In these latter tropical floodplains, primary productivity was therefore dominated by macrophytes. Despite

this, several studies have indicated that very little of the carbon from this source directly enters the aquatic food web (Hamilton *et al.*, 1992; Lewis *et al.*, 2000). Although algae are much less conspicuous, high turnover rates can maintain significant consumer biomass (Table 1, cf. $\sim$300 kg ha^{-1} for the Orinoco River floodplain (Lewis *et al.*, 2000)). Indeed, on the floodplain of the Orinoco River, carbon sources for consumers were mostly algal, despite macrophytes and litter fall providing 98% of potentially available carbon (Lewis *et al.*, 2001). The source of carbon for fish on the central floodplain of the Amazon River, where C$_4$ macrophytes were the greatest primary producer, was mostly from phytoplankton despite this being a minor contributor to overall catchment productivity (Forsberg *et al.*, 1993; Lewis *et al.*, 2001). However, notwithstanding the fact that algae are likely to be a critical basal source for the floodplain food web, biomass and rates of productivity of benthic and epiphytic algae on the floodplain are poorly known and have rarely been adequately quantified (Davies *et al.*, 2008).

Riparian and floodplain forests provide another source of allochthonous carbon in tropical floodplains. The Magela floodplain forest is dominated by *Melaleuca* spp. with few other overstorey species (see Cowie, Short & Osterkamp-Madsen, 2000). Leaves of *Melaleuca* spp., like those of other Myrtaceae genera, are highly lignified and refractory (Finlayson *et al.*, 1988) and, consequently, are not readily available as a food source for aquatic consumers. Leaves that break down quickly are used as food by organisms, and those that persist longer in aquatic environments are often used as habitat or substrate (Stout, 1980). The species-poor overstorey of the Magela floodplain is unlike other floodplain forests, such as the Amazon which has a high diversity of tree species and a variety of leaf types (Junk, 1993), with different decomposition rates providing a mixture of food and habitat sources for organisms (Goncalves *et al.*, 2006). However, some tree species that occur on the Magela Creek floodplain, including *Syzidium* spp., *Barringtonia acutangula*, *Ficus* spp. and *Pandanus aquaticus*, have fleshy fruits that may provide a food source for fish (Davis *et al.*, 2010) and other aquatic consumers such as turtles (Legler, 1982). The importance of this may be limited on the Magela floodplain, however, compared to the flooded forests of other tropical floodplains such as the Amazon where there are specialist frugivorous fish (Goulding, 1980).

The low relief, resistant rocks and lack of development within the catchment contribute to the low TSS and nutrient levels recorded for Magela Creek compared with other tropical systems (Lewis, 2008) and perhaps are most similar to levels recorded for the nutrient-poor blackwater streams such as the Rio Negro in the Amazon Basin (Davies *et al.*, 2008; Lewis, 2008). Therefore, the Magela Creek floodplain is probably more nutrient limited and consequently less productive than some other tropical floodplain systems such as the Llanos of the Orinoco in Venezuela and the Pantanal wetland in Brazil (Lewis, 2008). Diversity and abundance of phytoplankton, zooplankton and macroinvertebrates are similar in Magela Creek to values in other tropical floodplain systems (Dudgeon, 1992; Finlayson, 2005; Jacobsen *et al.*, 2008). Although fish productivity is similar in Magela Creek, diversity is much lower than in other tropical regions (Winemiller, 2004), in part because of the relatively recent creation of these wetlands (Wasson, 1992). The low nutrients and productivity for Magela floodplain may result in a less complex aquatic food web structure (Douglas *et al.*, 2005) with shorter food chain lengths (e.g., epiphytic algae > bony bream > barramundi > crocodiles). Similarly, river productivity in the Amazon Basin also affects trophic structures with food chain lengths longer in more productive whitewater rivers than nutrient-poor blackwaters (Jepsen & Winemiller, 2002).

Role of macrophytes on the floodplain

Macrophytes on the floodplain have crucial ecological roles in addition to primary production. Particularly in the wet season, macrophytes provide habitat in the form of refugia for aquatic prey animals and cover for aquatic predators. Macrophytes also provide substrates for the growth of epiphytic algae where shading, water depth and turbidity may inhibit the growth of benthic algae. Epiphytic N-fixing algae (e.g., *Nostoc* spp.), which enhance N sources for algal production in N-limited systems, characterise the floodplain of the East Alligator River in northern Australia (Douglas *et al.*, 2005; Davies *et al.*, 2008). Recycled macrophyte material is also likely to be an important source of soil nutrients on the floodplain

with grass detritus containing substantially higher levels of nutrients (N, P, K) than concentrations in the inputs of water from the creek (Finlayson, 1991).

Despite the widespread area of grasslands on the Magela Creek and other northern Australian floodplains, there are no large extant native herbivores to consume this biomass. This is in contrast to floodplain grasslands on other continents where medium to large native herbivores occur, such as hippopotamus (*Hippopotamus amphibius*) in Africa, capybara (*Hydrochoerus hydrochaeris*) in South America and moose (*Alces alces*) in North America. In pre-European times, manatees (*Trichechus inunguis*) and capybara were much more abundant on the Amazon floodplain, moving onto the floodplain in the wet season to feed on the macrophytes (Junk, 1997). This suggests that on the Amazon floodplain, macrophytes have perhaps become a more dominant feature of the floodplain in more recent times. On the Magela Creek floodplain, feral water buffalo have been a major herbivore since their introduction in the early 1800s before an extensive eradication programme initiated in 1985 greatly reduced numbers (Bayliss *et al.*, 2006). The cessation of traditional indigenous burning practices on the floodplain in the late-dry season, most likely in combination with a substantial reduction of buffalo numbers, has led to an increase in the area of the native grass *Hymenachne acutigluma* in the wetter areas and the exotic para grass *Urochloa mutica* in drier areas, where it has replaced native wild rice (*Oryza* spp.) (Ferdinands, Beggs & Whitehead, 2005). There is evidence however that this C_4 grass is not utilised in the aquatic food web on the floodplain (Bunn *et al.*, 1997; Douglas *et al.*, 2002). Feral pig numbers have increased rapidly since 1985 (corresponding to the decline in buffalo numbers), and they are now widespread consumers of plants, especially *Eleocaris dulcis* sedges, competing directly with waterbirds such as magpie geese (*Anseranas semipalmata*) and brolgas (*Grus rubicunda*) (Fig. 3; Bayliss *et al.*, 2006).

Water birds such as magpie geese consume macrophyte biomass including the tubers of the sedge *Eleocharis dulcis* and the seeds and probably some leaf and stem material of wild rice (Morton *et al.*, 1990a). Seeds of wild rice are also eaten by granivorous rodents that occupy the margins of the Magela floodplain (Wurm, 1998). Wild rice seeds are also eaten by some herbivorous fish species on the central Amazon River (Forsberg *et al.*, 1993). Possible indirect links of floodplain macrophytes to the aquatic food web could occur *via* terrestrial insects such as grasshoppers feeding on emergent macrophytes, which may then be eaten by insect predatory fish such as the archer fish (*Toxotes* spp.) or rainbow fish (*Melanotaenia* spp.). The importance of terrestrial subsides for the maintenance of aquatic ecosystems has been highlighted for riparian areas (Nakano & Murakami, 2001; Baxter, Fausch & Saunders, 2005) and is obviously important on floodplains; however, the distinction between terrestrial and aquatic subsidies is not clearly defined.

Conclusions

The interaction at the terrestrial–aquatic interface in river floodplain systems generally results in high diversity and productivity (Naiman & Decamps, 1997; Naiman, Décamps & McClain, 2005). This is because of the interactions between flooding, sediment transport, biotic processes (primary and secondary production and processing of organic matter) and hydrological connection and disconnection as waters inundate and recede from the floodplain (Fig. 3; Tockner *et al.*, 2000; Tockner, Lorang & Stanford, 2010a). Floodplain rivers have always been highly valued environments for people in terms of settlement and exploitation (Ward, 1998; Junk & Wantzen, 2004; Winemiller, 2004; Jackson *et al.*, 2005) and hence are impacted by multiple stressors (Tockner *et al.*, 2010a,b). Therefore, in the case of tropical floodplain rivers, knowledge of the seasonal and spatial links and exchange between the floodplain and the river is critical. Particular components of this include understanding the dynamics of primary producers such as algae that appear to be a critical basal carbon source in the aquatic food web. We also have little understanding under what conditions and scales the floodplain is either a source or a sink of organic matter to the river and how the biophysical heterogeneity of floodplains contributes to the storage, use, regulation and movement of organic matter. In terms of secondary consumers, there is a lack of information on the movement of fish on and off the floodplain, and the utilisation of the floodplain for feeding and/or reproduction. Food web effects of fish feeding on the floodplain and maintenance in dry season refugia are currently poorly understood. Other areas that require more information include the effects on food webs and the carbon budget of the feeding and migration

patterns of waterbirds, and the effects of feral animals and exotic plants. We also need to understand the importance of littoral areas of waterholes and floodplains in supporting biodiversity and as areas of high inputs of allochthonous and autochthonous organic matter as well as for nutrient cycling (Strayer & Findlay, 2010).

This paper has provided insights into the ecological functions that drive food webs in tropical floodplain rivers. This ecosystem function level of understanding is critical for the management of wet–dry tropical floodplains. For example, determining environmental flow requirements for rivers assumes that natural flow regimes and associated hydrological–ecological linkages are well known. This is clearly not the case in tropical floodplain rivers in many regions of the world. Most research on environmental flows has focused on predicting changes in aquatic habitat and then using this to predict likely responses of particular biota. Therefore, assessments of environmental flows need to include fundamental ecosystem processes related to the connectivity between the river and the floodplain, but very few studies have attempted this in tropical regions. We have highlighted the information that is known in this regard and the obvious gaps in our conceptual understanding of these systems, and thereby provided a conceptual framework for future work.

Acknowledgments

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