

# Do changes in flood pulse duration disturb soil carbon dioxide emissions in semi-arid floodplains?

R. Sánchez-Andrés · S. Sánchez-Carrillo ·  
M. J. Ortiz-Llorente · M. Álvarez-Cobelas ·  
S. Cirujano

Received: 28 October 2009 / Accepted: 14 May 2010 / Published online: 4 June 2010  
© Springer Science+Business Media B.V. 2010

**Abstract** In semi-arid floodplains the average times between floods have been cited to drive metabolic and biogeochemical responses during the subsequent flooding pulse. However, the interaction effects of flood pulse duration and the length of time between floods on the carbon budget are not well understood. Using field experiments, flood pulses—dry cycles were simulated (SF plots—short flood/dry cycles: 15 flood days + 7 dry + 15 flood and LF plots—long flood/dry cycles: 21 flood + 14 dry + 21 flood) in a semi-arid floodplain in Central Spain, in order to study the effects on soil CO<sub>2</sub> emissions. Differences on soil water content among SF, LF and control plots were statistically significant throughout the experiment ( $p < 0.01$ ). Soil CO<sub>2</sub> emission rates during drying time were significantly related with the duration of previous flooding and inter-flooding intervals ( $R^2 = 0.52$ – $0.64$ ,  $p = 0.03$ ). During the first stage of desiccation, the high soil water content appears to limit aerobic metabolism. Soil respiration rates similar to those of control plots measurements occurred 1–2 weeks later. Then, soil respiration increased to a

maximum rate which was delayed 5–8 weeks, as high soil water content limited microbial activity. While more than 7 days of inundation promoted denitrification, organic nutrients supplied by flood water increased 1% soil respiration during drying. Differences between SF and LF plots in soil CO<sub>2</sub> emissions only appeared after floodplain soil had been subjected to two consecutive flood-dry cycles; 70 days after the second inundation ended, CO<sub>2</sub> fluxes achieved similar values in all treatments. Daily soil CO<sub>2</sub> emission rates during the entire study period (117 days) were comparable, independently of the flood duration and the time between floods ( $75.76 \pm 1.59$  and  $77.94 \pm 0.45$  mmol CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup>, in SF and LF, respectively). Flood disturbance affects site-specific microbial processes, but only during very short time periods. The mechanism by which soil microbial communities cope or adapt to new conditions needs to be reassessed in future research in order to determine the long-term effects of hydrological changes in the soil carbon balance of semi-arid floodplains.

**Keywords** Soil CO<sub>2</sub> emission · Flood pulse · Wet–dry cycle · Drought · Semi-arid floodplain

R. Sánchez-Andrés (✉) · S. Cirujano  
Royal Botanic Garden, CSIC, Pza Murillo 2,  
28014 Madrid, Spain  
e-mail: rsanchez@rjb.csic.es

S. Sánchez-Carrillo · M. J. Ortiz-Llorente ·  
M. Álvarez-Cobelas  
Institute of Natural Resources, CSIC, Serrano 115 dpdo,  
28006 Madrid, Spain

## Introduction

Hydrology is recognized as a critical variable limiting biological activity and biogeochemical processes in floodplains (Valett et al. 2005). Pulsed flood events

directly control ground processes through wet–dry soil cycles (Bayley 1995). A flush flood into a dry soil immediately alters the C balance of the system: rapid soil microbial response to incident moisture availability often results in an increase of C and N mineralization (Degens and Sparling 1995), followed by shifts in C:N of microbial available substrate and an offset in the balance between nutrient immobilization and mineralization (Austin et al. 2004).

High respiration rates from biological processes have been observed in semi-arid terrestrial ecosystems, shortly after a wetting (rainfall) pulse resulting in substantial CO<sub>2</sub> release to the atmosphere (Huxman et al. 2004); these CO<sub>2</sub> effluxes often outweigh the subsequent photosynthetic CO<sub>2</sub> accumulation, resulting in a net loss of C from an ecosystem through a rainy period (Emmerich 2003). In semi-arid floodplains, inter-flood intervals (i.e. the average time between floods; Molles et al. 1998) have been cited to drive metabolic and biogeochemical responses during the subsequent flooding pulse (Valett et al. 2005). In floodplains, however, the effects of the interaction between flood pulse duration and the length time between floods on the carbon budget are not well understood.

It is recognized that, in arid and semi-arid climates, ecosystem processes in the floodplain may be limited by soil moisture availability (Ellis et al. 2002). During the inter-flood interval, floodplain soil moisture becomes almost zero, depending on physical soil properties as well as on previous flood size, rainfall episodes and evaporation during the inter-flood periods and time lapsed since the last flood (Huxman et al. 2004; Sponseller 2007). While the size of the precipitation pulse has been demonstrated to control net ecosystem exchange of CO<sub>2</sub> in semi-arid terrestrial regions (Jenerette et al. 2008), changes in the inundation duration and changes in the inter-flood interval in floodplains could promote strong disturbances (i.e. changes on temporal dynamics) in the soil CO<sub>2</sub> net exchanges during drainage. However, these disturbances have not been quantified yet.

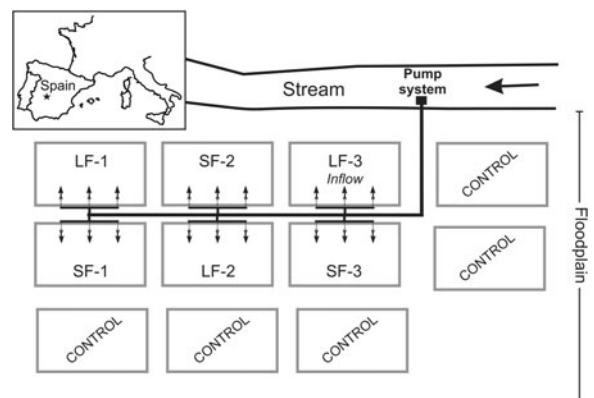
Semi-arid floodplains are important regulating the water quality of rivers, acting as landscape buffers (Castelle et al. 1994; Valett et al. 2005). Flooding plays a significant role on stream biogeochemistry, either as source or sink of carbon, nitrogen and phosphorus, through diverse biogeochemical processes mediated by soil microbial biomass (Benke

et al. 2000; Valett et al. 2005). Flood pulse changes alter subsidies provided by either streams or floodplains, modifying nutrient balances and, hence, ecosystem processes. The impact of these changes on floodplain nutrient inputs—as flood mediated—on floodplain CO<sub>2</sub> fluxes is unknown.

Because climate change predictions for semi-arid regions suggest a rainfall reduction accompanied by an increase in drought frequency (Gao and Giorgi 2008), it is necessary to know how changes in inundation patterns could feedback global warming through either an increase or decrease of greenhouse gas emissions from semi-arid floodplains. The objective of this study is to examine how changes in the flood pulse duration, as well as in the inter-flood interval, disturb soil CO<sub>2</sub> emissions during the subsequent drainage in semi-arid floodplains and to evaluate the importance of flood pulsed-event duration on soil biogeochemical processes.

## Materials and methods

The flooding experiment consisted in triplicate experimental plots (30 m<sup>2</sup>) constructed in a floodplain of a third order stream (Arroyo Grande) located in Central Spain at Santa Olalla (La Higuera Experimental Farm, Toledo province; 40°03'N and 04°25'W; Fig. 1). Since the floodplain is subject to sporadic inundation, it only supports herbaceous vegetation (mostly ruderal species, i.e. the first colonizers of



**Fig. 1** Scheme of the floodplain area where flood pulse experiments were performed, showing distribution of flood plots—*SF* short flood/dry cycles and *LF* long flood/dry cycles—and control plots, as well as the location of pump system and pipes distribution

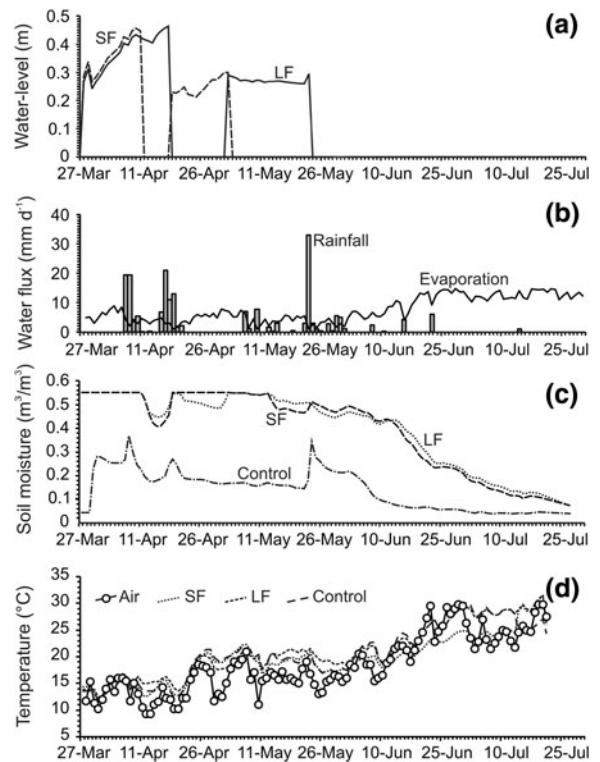
**Table 1** Water quality variables ( $\text{mg l}^{-1}$ ) of the floodwater used during flood pulse experiments

	Floodwater
Suspended solids	$111.26 \pm 68.66$
Total organic carbon	$3.75 \pm 1.25$
Dissolved organic carbon	$3.40 \pm 0.95$
Total nitrogen	$5.95 \pm 2.02$
Total organic nitrogen	$4.00 \pm 0.63$
Dissolved organic nitrogen	$3.54 \pm 0.54$
Dissolved inorganic nitrogen	$1.94 \pm 1.40$
N- $\text{NO}_3^-$	$1.79 \pm 1.21$
N- $\text{NO}_2^-$	$0.02 \pm 0.01$
N- $\text{NH}_4^+$	$0.14 \pm 0.18$
Total phosphorus	$2.44 \pm 0.72$

Values are averages ( $\pm$ SD) of measurements at weekly intervals

disturbed lands: *Galium tricornerutum*, *Scandix pecten-veneris*, *Convolvulus arvensis*). Floodplain soils are eutric fluvisols, which are characterized by the occurrence of stratification as gleyic phenomenon, and whose texture is of a sandy-loamy nature (for a comprehensive summary of soil at this location, see López-Fando and Bello 1987). Floodwater used in the experiment was pumped from the nearby stream, which received wastewater discharges from neighboring towns and pig-farms. Wastewater discharges represent more than 90% of its water flow. Average water quality variables of the stream during the experimental period are summarized in Table 1.

At the beginning of the experiment, the floodplain presented very scarce vegetation (<5% of cover) given that the growing season had not started. Pump-controlled floods were performed from March to July 2008, and included the repetition of two flood cycles, separated by a dry one, during a sampling period of 117 days. Two distinctive flood treatments (short flood/dry cycles—SF and long flood/dry cycles—LF) were applied following these schemes: SF: 15 flood days + 7 dry days + 15 flooding days + 80 dry days; and LF: 21 flood days + 14 dry days + 21 flooding days + 59 dry days (Fig. 2a). These flood pulses were designed to simulate a hydroperiod typical of Mediterranean floodplains receiving floodwater in autumn and spring (Sánchez-Carrillo 2009). Water in flooded plots was lost exclusively by infiltration and evaporation, preventing surface outflows. Five plots of identical size were also used as



**Fig. 2** Time course of the main hydrological variables during the experimental flooding period in SF (short flood/dry cycles), LF (long flood/dry cycles) and control plots. Only daily mean values are shown to improve visualization. **a** Water level trends in SF and LF plots, **b** rainfall and evaporation rates, **c** soil moisture records at SF, LF and control plots, and **d** air temperature compared to soil temperature measurements in flooded and control plots

controls where no flooding was applied during the experiment (Fig. 1).

The pumping system was automatically programmed to operate 8–12 h  $\text{day}^{-1}$  to maintain high water-levels through the lowest water-level fluctuations (depth range 25–45 cm). Water flow measurements were obtained using inflows entering in each experimental plot. During the first day of flood pulses, the experimental plots received water at an average rate of  $0.67 \text{ m}^3 \text{ m}^{-2} \text{ day}^{-1}$ ; during the remainder time the flow rate averaged  $0.25 \text{ m}^3 \text{ m}^{-2} \text{ day}^{-1}$  in the first flood, whilst the rate was reduced to  $0.13 \text{ m}^3 \text{ m}^{-2} \text{ day}^{-1}$ . Soil moisture and soil temperature (0–10 cm of soil depth) were sampled using EC-10 and EC-T probes (Decagon Devices Inc.) at 1 h intervals and 24-h-integrated averages were recorded in data loggers (ECH<sub>2</sub>O, Decagon Devices Inc.). Soil moisture probes were previously gravimetrically

calibrated in the laboratory, using soil samples ( $450 \text{ cm}^3$ ) taken in the experimental area [soil water content,  $\text{SWC} (\%) = -0.63755 + \text{mV} \times 0.0009057$ ;  $R^2 = 0.99$ ,  $\text{SE} = 0.009$ ]. Each probe was installed at the center of the plot. Meteorological data were taken from a weather station located in the Experimental Farm (100 m from the experimental plots).  $\text{CO}_2$  soil fluxes were measured weekly, using a closed soil respiration chamber SRC-1 connected to an EGM-4  $\text{CO}_2$  gas analyzer (PP-systems) after each simulated inundation cycle and biweekly when the flooding ceased, until the end of the experiment. Because this chamber method does not require the use of flux collars,  $\text{CO}_2$  soil fluxes were measured randomly in each sampling plot ( $n = 5$ ) by placing the metal frame of the chamber into the ground (2.5 cm). Measurements were taken at hourly intervals from 11:00 to 13:00 hours. Water samples were taken weekly at the inflow during flooding periods, stored in 2-l, acid-rinsed, high density polyethylene bottles, and held at  $<4^\circ\text{C}$  during the trip to the laboratory, where a portion of each were immediately vacuum filtered (within 2 h; Whatman GF/C  $0.45 \mu\text{m}$  of pore diameter glass-fiber filter) for dissolved carbon and nitrogen measurements and then frozen. Samples were analyzed for total organic carbon (TOC), dissolved organic carbon (DOC), total organic nitrogen (TON) and dissolved organic nitrogen (DON) using a Shimadzu TOC-V combined with TN M-1 unit. Dissolved inorganic nitrogen fractions ( $\text{DIN} = \text{N-NO}_3^- + \text{N-NO}_2^- + \text{N-NH}_4^+$ ) and total phosphorus were measured following APHA (2005). Finally, C and N contents of soil plots (0–20 cm of depth) were measured twice before the inundation and to the end of the experiment by means of a CHNS/O Analyzer series II 2400 (Perkin–Elmer Instruments).

Carbon and nitrogen inputs ( $I$ ; in  $\text{g m}^{-3}$ ) supplied by flood waters into the inundation plots were calculated by the *Eulerian* method ( $I = vc$ ), using the instantaneous values for nutrient concentrations ( $c$  in  $\text{g m}^{-3}$ ) and inflow records ( $v$  in  $\text{m}^3$ ). Input data then were normalized by the plot surface ( $\text{g m}^{-2}$ ). The ratio of flooded to dry days and the flood frequency (total flood days divided by total days of the experiment) were used as relative measurements of both the inter-flood duration and the flood duration during the experiment. Long-term (as referring to the total experiment duration) changes of soil water contents, as well as of  $\text{CO}_2$  respiration rates, were calculated as

the slope of the lineal tendency through weekly changes. Short-term changes of soil moisture were computed through the difference between the values in the last 96 h. Data on  $\text{CO}_2$  fluxes, soil moisture, flood frequencies and flood to dry day ratio were root-squared transformed prior to statistical analyses. A  $t$  test was used to find hourly differences on soil  $\text{CO}_2$  fluxes in treatments. Differences on soil  $\text{CO}_2$  fluxes between experimental flooding treatments were tested using one-way ANOVA with Type III (orthogonal) sums of squares (as unequal number of observations between flooding treatments due to distinctive durations of applied wet–dry cycles). The Tukey HSD test was used for post hoc analyses. Water level, rainfall, evaporation, soil moisture and nutrient input between experimental plots were compared using the non-parametric Friedman ANOVA test. The non-parametric Spearman rank order correlations were used to describe significant relationships between hydrological variables whilst Pearson correlations were applied to  $\text{CO}_2$  fluxes and nutrient data. All data analyses were undertaken using Statistica 7.0 (Statsoft Inc.).

## Results

### Meteorology, inundation and soil moisture during the experiment

Annual rainfall was 355 mm in 2008 at the experimental site. Total rainfall during the experiment period amounted to 194 mm (April–July), 92% occurring in April and May (Fig. 2b). Mean daily air temperature during the experiment averaged  $19.1 \pm 5.6^\circ\text{C}$ , rising from  $13.6^\circ\text{C}$  in April to  $25.2^\circ\text{C}$  in July. Soil temperatures did not show significant differences between flooding treatments and control plots during the field experiment (Friedman test  $p > 0.05$ ), averaging  $20.4 \pm 4.8^\circ\text{C}$  (Fig. 2). Evaporation totaled 944.5 mm (Fig. 2b) during this period. No statistically significant differences in soil moisture were found between SF plots (Friedman test  $p > 0.05$ ), as well as between LF plots ( $p > 0.05$ ); however, both SF and LF plots behaved differently from control plots (Friedman test  $p < 0.01$ ). Differences in soil water contents among SF and LF were statistically significant along the experiment (Friedman test  $p < 0.01$ ). Water level recorded in SF and LF plots did not significantly influence the soil

**Table 2** Spearman rank order correlations ( $r$ ) between mean daily soil water content in flooding treatment plots and the total daily main water fluxes, measured throughout flood-pulse experiments

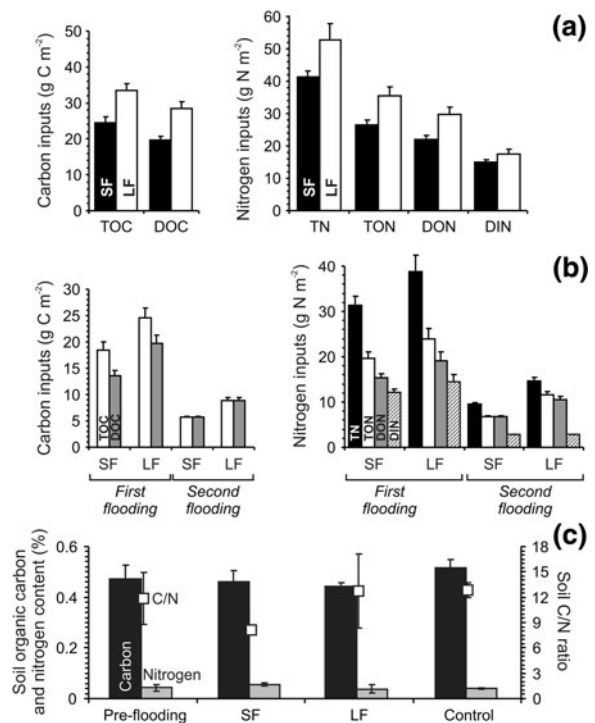
	Soil moisture (%)		
	SF	LF	Control
Water level (cm)	0.60	0.75	0.13 <sup>ns</sup>
Rainfall (mm day <sup>-1</sup> )	0.14 <sup>ns</sup> (0.37)	0.39 (0.48)	0.41
Evaporation (mm day <sup>-1</sup> )	-0.61 (-0.79)	-0.66 (-0.76)	-0.71

Data in parentheses show correlations between soil moisture records in SF and LF plots exclusively during drainage periods. The comparison between water level and soil moisture at control plots was undertaken using water depth values of the nearest flooding plot, regardless of its being on SF or LF treatment. SF is the short flood/dry cycle treatment and LF is the long flood/dry cycle treatment. All correlations are statistically significant at  $p$ -level < 0.05, with the exception of those noted by ns

moisture at the control plots ( $p > 0.05$ , Table 2); on the contrary, soil moisture variations at the flooding plots were dependent on inundation (Table 2). In fact, inundation increased soil moisture by 30–50% in flooding treatment plots (Fig. 2c). Evaporation exerted a strong control on soil water content in both the control and treatment plots (Table 2). Obviously, the shorter the drying period, the lower the loss of soil moisture. During the entire experiment (including flood pulses), the weight of rainfall events on soil moisture variability increased in the control plots, being negligible in the SF plots (Table 2). However, the trend of soil water content during drainage was dependent on rainfall events in both flood treatments (Table 2). Graphically, a strong correlation of peaks appearing in soil water content and rainfall events could be observed, mainly at the end of the latter inundation cycle (Fig. 2). For example, during drying of SF plots, after the second inundation, rainfall events occurred from May 22 to 24, accounting for 39 mm, which increased soil water content from 46 to 52% (Fig. 2).

#### Carbon and nitrogen inputs during flooding and soil transformations

Carbon and nitrogen supplied by flood water were significantly higher in LF treatments (Friedman test  $p < 0.05$ ; Fig. 3a). Total organic nitrogen supplied by flooding was close to or slightly above total organic



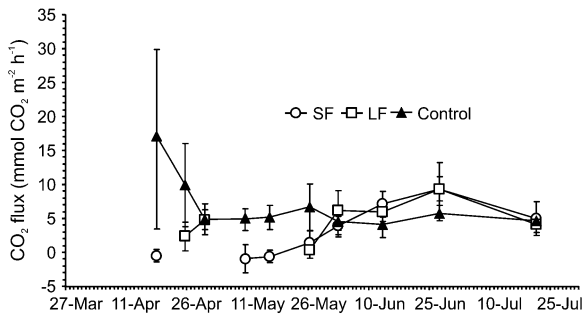
**Fig. 3** **a** Carbon and nitrogen supplied by floodwater at SF and LF plots during the entire experimental period (*TOC* total organic carbon, *DOC* dissolved organic carbon, *TON* total organic nitrogen, *DON* dissolved organic nitrogen, *DIN* dissolved inorganic nitrogen), **b** differences on carbon and nitrogen inputs in SF and LF plots provided by each experimental floods, and **c** changes on mean soil carbon and nitrogen contents and soil C:N ratio caused by experimental inundations. SF is the short flood/dry cycle and LF the long flood/dry cycle experiments

carbon (Fig. 3a). Organic nitrogen made up more than 65% of total nitrogen inputs. Dissolved organic fractions of C and N were dominant in both flooding treatments (Fig. 3a). Significantly, the first inundation supplied more C and N than the second one (Friedman test  $p < 0.05$ ; Fig. 3b). After inundations, C soil contents did not significantly change in flooding plots ( $p < 0.05$ ), whilst N content at SF plots increased significantly ( $p < 0.05$ ; Fig. 3c). The C:N ratio decreased significantly in SF (from 11.8 to 8.1;  $p < 0.05$ ), while slightly increasing in LF and control plots (from 11.8 to 12.7 in LF and 12.9 in control; Fig. 3c).

#### Inundation effects on soil CO<sub>2</sub> fluxes

In both flood treatments, hourly differences of measured soil CO<sub>2</sub> fluxes were not statistically





**Fig. 4** Averages of soil  $\text{CO}_2$  fluxes measured during the drainage periods in flood plots (SF short flood/dry cycles and LF long flood/dry cycles) compared to control plot records. Vertical bars represent standard deviations

significant ( $t$  test  $p > 0.05$ ). Significant hourly differences of soil  $\text{CO}_2$  fluxes were recorded in control plots at the beginning of the experiment (April 18,  $t$  test  $p < 0.05$ ; Fig. 4) as related to rainfall occurred during sampling time (Fig. 2). However, this variability did not display any hourly trend. Early measurements of  $\text{CO}_2$  fluxes on control plots showed the highest values, decreasing from April 30, when the rate was stabilized, until the end of the experiment (average  $4.99 \pm 0.91 \text{ mmol CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ ; Fig. 4). These highest  $\text{CO}_2$  fluxes matched rainfall events occurring within 48–72 h before measurements were taken (16–18 April 38.7 mm; 23–26 April 37.3 mm), when soil moisture peaked at the control plot (Fig. 2); however, they could not be statistically confirmed because of the lack of enough rainfall pulses (Spearman correlation  $p > 0.1$ ).  $\text{CO}_2$  flux in the control plots was not related to soil temperature trends ( $p > 0.05$ ).

After flooding ended and when soil started to dry,  $\text{CO}_2$  fluxes were lowest in both SF and LF treatments as compared to control plots (91–97 and 76–94%

lower than control, in SF and LF respectively; Fig. 4). Soil respiration increased during the following weeks after drying, achieving rates as high as those measured in control plots (Fig. 4). Recovery up to comparable control flux measurements was faster in LF plots (1 week) than in SF (2 weeks). After this time, soil  $\text{CO}_2$  fluxes in flooding treatments reached higher values than control plots, with maxima occurring 54 (SF) and 34 (LF) days after flooding ceased (140–170% of the measured  $\text{CO}_2$  flux in control plots; Fig. 4); 70 days after the second inundation concluded,  $\text{CO}_2$  fluxes achieved similar values ( $4.77 \pm 2.27$ ,  $4.09 \pm 1.36$  and  $4.54 \pm 0.91 \text{ mmol CO}_2 \text{ m}^{-2} \text{ h}^{-1}$  in SF, LF and control plots, respectively; Fig. 4).

Flooding treatments significantly explained the variance of soil  $\text{CO}_2$  fluxes up to 45 days after inundation (Table 3). All treatments showed significant differences from control plots in soil respiration rates until 45 days after the second inundation, while differences between flooding treatments were only confirmed after the first inundation (Tukey test  $p < 0.05$ ). Soil respiration in SF and LF plots was statistically different during 30 days after the second inundation (Tukey test  $p < 0.05$ ). Seventy days after the second inundation, the effects of flooding on soil respiration were negligible (Table 3).

During the experimental period (117 days), considering both flooded and dry periods, the mean daily rate of soil  $\text{CO}_2$  emissions were very close in SF and LF plots ( $75.76 \pm 1.59$  and  $77.94 \pm 0.45 \text{ mmol CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ , respectively), being half of those recorded in control plots ( $177.91 \pm 2.04 \text{ mmol CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ ). Therefore, for the entire period (117 days), the difference of total rate of soil  $\text{CO}_2$  flux between flood treatments accounted for 0.25 mol  $\text{CO}_2 \text{ m}^{-2}$  (8.86 and 9.13 mol  $\text{CO}_2 \text{ m}^{-2}$  in SF and LF,

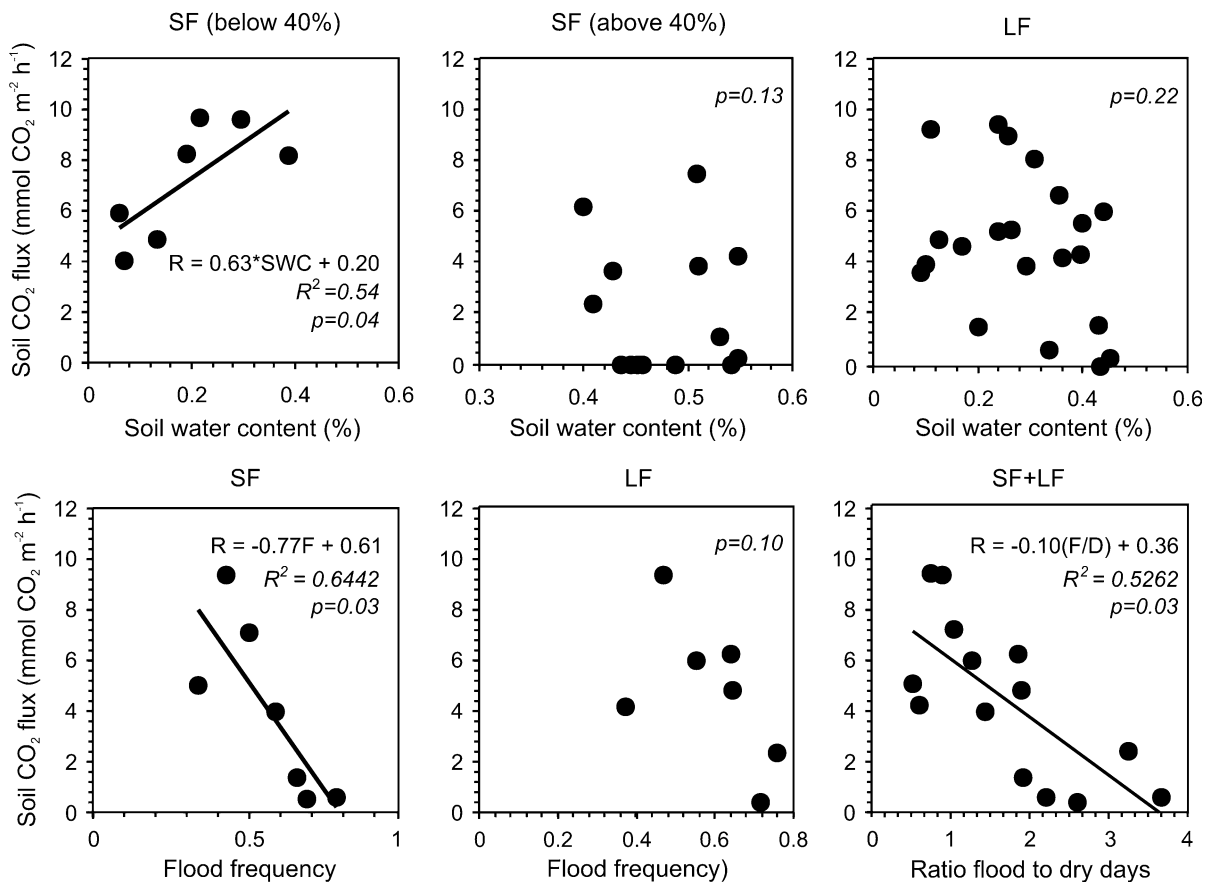
**Table 3** One way ANOVA (Type III sums of squares) showing overall effects of inundation and inter-flood intervals on  $\text{CO}_2$  fluxes at the floodplain

	$R^2$	Mean squares	MS residuals	$F$ ratio	$p$ -Value
After First flood	0.33	4.90	0.66	7.38	0.003
After Second flood + 10 days	0.73	0.23	0.01	35.32	0.00001
After Second flood + 20 days	0.46	0.11	0.01	12.25	0.0002
After Second flood + 30 days	0.27	0.02	0	5.82	0.009
After Second flood + 45 days	0.37	0.05	0.01	8.66	0.001
After Second flood + 70 days	0.003	0.002	0.002	1.03	0.371

respectively). Total  $\text{CO}_2$  flux in control plots ( $20.82 \text{ mol CO}_2 \text{ m}^{-2}$ ) demonstrated that inundation substantially reduced  $\text{CO}_2$  emissions by floodplain soils. However, comparing only dry periods after the second flood pulse, averages of  $\text{CO}_2$  respiration rates were very similar in both flood treatments and controls ( $128.38 \pm 70.66$ ,  $124.52 \pm 75.21$  and  $122.02 \pm 20.0 \text{ mmol CO}_2 \text{ m}^{-2} \text{ day}^{-1}$  in SF, LF and control, respectively).

Finally, in flooding plots, instantaneous soil moisture records during drying were not correlated to soil  $\text{CO}_2$  flux measurements ( $p > 0.05$ ).  $\text{CO}_2$  fluxes in SF plots showed a significant relationship when soil water content was below 40% ( $R^2 = 0.60$ ,  $p = 0.04$ ; Fig. 5). However, above this soil moisture value, this relationship was not significant ( $p > 0.1$ ; Fig. 5).  $\text{CO}_2$  emissions at LF plots did not show any significant relationship with soil water content

( $p > 0.1$ ; Fig. 5). Total changes in soil water content (slope of weekly changes) during drying did not significantly correlate with soil  $\text{CO}_2$  emissions, nor with changes in  $\text{CO}_2$  respiration rates (slope of weekly observations;  $p > 0.1$ ). Very short-term reductions of soil water content (changes in the last 96 h onwards) during drainage appeared not to have any significant influence on soil microbial activity (i.e. respiration  $p > 0.05$ ), not considering both short-changes and the present soil water content conditions together (SWC present—SWC previously/SWC present;  $p > 0.05$ ). On the contrary, soil  $\text{CO}_2$  fluxes in SF plots showed a statistically significant positive relationship with increases of soil moisture recorded 72 h before taking respiration measurements ( $R^2 = 0.77$ ,  $p = 0.001$ ), which matched rainfall events recorded during drying. The mean daily rate of soil  $\text{CO}_2$  emissions ( $\text{g CO}_2 \text{ day}^{-1}$ ) in flooded plots during the



**Fig. 5** Relationships between soil moisture, flood frequency (ratio of total to flooded days) and the ratio of flood to dry days with soil  $\text{CO}_2$  fluxes measured in SF (short flood/dry cycles) and LF (long flood/dry cycles) plots

entire experimental period depended on organic inputs ( $\text{g m}^{-2}$ ) during the inundation [ $R^2$  values  $\text{TOC} = 0.61$ ,  $\text{DOC} = 0.60$ ,  $\text{TON} = 0.60$  and  $\text{DON} = 0.59$ , at  $p < 0.04$ ;  $\text{CO}_2$  flux =  $0.01 \cdot (\text{TOC or DOC}) + 3.10$  and  $\text{CO}_2$  flux =  $0.01 \cdot (\text{TON or DON}) + 3.04$ ]. Flood frequency accounted for 64% of  $\text{CO}_2$  flux variability in the SF plots ( $p = 0.03$ ), whilst it was not significant at LF plots ( $p > 0.05$ ; Fig. 5). Using the entire soil  $\text{CO}_2$  flux database, joining both SF and LF treatment plots, the flood to dry ratio showed a significant relationship with soil respiration rates ( $r^2 = 0.52$ ,  $p = 0.03$ ; Fig. 5).

## Discussion

Ellis et al. (2002) and Valett et al. (2005) have demonstrated the importance of inter-flood intervals in biogeochemical responses occurring during the subsequent flooding pulse in floodplains. Our results demonstrate that interactions linking inter-flood intervals and flood episodes exert a strong control on carbon-related soil processes during drying cycles.

The aim of this study was to know whether the dynamic response of floodplain soil respiration operates differently during the drying period after an inundation as compared to normal conditions (i.e. only subject to rainfall/evaporation). Thus, we will first discuss control plot responses, in order to set the framework for further comparisons. In contrast to the continuous response of soil respiration to temperature, a growing number of studies have suggested that  $\text{CO}_2$  emission has a pulsed response to precipitation events, depending on rainfall size (Huxman et al. 2004; Jarvis et al. 2007). Although the lack of replicates (i.e. not enough rainfall events) of our data in control plots did not demonstrate this statistical relationship, observed  $\text{CO}_2$  peaks (Fig. 4) suggest that heterotrophic respiration was fueled when rain pulses were greater than 30 mm during the last 48–72 h. In fact, the positive relationship found in SF plots between increasing soil moisture and soil respiration during drying (Fig. 5) confirmed this statement. Despite the fact that soil heterotrophic metabolism under pulsed rainfall events was out of the scope of this study, our soil  $\text{CO}_2$  records during drying could support the hypothesis of a pulse trajectory response: an initial maximum increase in metabolism was followed by a rapid return to

pre-event conditions, likely related to substrate limitation rather than to soil drying (Jenerette et al. 2008). This initial burst of  $\text{CO}_2$  flux was caused by a mixture of biogeochemical mechanisms, including the instantaneous physical displacement of  $\text{CO}_2$ -rich soil air (Knorr et al. 2008) and, mostly, to microbial respiration (Huxman et al. 2004).

Few attempts have been made to characterize the effect of water table fluctuations on soil carbon emissions during subsequent dryness. Most studies have investigated the effect of hydrological fluctuations by means of soil core experiments (e.g. Kettunen et al. 1999; Blodau and Moore 2003; Knorr et al. 2008) but few have characterized in situ responses of carbon flux rates to flooding disturbance. Since flooding saturates soil pores, the effect of soil moisture in soil  $\text{CO}_2$  emissions is quite different to that observed in terrestrial dry systems. During drying after the flood pulse, the  $\text{CO}_2$  emission trajectory inversely responds to that observed in terrestrial systems: an initial lower (almost zero) soil respiration metabolism followed by a burst of  $\text{CO}_2$  flux, returning to “normal” conditions 45 days after flooding ends (Fig. 4). This complex pattern has also been observed in wetland peat soils after flooding (Blodau and Moore 2003) and after rewetting of unsaturated soils (Borken et al. 1999). These authors observed how flood/rewetting resulted in rapid depletion of  $\text{O}_2$  and complex patterns of soil  $\text{CO}_2$  fluxes during subsequent drying. Our results have demonstrated that the pattern of soil  $\text{CO}_2$  emission rates during drying can be understood by knowing previous flooding characteristics. Flood frequency (or the ratio of flooded to dry days) affects the pathway of aerobic respiration throughout drying cycles as microbial activity adapts to new soil conditions.

Soil microbial communities shallowly located (2 mm) have been reported to be highly responsive to small wetting events (Austin et al. 2004). A rapid change in soil water potential associated with flooding may cause aerobic microbial populations to undergo osmotic shock, including microbial cell lysis (Bottner 1985; Van Gestel et al. 1993). It could explain how the high soil water content appears to limit aerobic metabolism during the early stages of the drying cycle (Potts et al. 2006). A few weeks (1–2) after flooding ceases, soil moisture declines and microbial activity is triggered, raising soil  $\text{CO}_2$  emissions. It is unclear so far whether this strong



increase in soil CO<sub>2</sub> emission was caused by an increase in either root or heterotrophic respiration. A feature of our experiments (bare soil) explains why these enhanced CO<sub>2</sub> fluxes are related to the heterotrophic respiration, as pointed out by Borken et al. (1999). At this point, the heterotrophic microbial activity responds to enhanced oxygen diffusion in the uppermost soil layers, and also the accumulated labile soil organic matter and previously dead microbial biomass, with their low C:N ratios, become available for microbial populations (Austin et al. 2004), increasing soil respiration rates.

The delayed time of maximum CO<sub>2</sub> release rate from soil appears as a common pattern in soil rewetting experiments. In a rewetting field experiment, Borken et al. (1999) cited a time lag of 2–3 weeks, which was explained by the slower rewetting applied. Our longer time lags of CO<sub>2</sub> peaks (5–8 weeks) could be explained by the adaptation of aerobic microbial processes to the strong environmental shift (i.e. aerobic microbial populations were either quiescent or died during water saturation stage and, hence, biomass slowly recovered when soil was drying). Since additions of dissolved organic matter have been observed to cause rapid and large increases in soil CO<sub>2</sub> flux (Cleveland and Nemergut 2007), supply of dissolved organic carbon by floodwaters might have stimulated soil respiration instead of inhibiting it. The delay of CO<sub>2</sub> flux peak can then be related only to the excess of soil water content, where anaerobic conditions prevailed in the soil column for a long time. In fact, the relationship between soil moisture below 40% and soil emission CO<sub>2</sub> rates (Fig. 5) could be showing the limit of water content for the dominance of aerobic microbial processes. Soil CO<sub>2</sub> production decline during drying after a flooding episode also appears as a common pattern of drying soils (Matthews et al. 2005).

The absence of significant changes in soil C contents after inundations seems reasonable, as soil C and N contents are very large compared to soil respiration over short period of times. It may also be related to the magnitude of organic carbon supplied by floodwater, which would increase soil organic carbon reserves by less than 1% (considering a soil thickness of 20 cm, 1,880 g of stored organic carbon). Observed changes of soil nitrogen content, as well as C:N ratio in SF treatment plots (Fig. 3), should respond to a lower denitrification rate due to reduced flood

duration compared to LF plots, caused by longer water renewal time. Denitrification rate, which is the primary mechanism of nitrogen removal in aquatic ecosystems, increases with water residence time (Saunders and Kalff 2001). Likewise, in soil systems a poor drainage tends to increase denitrification rates (Hofstra and Bouwman 2005). Therefore, more than 7 days of flooding appears to significantly enhance denitrification process at these floodplain soils.

Slopes of linear functions indicate that, when a flooding occurs, heterotrophic microbial activity in the floodplain would only be increased by 1% (0.01 g by 1 g of organic carbon or nitrogen inputs). Nevertheless, our experiment was performed using nutrient-rich flood water and, therefore, the effects of low nutrient discharges on CO<sub>2</sub> fluxes need to be explored in the future, in order to ascertain whether microbial processes during drying follow the same patterns.

Our results demonstrate that the effects of flood duration and inter-flood interval on soil CO<sub>2</sub> emissions only occur when floodplain soil has been subject to two consecutive flood-dry cycles. Heterotrophic soil respiration rates in the floodplain depended on the applied flood-dry pulse in a short-time (throughout 30 days after the second flooding, Table 3), then the effects disappeared. However, computed mean daily soil CO<sub>2</sub> emission rates were comparable during the entire flood experiment (117 days), independently of the flood duration and the time between floods. This similarity of mean CO<sub>2</sub> flux rates for long periods of time has been cited from various wetland habitats in spite of pronounced differences of flooding regimes (Pulliam 1993). This could suggest that total amount of CO<sub>2</sub> emitted by semi-arid floodplains to annual scales will remain unchanged although the flooding frequency did. However, the limited temporal scope of our experiment (two floods) does not allow us verify that assumption. Relative to very short periods of time, our results highlight the weight of site-specific microbial processes as dependent on environmental changes. Probably, as suggested by Cleveland and Nemergut (2007), the importance of soil microbial community composition on soil respiration during the new conditions provided by wet–dry cycles should be reassessed.

Finally, if changes in the inundation patterns do not promote changes on the total amount of CO<sub>2</sub> emitted by semi-arid floodplain soils, their carbon

budget could only be changed by variations in methane emissions. Methane emissions have been shown to be significantly lower in wetlands subject to flood pulses, as compared to those occurring under steady flow hydrology (Altor and Mitsch 2008). Nevertheless, since Mediterranean regions are among the ones to suffer most hydrological alterations due to climate changes (Gao and Giorgi 2008), further research on semi-arid floodplains is necessary to test how methane emissions might respond to flood pulse changes, in order to assess feedback effects on soil and atmospheric carbon budgets.

## Conclusions

Soil CO<sub>2</sub> emission pattern during drying in semi-arid floodplains has been analyzed through the duration of previous flooding and inter-flooding intervals. The soil CO<sub>2</sub> emission curve after flooding responds inversely during desiccation to that observed in drying after rain pulse episodes. During the first stages, the limited transport of oxygen under water saturated conditions constrains the aerobic metabolism. Thereafter, soil respiration increases to a maximum rate, which is delayed as heterotrophic microbial activity manages to adapt to new conditions. CO<sub>2</sub> emissions return to “normal” (control) conditions only 45 days after flooding ceased.

Whilst longer inundation (more than 7 days) promotes denitrification during the stagnant water period, organic nutrients supplied by flood water only increase soil respiration by 1% during drying. The effects of flood duration and inter-flood interval on soil CO<sub>2</sub> emissions occur only when floodplain soil has been subject to two consecutive flood-dry cycles. Heterotrophic respiration then depicts different emission rates over the next 30 days, depending on the value of the flood-dry pulse. For the entire flood experiment (4 months), however, mean daily soil CO<sub>2</sub> emission rates were independent of the flood duration and the time between floods. Site-specific microbial processes are altered with environmental changes only in very short-time periods. It is not entirely clear if soil microbial communities are either sufficiently robust to cope with flood events or adapt fast enough to compensate the flood disturbance. More emphasis should be given to changes on soil microbial community composition during flood events, as well as to

the time scale at which microbial processes adapt to new conditions, in order to determine the long-term effects of hydrological changes in the soil carbon balance of semi-arid floodplains.

**Acknowledgements** This research was granted by a PIE-CSIC project “Flood pulse effects on the carbon biogeochemistry of Mediterranean wetlands”. RSA was supported by a JAE-Doc contract at RJB-CSIC. The authors are very grateful to the Finca La Higuera Staff: Carlos Lacasta, José María Gómez, Gregorio Gómez and José R. Vadillo. Our thanks as well to M. Benítez and José L. Ayala for soil laboratory assistance. Finally, the authors thank two anonymous reviewers for their helpful suggestions to a previous version of the manuscript.

## References

- Altor AE, Mitsch WJ (2008) Pulsing hydrology, methane emissions and carbon dioxide fluxes in created marshes: a 2-year ecosystem study. *Wetlands* 28:423–438
- APHA (2005) Standard methods for the examination of water and wastewater, 21st edn. American Public Health Association (APHA), American Water Works Association (AWWA) & Water Environment Federation (WEF), Washington, DC
- Austin AT, Yahdjian L, Stark JM, Belnap J, Porporato A, Norton U, Ravetta DA, Schaeffer SM (2004) Water pulses and biogeochemical cycles in arid and semi-arid ecosystems. *Oecologia* 141:221–235
- Bayley PB (1995) Understanding large river—floodplain ecosystems. *Bioscience* 45:153–158
- Benke AC, Chaubey I, Ward GM, Dunn EL (2000) Flood pulse dynamics of an unregulated river floodplain in the Southeastern US coastal plain. *Ecology* 81:2730–2741
- Blodau C, Moore TR (2003) Micro-scale CO<sub>2</sub> and CH<sub>4</sub> dynamics in a peat soil during a water fluctuation and sulfate pulse. *Soil Biol Biochem* 35:535–547
- Borken W, Xu YJ, Brumme R, Lamersdorf N (1999) A climate change scenario for carbon dioxide and dissolved organic carbon fluxes from a temperate forest soil drought and rewetting effects. *Soil Sci Soc Am J* 63:1848–1855
- Bottner P (1985) Response of microbial biomass to alternate moist and dry conditions in a soil incubated with <sup>14</sup>C- and <sup>15</sup>N-labelled plant material. *Soil Biol Biochem* 17:329–337
- Castelle AJ, Johnson AW, Conolly C (1994) Wetlands and stream buffer size requirements—a review. *J Environ Qual* 23:878–882
- Cleveland CC, Nemergut DR (2007) Increases in soil respiration following labile carbon additions linked to rapid shifts in soil microbial community composition. *Biogeochemistry* 82:229–240
- Degens BP, Sparling GP (1995) Repeated wet–dry cycles do not accelerate the mineralization of organic C involved in the macro-aggregation of a sandy loam soil. *Plant Soil* 175:197–203

- Ellis LM, Crawford CS, Molles MC (2002) The role of the flood pulse in ecosystem-level processes in southwestern riparian forests: a case study from the Middle Rio Grande. In: Middleton BA (ed) *Flood pulsing in wetlands: restoring the natural hydrologic balance*. John Wiley and Sons, Hoboken, New Jersey, pp 51–108
- Emmerich WE (2003) Carbon dioxide fluxes in a semi-arid environment with high carbonate soils. *Agric For Meteorol* 116:91–102
- Gao X, Giorgi F (2008) Increased aridity in the Mediterranean region under greenhouse gas forcing estimated from high resolution simulations with a regional climate model. *Glob Planet Change* 62:195–209
- Hofstra N, Bouwman AF (2005) Denitrification in agricultural soils: summarizing published data and estimating annual rates. *Nutr Cycl Agroecosys* 75:267–278
- Huxman TE, Snyder KA, Tissue D, Leffler AJ, Ogle K, Pockman WT, Sandquist DR, Potts DL, Schwinning S (2004) Precipitation pulses and carbon fluxes in semi-arid and arid ecosystems. *Oecologia* 141:254–268
- Jarvis P, Rey A, Petsikos C, Wingate L, Rayment M, Pereira J, Banza J, David J, Miglietta F, Borghetti M, Manca G, Valentini R (2007) Drying and wetting of Mediterranean soils stimulates decomposition and carbon dioxide emission: the ‘Birch effect’. *Tree Physiol* 27:929–940
- Jenerette GD, Scott RL, Huxman TE (2008) Whole ecosystem metabolic pulses following precipitation events. *Funct Ecol* 22:924–930
- Kettunen A, Kaitala V, Lehtinen A, Lohila A, Alm J, Silvola J, Martikainen PJ (1999) Methane production and oxidation potentials in relations to water table fluctuations in two Boreal mires. *Soil Biol Biochem* 31:1741–1749
- Knorr K-H, Oosterwoud MR, Blodau C (2008) Experimental drought alters rates of soil respiration and methanogenesis but not carbon exchange in soil of a temperate fen. *Soil Biol Biochem* 40:1781–1791
- López-Fando C, Bello A (1987) Description of La Higuera experimental farm (in Spanish). CSIC, Madrid
- Matthews CJD, Joyce EM, St. Louis VL, Schiff SL, Venkiteswaran JJ, Hall BD, Bodaly RA, Beaty KG (2005) Carbon dioxide and methane production in small reservoirs flooding upland boreal forest. *Ecosystems* 8: 267–285
- Molles MC, Crawford CS, Ellis LM, Valett HM, Dahm CN (1998) Managed flooding for riparian ecosystem restoration. *Bioscience* 48:749–756
- Potts DL, Huxman TE, Cable JM, English NB, Ignace DD, Eilts JA, Mason MJ, Weltzin JF, Williams DG (2006) Antecedent moisture and seasonal precipitation influence the response of canopy-scale carbon and water exchange to rainfall pulses in a semi-arid grassland. *New Phytol* 170:849–860
- Pulliam W (1993) Carbon dioxide and methane exports from a Southeastern floodplains swamp. *Ecol Monogr* 63:29–53
- Sánchez-Carrillo S (2009) Hydrology and biogeochemistry of Mediterranean temporary ponds. In: Fraga P (ed) *International conference on Mediterranean temporary ponds*. Consell Insular de Menorca, Mahón, pp 71–82
- Saunders DI, Kalff J (2001) Nitrogen retention in wetlands, lakes and rivers. *Hydrobiologia* 443:205–212
- Sponseller R (2007) Precipitation pulses and soil CO<sub>2</sub> flux in a Sonoran Desert ecosystem. *Glob Change Biol* 13:426–436
- Valett HM, Baker MA, Morrice JA, Crawford CS, Molles MC, Dahm CN, Moyer DL, Thibault JR, Ellis LM (2005) Biogeochemical and metabolic responses to the flood pulse in a semi-arid floodplain. *Ecology* 86:220–234
- Van Gestel M, Merckx R, Vlassak K (1993) Microbial biomass responses to soil drying and rewetting: the fate of fast- and slow-growing microorganisms in soils from different climates. *Soil Biol Biochem* 25:109–123