ECOSYSTEM ECOLOGY - ORIGINAL RESEARCH

Provisioning of bioavailable carbon between the wet and dry phases in a semi-arid floodplain

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Abstract Ecosystem functioning on arid and semi-arid floodplains may be described by two alternate traditional paradigms. The pulse-reserve model suggests that rainfall is the main driver of plant growth and subsequent carbon and energy reserve formation in the soil of arid and semi-arid regions. The flood pulse concept suggests that periodic flooding facilitates the two-way transfer of materials between a river and its adjacent floodplain, but focuses mainly on the period when the floodplain is inundated. We compared the effects of both rainfall and flooding on soil moisture and carbon in a semi-arid floodplain to determine the relative importance of each for soil moisture recharge and the generation of a bioavailable organic carbon reserve that can potentially be utilised during the dry phase. Flooding, not rainfall, made a substantial contribution to moisture in the soil profile. Furthermore, the growth of aquatic macrophytes during the wet phase produced at least an order of magnitude more organic material than rainfall-induced pulse-reserve responses during the dry phase, and remained as recognizable soil carbon for years following flood recession. These observations have led us to extend existing paradigms to encompass the reciprocal provisioning of carbon between the wet and dry phases on the floodplain, whereby, in addition to carbon fixed during the dry phase being important for driving biogeochemical transformations upon return of the next wet phase, aquatic macrophyte carbon fixed during the wet phase is recognized as an important source of energy for the dry phase. Reciprocal provisioning presents a conceptual framework on which to formulate questions about the resistance and ecosystem resilience of arid and semi-arid floodplains in the face of threats like climate change and alterations to flood regimes.

Keywords Pulse-reserve · Flood pulse concept · Soil carbon · Ecosystem resilience · Rainfall

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Introduction

A spatial subsidy is the transfer of a resource (including prey, detritus and nutrients) from one habitat to another (Polis et al. 1997). The spatial subsidy of material and energy from riparian zones (including floodplains) to their adjacent water bodies is well documented in freshwater ecology (see reviews by Naiman et al. 2005; Ballinger and Lake 2006). For lowland river floodplain ecosystems research, probably one of the most important formulations of cross-subsidisation has been the flood pulse concept (FPC). The FPC extended previous models of riverine functioning, such as the river continuum concept (Vannote et al. 1980),

to describe the interaction between a river channel and its adjacent floodplain (Junk et al. 1989). The cornerstone of the FPC is that the flood pulse facilitates the two-way transfer of materials, including carbon, between a river and its adjacent floodplain during floods, with most carbon moving from the floodplain to the river (Cuffney 1988). Also central to the FPC is that extended periods of floodplain inundation can promote growth of aquatic macrophytes (Junk et al. 1989). Aquatic macrophytes, and especially emergent macrophytes, have long been known to be highly productive in terms of the quantity of biomass produced. Despite this, the carbon fixed by aquatic macrophytes on the floodplain does not appear to be an important resource for aquatic food webs (Bunn and Boon 1993).

Human interventions such as river regulation, water extraction and erection of dams, weirs, locks and flood protection barriers have changed the incidence, timing and, most importantly, the extent and duration of floods on floodplains worldwide (Sparks 1995; Poff et al. 1997; Tockner and Stanford 2002). The impacts of the loss of flows on in-channel processes (Kingsford 2000) and on the health of floodplain trees has received significant attention (Jolly 1996; George et al. 2005; Cunningham et al. 2009; Wen et al. 2009), but the effects on floodplain biogeochemical processes, particularly the formation of soil carbon, has not been studied in detail (Baldwin and Mitchell 2000; Humphries and Baldwin 2003).

Soil carbon can be considered as a slow-moving state variable (sensu Scheffer et al. 2001). Indirectly, soil carbon affects soil physiochemical properties including water retention, aggregation, pH buffering and cation exchange capacity (Stevenson 1994). It has been postulated that a positive feedback between soil carbon, soil moisture, vegetation and soil biota could impart resilience to arid and semi-arid floodplains in the face of river regulation and a drying climate (Colloff and Baldwin 2010).

An alternate stimulus for soil carbon production in arid and semi-arid floodplain ecosystems is rainfall. In arid and semi-arid regions, soil moisture from rainfall generally governs the rates of production and decomposition of soil organic matter. This has led to the formulation of the pulse-reserve model for ecosystem functioning in these ecosystems (Noy-Meir 1973; Reynolds et al. 2004). In this model, first postulated by Westoby and Ridges in the early 1970s (Noy-Meir 1973), rainfall events are triggers for pulses of plant growth and the subsequent formation of reserves of organic carbon (Ogle and Reynolds 2004, Morton et al. 2011). The reserves of carbon (and nutrients) in the soil and litter are then cycled through higher soil trophic levels via the activity of micro-organisms (Collins et al. 2008).

The aim of this study was to determine to what extent floodplain soil carbon production is affected by flooding, compared to rain events, and by inference the effect of

reducing flood frequency and extent on floodplain functioning. We examine the long-term effects of flooding and drying on organic matter dynamics in a semi-arid floodplain using a phenomenological space-for-time experimental design. We also compare the effects of both rainfall and flooding on soil moisture to determine the relative importance of each for soil moisture recharge (and associated potential biological response). We show that growth of aquatic macrophytes during the wet phase produces at least an order of magnitude more organic material than any rain-induced pulse-reserve response. Furthermore, we show that organic matter fixed during the wet phase slowly declines during the dry phase and therefore can potentially serve as an energy source for years after flood recession. These observations have led us to propose a model of lowland river–floodplain functioning that encompasses the reciprocal provisioning of carbon between the dry and wet phases on arid and semi-arid floodplains.

Materials and methods

Study area

The study was conducted in the river red gum (*Eucalyptus camaldulensis* Dehnh.) forest of Yanga National Park (hereafter 'Yanga') on the lower Murrumbidgee River floodplain near Balranald, New South Wales, Australia (34°39′S, 143°35′E). The Murrumbidgee River is heavily regulated, with four major irrigation areas, over 10,000 km of irrigation canals and 24 dams and weirs. The catchment is ca. 84,000 km^2, extending from the alps in New South Wales, where annual rainfall is >1,500 mm, to a semi-arid region in the west that receives an average of 320 mm of rainfall per year (Hutchinson et al. 2005). Overbank flows in the lower Murrumbidgee floodplain prior to river regulation were derived from winter and spring rain and snow melt in the upper catchment and occurred every 2–3 years (Kingsford and Thomas 2004). River regulation and water resource development has doubled the average return interval and halved the duration and volume of flooding flows (Page et al. 2005). Furthermore, the lower Murrumbidgee floodplain area that includes Yanga received well below average rainfall for 10 of the 15 years prior to our study, including the 4 years immediately prior to the start of sampling (Bureau of Meteorology 2010).

Yanga has a system of channels and regulators, constructed prior to the establishment of the National Park, allowing water delivery to different parts of the floodplain. A large overbank flood occurred in 1997 and, since then, the park has received a series of targeted environmental water deliveries through regulators in 2000, 2005, 2008 and 2009, creating a mosaic of flood histories throughout the park. The

extent of flooding for each event was determined by examining aerial photographs, satellite images, available hydrographs and on-ground observation of high-water marks.

Study design

The mosaic of different flood histories allowed us to use a space-for-time substitution approach to assess long-term changes in soil carbon and above-ground biomass as a function of time since last flood. Five different inter-flood periods, ranging from presently flooded to nearly 10 years since last flooding, were achieved by sampling 27 sites from nine locations, at four different regions of the park (Fig. 1; see also Electronic Supplementary Material Table 1). Locations were defined by the date of the most recent flood or watering event. Sites were selected from similar landforms and sampled at multiple times, providing a finer-scale response within the space-for-time design (Table 1). While common in ecological research, the inappropriate use of space-for-time substation has received some criticism (Walker et al. 2010). We validated our space-for-time substitution approach by including sites that were last flooded in 2005 (representing the period approximately 3–4 years after flood) from each of the park locations. We also included two sites last flooded in 2000 (representing the period >8 years post-flood) at two regions. Including multiple sites with the same flood history allowed assessment of variability within the park.

Soil moisture response to rainfall and flooding

To determine changes in soil moisture in response to rainfall, four automatic monitoring stations for soil moisture, temperature and rainfall were installed in three regions in the park (Shaws, Avenue and Levee; Fig. 1). Each station used capacitance probes (EC-5; Decagon Devices, USA) to measure volumetric soil moisture at 5, 15 and 30 cm depth; soil temperature (S-TMB-M0XX; Onset Computer, USA) at 5 cm depth; and rainfall (S-RGB-M002, Onset Computer) on an hourly basis with a HOBO H21-001 weather station (Onset Computer). Soil moisture values at 5 and 15 cm depth were corrected for diurnal temperature fluctuations. The temperature correction factor was determined by multiple linear regression of measured soil moisture and temperature values against a linear interpolation of soil moisture values over a 12-day period with no rain (see Electronic Supplementary Material for more details). Data from the Levee region, which did not receive flooding during the study period, were used to examine the effect of rain on soil moisture. The daily average soil moisture data from all four loggers deployed at this site were averaged prior to analysis. Rain events were defined as periods of rain interrupted by not more than 1 day without precipitation.

Historic climate data for the Yanga area were obtained from the Balranald meteorological station (number 049002, 34°38′23.28″S, 143°33′39.6″E), which is situated approximately 30 km from the centre of the park (Bureau of Meteorology 2010).

Soil properties, above-ground biomass and soil carbon fractions

Physical soil characteristics (gravimetric moisture, bulk density, particle size and water holding capacity), soil pH and soil salinity ($EC_{1:5}$) were measured as described previously (Wilson et al. 2011). At each site, five replicate above-ground biomass and soil samples from within a 10-m radius were collected on a minimum of four occasions between July 2008 and December 2009. Above-ground biomass was harvested from a 0.3 m × 0.3 m quadrat and sorted into six categories: scats (animal faeces), eucalypt leaves, small woody debris (<2 cm diameter; which includes sticks, twigs and woody fruit), aquatic macrophytes (predominantly *Eleocharis* sp.), terrestrial understorey vegetation and unidentifiable material. All above-ground biomass is reported on a dry weight basis.

Soil was collected to a depth of 5 cm from within the same quadrats. Coarse root material >10 mm long was determined by sieving air-dried soil through 10-mm mesh-size sieves and manually sorting the retained material after drying at 50 °C to constant weight. Total soil organic matter ($T\text{-}OM_{<10\ mm}$) was determined from soil that had previously been sieved to remove the coarse root material. Approximately 5 g of soil was ground, passed through a 2-mm mesh-size sieve, then ashed at 550 °C for 2 h. Labile or bioavailable carbon was measured as permanganate-oxidizable carbon [$KMnO_4$-C] (Blair et al. 1995).

Microbial biomass carbon (MB-C) was determined by fumigation extraction (Brookes et al. 1985) and calculated as described by Horwath and Paul (1994). Briefly, approximately 12 g of field moist soil was fumigated with ethanol-free chloroform ($CHCl_3$) at 20 °C for 24 h, extracted with 40 ml 0.5 M K_2SO_4 (1:4 soil solution ratio) for 1 h at 20 °C and the carbon content measured using a 1010 total carbon analyzer (I.O. Analytical, USA).

All statistical tests and curve fitting were performed using Sigmaplot v.11 (Systat Software). Unless otherwise stated. the mean and standard error are calculated for each site on each sampling occasion ($n = 15$). Exponential decay curves for root material and above-ground aquatic plant material were fitted to mean data for each site and sampling occasion (excluding sites inundated at the time of sampling) to estimate the first-order decay constant (k). Estimated decay time ($t_{0.95}$) was defined as the time taken for 95 % of the material to disappear and was calculated by: $t_{0.95} = \ln(0.5)/k$.

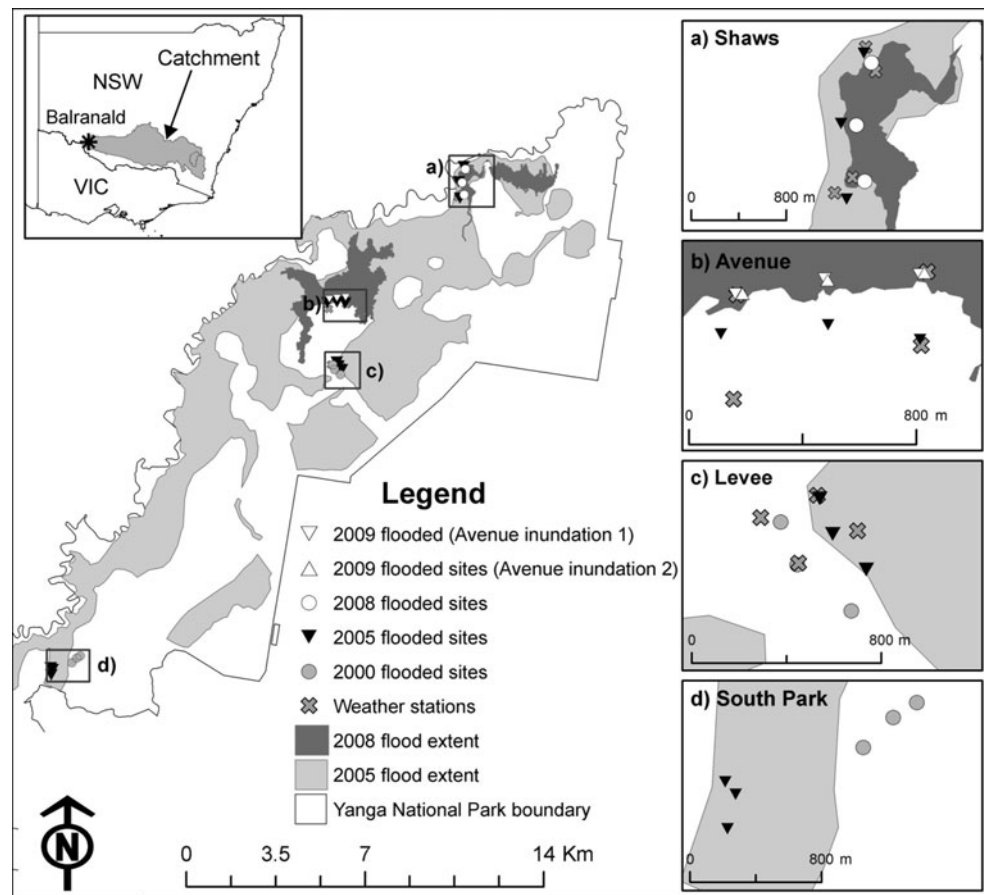**Fig. 1** Locality map showing sampling sites

Table 1 Location of the study sites and the range of periods since last inundation at each site from the space-for time experimental design

Region	Location of sampled sites	Range in the period since last inundation
Shaws	2005 flooded	2 years 7 months–4 years
	2008 flooded	2 months–1 year 7 months
Avenue	2005 flooded	3–4 years
	Avenue inundated 1	0–3 months
	Avenue inundated 2	0–3 months
Levee	2005 flooded	3–4 years
	2000 flooded	8–9 years
South Park	2005 flooded	3–4 years
	2000 flooded	8–9 years

A detailed account of all sampling times and period since last flood is presented in Electronic Supplementary Material Table 1

Results

Soil moisture in response to rainfall and flooding

Daily rainfall on the semi-arid floodplain at Yanga was highly variable, but rarely exceeded 20 mm (Electronic Supplementary Material Fig. 1). To effect a substantial (>0.05 m^3 m^{-3}) increase in soil moisture at a depth of 5 cm, approximately 20 mm of rain was required over the course of a rain event (Fig. 2). Approximately 30–40 mm of rainfall was required before a response was observed at 15 cm soil depth and approximately 45–55 mm of rain was required to increase soil moisture at 30 cm. (There was one instance where a 20-mm rain event increased the soil moisture at 30 cm by about 0.15 m^3 m^{-3} as it followed a 40-mm rain event that had occurred 5 days earlier.) Conversely, flooding resulted in the rapid (within 1–5 h of flooding) saturation (to approximately 0.40 m^3 m^{-3}) of the soil profile (e.g. see Electronic Supplementary Material Fig. 2).

The rate of soil drying following rain events was dependent on soil depth, the amount of water in the soil profile at the end of the rain event and the soil temperature (Electronic Supplementary Material Figs. 3, 4). The rate of soil drying after the flood recession was independent of soil depth (-0.017 ± 0.006, -0.019 ± 0.002 and -0.014 ± 0.004 m^3 m^{-3} day^{-1} for 5, 15 and 30 cm, respectively).

Soil properties

The sand content of soils ranged from 24 ± 1.5 to 53 ± 2.1 % across the study area, consistent with a clay to sandy clay soil texture. The mean bulk density across all
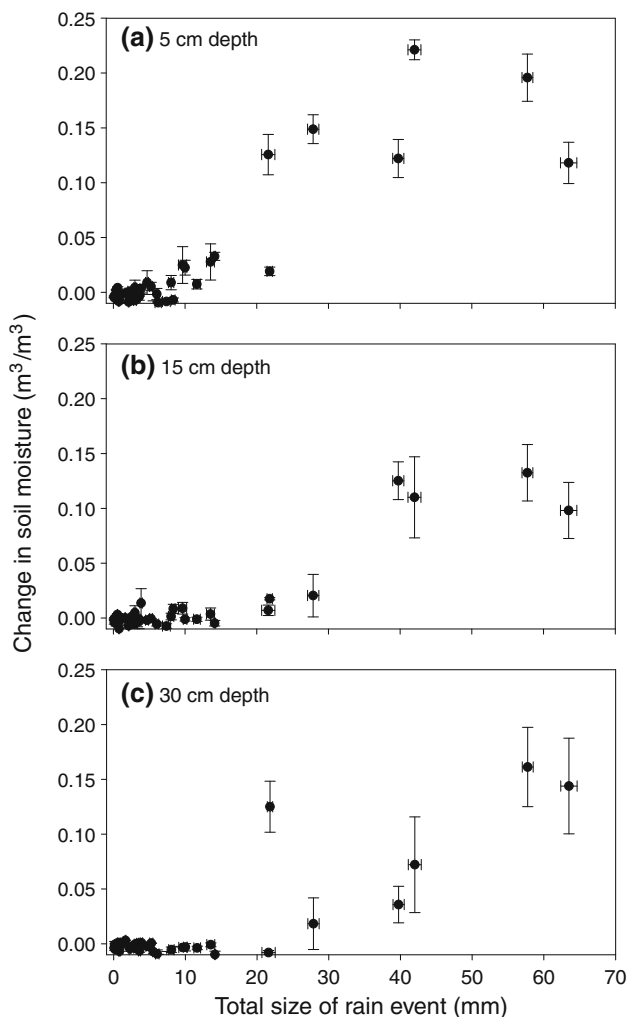
Fig. 2 Average change in soil moisture at the Levee site at different depths: **a** 5 cm, **b** 15 cm and **c** 30 cm, from the day prior to a rain event to the day after the end of the rain event, as a function of the size of the rain event

sites and times was 0.87 ± 0.06 g cm^{-3} ($n = 664$). The Avenue, Levee and South Park regions had very similar sand content while the Shaws region had a lower sand content. However, this did not affect the soil water-holding capacity, which was instead negatively correlated with time since last flood (data not shown). The water-holding capacity ranged from 37 ± 0.8 to 42 ± 2 % and was highest in recently flooded soils. Soil pH values ranged from 4.3 ± 0.5 to 6.5 ± 0.3 and were highest when sites were flooded. Soil salinity was low in flooded sites (EC$_{1:5}$ 0.07 ± 0.002–0.13 ± 0.008 dS m^{-1}) and higher in dry sites (EC$_{1:5}$ 0.09 ± 0.01–0.27 ± 0.03 dS m^{-1}).

Response of soil organic matter since last flood

Coarse root material was 43.8 ± 10.2 g kg^{-1} in the most recently flooded soils and steadily declined over 3 years

post-flooding, remaining at 0.6 ± 0.2 g kg^{-1} during the remaining 6 years (Fig. 3a). Loss of root material from the soil profile could be fitted to an exponential decay model ($r^2 = 0.72$; $k = 0.76$ years^{-1}) which equates to an estimated decay period ($t_{0.95}$) of about 4 years. Most of the root material in recently flooded soils was from aquatic macrophytes, particularly *Eleocharis* sp. (see below).

Total organic matter <10 mm in diameter (T-OM$_{<10\ mm}$) ranged from 60 to 135 g kg^{-1} in soils that had recently been flooded, with 61–85 g kg^{-1} remaining in the soil samples that had not been flooded for between 8 and 9.5 years (Fig. 3b). Total soil carbon (TC$_{<10\ mm}$) was highly correlated with T-OM$_{<10\ mm}$, (Pearson's $r = 0.949$; $P < 0.001$; Electronic Supplementary Material Fig. 5). Soil water holding capacity increased with increasing T-OM$_{<10\ mm}$, but not linearly (Electronic Supplementary Material Fig. 6).

The labile carbon fraction was relatively low in all soils. KMnO$_4$-C concentration was greatest in soils 6 months after flooding (approximately 3 g kg^{-1}), then declined to 1.5 g kg^{-1} by 9 years after flooding (Fig. 4).

Microbial biomass carbon (MB-C) tended to be lower in soils that had not been flooded for 8 years or longer, compared to soils that had only recently been inundated (Fig. 5). However, there is an indication MB-C can increase rapidly in response to rain events as the MB-C was higher in samples that were collected the day after 17 mm of rain had fallen (Fig. 5, open symbols).

Above-ground biomass–response since last flood

Total above-ground biomass showed no trend in response to drying and was highly variable (data not shown). However, trends emerged when individual components were examined. Mean above-ground aquatic macrophyte matter peaked at 122–753 g m^{-2} between 6 months and 2 years after flooding, but by 3 years only 0–26 g m^{-2} was present (Fig. 6a). Loss of above-ground aquatic macrophyte matter could be fitted to an exponential decay model ($r^2 = 0.86$; $k = -1.01$ years^{-1}) which equates to an estimated decay period ($t_{0.95}$) of about 3 years. The biomass of terrestrial understorey vegetation ranged from 0 to 114 g m^{-2}, almost an order of magnitude less than the aquatic macrophyte biomass (Fig. 6b). On two sampling occasions (August and December 2009, indicated in grey in Fig. 6b), terrestrial vegetation was dominated by an exotic mustard (most likely *Sisymbrium* sp.) in sites that had been dry for at least 3 years. Although visually dominant, the plant only accounted for between 6 and 104 g m^{-2} of the above-ground biomass and made little difference to the root biomass (Fig. 3a, with the August and December 2009 sampling marked in grey). The mass of scats (almost entirely from kangaroos) increased rapidly after flooding,
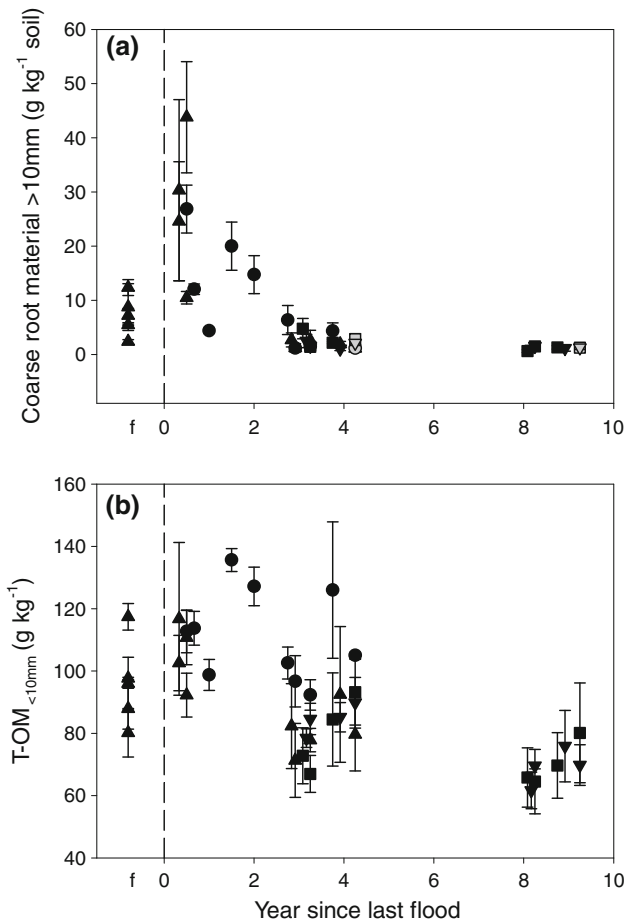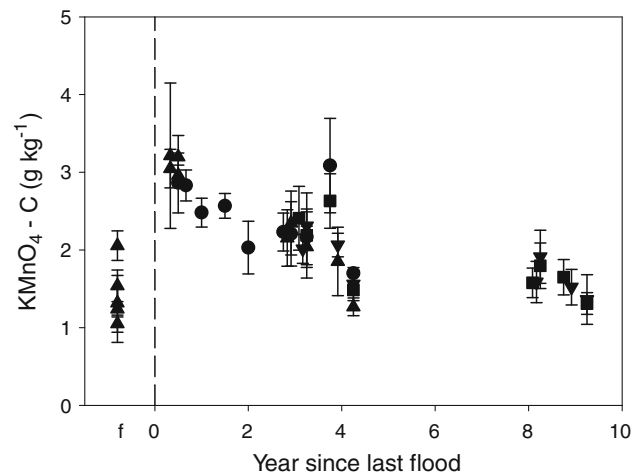
Fig. 4 The amount of readily available carbon measured as KMnO₄-C in a space-for-time substitution with respect to time since last flood across four different regions (*upward pointing triangles* Avenue, *circles* Shaws, *squares* Levee and *downward pointing triangles* South Park); *f* on the *x* axis indicates samples were flooded at the time of sampling

Fig. 3 **a** Coarse root material and **b** T-OM$_{<10 \text{ mm}}$ in a space-for-time substitution with respect to time since last flood across four different regions (*upward pointing triangles* Avenue, *circles* Shaws, *squares* Levee and *downward pointing triangles* South Park); *f* on the *x*-axis indicates samples were flooded at the time of sampling. In (**a**), August and December 2009 samples, following rain events, are marked in *grey*
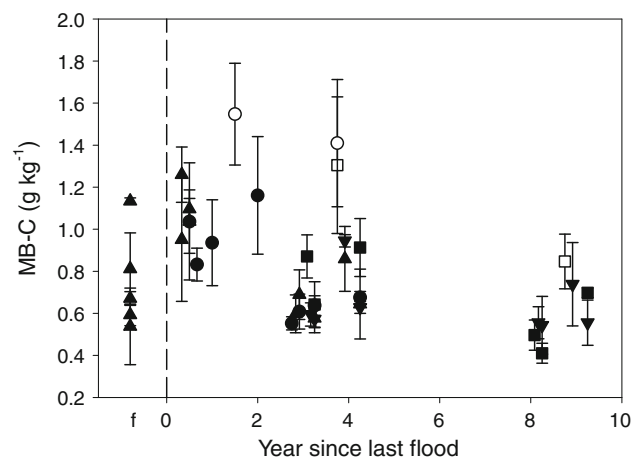

Fig. 5 MB-C in a space-for-time substitution with respect to time since last flooded across four different regions (*upward pointing triangles* Avenue, *circles* Shaws, *squares* Levee and *downward pointing triangles* South Park); *f* on the *x* axis indicates samples were flooded at the time of sampling. *Open symbols* indicate samples taken after a high rainfall event in the 24 h prior to sampling

reaching a maximum of 193 g m^{-2} 1 year after flooding then declining to between 8 and 80 g m^{-2} by 3 years (Fig. 7).

Tree detritus, almost all derived from *E. camaldulensis*, was also present on the floodplain. Overall, small woody debris (244 ± 18 g m^{-2}; *n* = 664) was much more dominant than leaf material (45 ± 3.2 g m^{-2}; *n* = 664), with tree detritus reaching a maximum between 2 and 4 years after flooding (data not shown).

Discussion

Relative importance of rainfall versus flooding for soil carbon reserves

The pulse-reserve model for arid and semi-arid ecosystems describes their dependence on discrete inputs of moisture,

usually provided by irregular rainfall (Morton et al. 2011; Noy-Meir 1973). While vegetation responses can be complex, rainfall is the main limiting factor for plant productivity (Noy-Meir 1973; Reynolds et al. 2004). In addition to rainfall, semi-arid floodplains can receive moisture inputs from flooding. Understanding the relative importance of each as a source of soil moisture is important for a clear understanding of how semi-arid floodplain ecosystems function, particularly those that are likely to be subjected to drier conditions in the future, whether due to climate change or diversions of water resources.
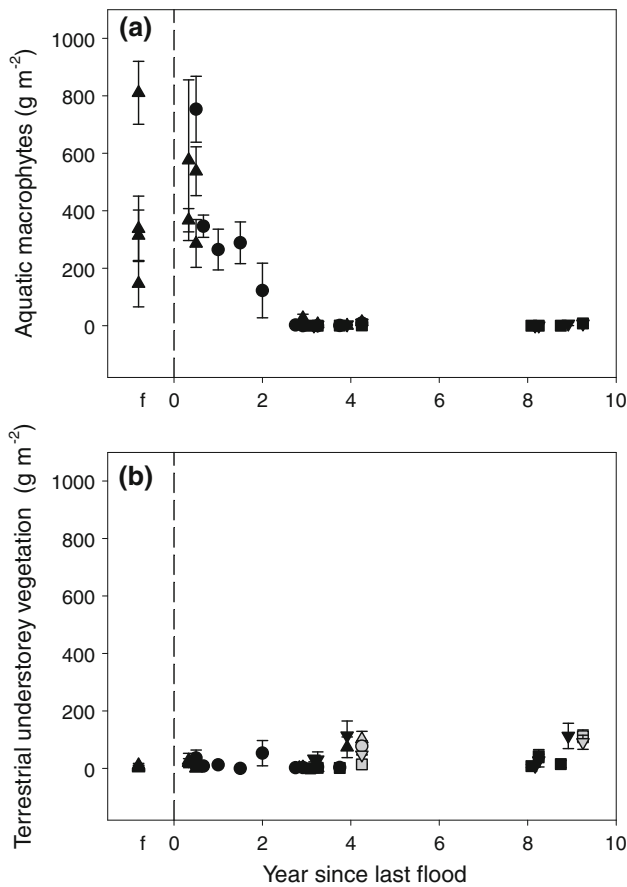
Fig. 6 **a** Aquatic macrophyte material, and **b** terrestrial understorey litter, in a space-for-time substitution with respect to time since last flood across four different regions (*upward pointing triangles* Avenue, *circles* Shaws, *squares* Levee and *downward pointing triangles* South Park); *f* on the *x* axis indicates samples were flooded at the time of sampling. August and December 2009 samples are marked in *grey*
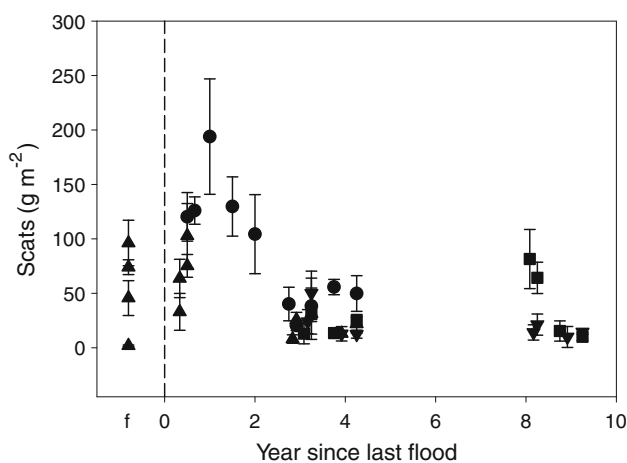

Fig. 7 Distribution of scats in a space-for-time substitution with respect to time since last flood across four different regions (*upward pointing triangles* Avenue, *circles* Shaws, *squares* Levee and *downward pointing triangles* South Park); *f* on the *x* axis indicates samples were flooded at the time of sampling

We showed that the minimum rain event sizes in a given 24-h period required to effect a significant increase in soil moisture at 5, 15 and 30 cm depth were approximately 20, 30–40 and at least 45–55 mm, respectively. Historic climate records from a nearby meteorological station showed that events >30 mm occur on average only about 2.5 times per year and events >40 mm occur less than once per year (Electronic Supplementary Material Fig. 7). This low large-rain-event frequency, combined with rapid drying after the cessation of a rain event, are consistent with the overall observation that rain makes only a minimal contribution to the support of an understorey vegetation community in this environment (see also Electronic Supplementary Material Fig. 8(a)). On two sampling occasions (August and December 2009), there was a visually dominant terrestrial understorey comprised mostly of an exotic mustard. The growth of the mustard followed a wet period in June 2009, suggesting that pulse-reserve responses can occur on this floodplain. However, the amount of biomass produced by the pulse-reserve response was substantially smaller than the amount produced in response to flooding. Sites sampled after flood recession had large stores of above-ground carbon in the form of dead and dying shoots and leaves of aquatic macrophytes, below-ground carbon (as roots and rhizomes) as well as the T-OM$_{<10\text{ mm}}$ pool (see also Electronic Supplementary Material Fig. 8b). There was approximately 3,000 g m^{-2} difference in total organic matter between the sites sampled after flood recession and sites that had been dry for more than 8 years (Fig. 8). About half of this difference can be attributed to the combined loss of above-ground (ca. 430 g m^{-2}) and below-ground (ca. 840 g m^{-2}) aquatic macrophyte tissue. Labile carbon fractions were in low amounts, and the undifferentiated T-OM$_{<10\text{ mm}}$ soil pool (ca. 1,540 g m^{-2}) accounted for much of the remainder of the loss. Given that this pool is substantially higher in sites immediately after flooding, it appears that at least some (if not most) of the carbon in this pool was fixed during the wet phase. Although not measured in this study, flooding may stimulate other types of primary production, for example algal growth on the floodplain, which is likely to be an important contributor to both floodplain soil organic matter and floodplain carbon subsidies to the river (Burford et al. 2008). Deposition of littoral and riparian organic debris in floodplain wetland basins is also characteristic of large flood events (Burns and Ryder 2001), although this may not occur during small floods or managed environmental flow events where lateral and longitudinal connectivity is restricted, and the kinetic energy required to mobilise and transport material from upstream sites is absent.

Although not sampled in our study, the largest pool of recognizable carbon was large woody debris from *E. camaldulensis*, the dominant tree species on the floodplain. Its

wood is highly resistant to decomposition and, with an estimated decay period ($t_{0.95}$) in the order of 375 years (Mackensen et al. 2003), is probably not an important reserve of bioavailable floodplain carbon in the short to medium (years–decades) term. Similarly, small woody debris, while relatively abundant on the flood plain, is also likely to be recalcitrant. Leaves of *E. camaldulensis* are much more readily degradable, with a half-life of 6–12 months (Glazebrook and Robertson 1999), but the standing load of leaf material on the floodplain was low (averaging 45 g m^{-2}; compared with about 130 g m^{-2} reported in Glazebrook and Robertson (1999) and 150 g m^{-2} reported by Francis and Sheldon (2002) from other *E. camaldulensis* floodplains).

In semi-arid floodplains such as Yanga, rainfall is more likely contributing to depletion of soil carbon reserves derived from aquatic macrophytes rather than to deposition of additional organic carbon from new plant growth. Wetting can increase microbial activity and associated carbon mineralisation within minutes to hours, particularly in soil biocrusts (Collins et al. 2008; Lee et al. 2004; Zhang et al. 2010). We demonstrated increases in microbial biomass carbon on sampling occasions that occurred within 24 h of a large rainfall event.

## Reciprocal provisioning model of floodplain ecosystem function

It is well documented that carbon fixed on the floodplain during the dry phase can provision the overlying water column and adjacent river on inundation (Robertson et al. 1999; Valett et al. 2005); indeed, this is a cornerstone of the FPC. The principal source of carbon to the overlying water column is dissolved organic carbon leached from accumulated leaf litter, understorey vegetation and soil on the floodplain (O'Connell et al. 2000; Valett et al. 2005; Howitt et al. 2007; Whitworth et al. 2012), as well as

particulate organic matter mobilised from the floodplain (Robertson et al. 1999). Dissolved organic carbon from the floodplain can make a substantial contribution to heterotrophic activity (e.g. Whitworth et al. 2012), while particulate carbon from floodplain vegetation (such as leaf litter, woody debris, roots, fruits and detritus) is utilised by aquatic consumers including microbial biofilms, macroinvertebrates and fish (Gregory et al. 1991; Hall et al. 2000; Banack et al. 2002; Pusey and Arthington 2003; Baxter et al. 2005). Furthermore, nutrients released from soil microbiota (Birch 1960; Baldwin and Mitchell 2000; Heffernan and Sponseller 2004) or litter (Baldwin 1999) upon inundation have the potential to stimulate algal production.

Therefore, it is inherent to the FPC that material fixed during the dry phase provisions the community that develops during the wet phase. What the FPC does not explicitly take into account is the role that carbon fixed during the period of inundation can play in subsidising the function of the floodplain when it is not inundated (in other words, temporal subsidisation).

While carbon from aquatic macrophytes formed during floodplain inundation is not thought to be an important component of some aquatic food webs (Bunn and Boon 1993), plant residues can be directly incorporated into the microeukaryotic soil community during dry conditions (Murase et al. 2012). Our study suggests that carbon that has been fixed in aquatic macrophyte tissue during the wet phase potentially represents an important source of bioavailable carbon for ecosystem processes during the dry phase. This is demonstrated by its depletion with time since flood recession. Without this carbon source, biotic processes within soils during the dry phase may be substrate-limited. A correlation between the magnitude of this carbon and the water-holding capacity of the soil also suggests that there is potential for a positive feedback for a certain period following flooding.

Fig. 8 Average gain or loss of floodplain organic matter with time since last flood
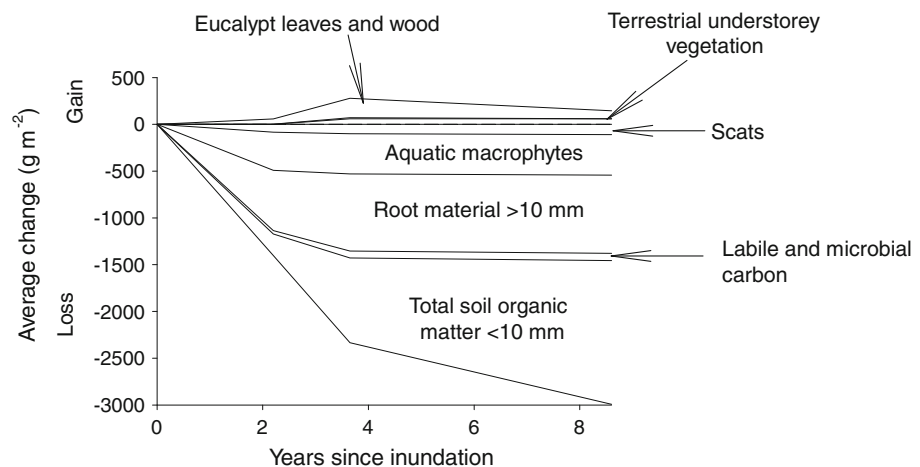
Macrophyte photosynthesis during the wet phase results in carbon fixation, the bulk of which is in the form of stems, leaves and roots. As floods recede and macrophytes senesce, this organic material becomes available for decomposition. During the wet phase, decomposition is relatively low; rate-limited by oxygen or other electron-acceptor availability (the concentration of oxygen in air is about 20 %; in water at 15 °C, it is about 0.0001 % at most). On semi-arid floodplains, the bulk of decomposition occurs during the dry phase in aerated soil and litter and is dependent upon large, sporadic rainfall events and high ambient temperatures. Because both photosynthesis and decomposition during the dry phase are limited by water, the supply of wet-phase macrophyte carbon represents a major subsidy to the pool available during the dry phase.

The reserve of carbon produced during flooding is not only important for soil processes but, as the increase in scats soon after flood recession attests, the flood pulse-reserve can also subsidize (sensu Anderson et al. 2008) other components of the ecosystem. This is consistent with observations made by Iles et al. (2010) that kangaroos at Yanga selectively grazed on wetland plants at recently flooded floodplain sites compared to adjacent non-flooded woodland.

They also showed that wetland plants are a main component of the kangaroos' diet during the post-flood period.

Therefore, as well as the dry phase provisioning the wet phase as outlined in the FPC, we also see a substantial reserve of carbon fixed in the wet phase potentially providing energy for ecosystem functioning during its dry phase—hence a reciprocal provisioning of carbon between the two phases (Fig. 9). In this context, we use the term reciprocal to mean interdependent and/or complementary interactions, influences and exchange (Oxford English Dictionary 2012). The aquatic macrophyte carbon reserve in the soil can potentially support dry phase processes for many years, indicating that the reciprocal provisioning of carbon is likely to be an important process for arid and semi-arid floodplains.

The reciprocal provisioning model of floodplain functioning presents a conceptual framework on which to formulate questions about the resilience and persistence of these ecosystems in the face of river regulation, climate change and extended periods of drought. We have suggested that macrophyte-derived carbon fixed during the wet phase is an important source of carbon for the functioning of the floodplain during its dry phase. In terms of
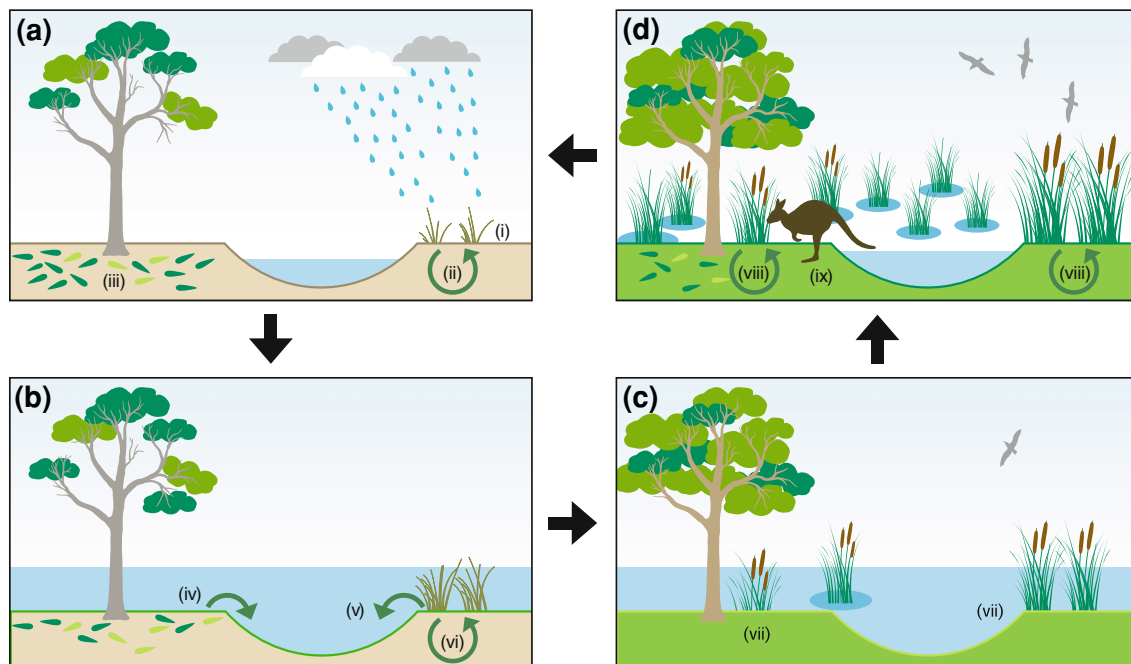

Fig. 9 Schematic representing the reciprocal provision of carbon model of flood plain functioning. **a** After a sustained period without flooding carbon fixation in terrestrial plants (*i*) and carbon processing in the soil (*ii*) is dependent on sporadic rainfall events—the pulse reserve model. Litter from terrestrial plants also accumulates on the floodplain (*iii*). **b** Immediately following inundation carbon and nutrients are leached from leaf litter (*iv*) and submerged terrestrial vegetation (*v*). This carbon is important for the functioning of the river system (the flood pulse concept). Mineralisation rates in the flooded soils are accelerated and readily bioavailable carbon is rapidly consumed (*vi*). **c** After sustained inundation submerged and emergent aquatic vegetation growth occurs (*vii*). The amount of C fixed in the aquatic vegetation following flooding can be substantially greater than that fixed during rain events. **d** On flood recession, the carbon fixed in aquatic macrophytes can sustain ecosystem functions, including (*viii*) soil microbial activity and terrestrial food webs, (*ix*) for years following flood recession

ecosystem resilience, the ecological threshold (sensu Groffman et al. 2006) for irreversible change in carbon dynamics on semi-arid floodplain ecosystems would therefore be represented by a period of drying, after which the floodplain has lost the ability to redevelop its wet phase community structure, particularly with regard to the growth of aquatic macrophytes (Cassanova and Brock 1998; Brock et al. 2003). This capacity will depend on the persistence of seed banks in floodplain soils (Brock 2011) and/or the ability of aquatic macrophytes to recolonise the floodplain following inundation via dispersal of propagules (either seed or viable plant fragments) from elsewhere. Seed bank persistence can depend on the time since last flood, or on the number of successive wetting/drying events without propagule replenishment. Brock (2011) demonstrated that viable seed for more than 70 % of the species originally present in wetland soil cores survived drought conditions for longer than 5 years. Furthermore, germination of almost half of the original species occurred in seven consecutive annual wetting events even though replenishment of the seed bank by development of new seed was deliberately prevented. This indicates that soil seed banks are highly resilient. However, the risk of loss of taxa during long droughts is real. Once the soil seed bank of flood-dependent and amphibious species has been depleted, a single flood event is likely to produce a suppressed response (Nicol et al. 2010). Re-establishment will be heavily dependent on the distribution of propagules elsewhere in the landscape and factors (flow direction and connectivity, wind and biota) facilitating dispersal among wetlands (Green et al. 2008; Questad and Foster 2008).

The relevance of this reciprocal provisioning model to the function of other ecosystems is open to investigation. Generally, the reciprocal provisioning model for floodplain functioning is more likely to be important on those floodplains where flooding persists for several months, allowing the generation of substantial macrophyte biomass, and where the floodplain dries for months or years at a time and terrestrial vegetation growth is limited by soil moisture availability due to low annual rainfall. Regional climate characteristics of the type of floodplain we describe in this paper include relatively high ambient summer temperatures, average rainfall typically <500–600 mm a year or higher, but with pronounced wet and dry seasons, and with an excess of average annual evaporation over precipitation of at least 1.5-fold. Therefore, the reciprocal provisioning model potentially applies to floodplains in steppe, desert, subtropical, savannah and Mediterranean climate zones around the world (e.g. see Electronic Supplementary Fig. 9).

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