

El Niño southern oscillation and seasonal drought drive riparian input dynamics in a Mediterranean stream

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Abstract

Inland waters substantially contribute to global carbon fluxes, and within them, low-order forested streams are important processors of allochthonous organic matter (OM) inputs. Leaf litter quantity and quality are expected to change in response to global change (e.g., climate change, land use change) but few long-term studies exist to better understand these shifts. The goal of this study was to assess the quantity and quality of OM sources to determine which global and local environmental factors control the dynamics of OM at the reach scale. The study was performed on a Mediterranean stream edged by a deciduous riparian forest over a 10-yr-time period. Riparian inputs, benthic and transported OM, and its carbon and nitrogen content were determined. The quantity of riparian inputs (912 ± 56 g dry mass m^{-2} yr^{-1}) was comparable to temperate regions with deciduous riparian forests, but the Mediterranean climate determined the different dynamics of these inputs. El Niño Southern Oscillation was strongly related to the interannual variability in riparian inputs through changes in precipitation. The annual amount of inputs depended on previous cumulated nonflow periods, with successive nonflow periods causing a progressive decrease in riparian inputs. The distribution of inputs throughout the year followed either a unimodal or bimodal pattern according to the absence or presence of a nonflow period in summer. In addition, drought caused lower quality (higher carbon : nitrogen molar ratio) riparian inputs. Changes in the quantity and quality of OM were explained by both present and past local and global factors.

Introduction

Inland waters contribution to global carbon (C) fluxes is substantial, although they only cover 1% of the Earth's surface. Inland waters receive about 2.7 Pg C per year from terrestrial ecosystems (Battin et al. 2009) and streams and rivers are important processors of these C inputs, with low-order streams having a disproportionately high contribution (Raymond et al. 2013). Low-order forested streams receive this allochthonous C from riparian forests. Global change, through climate change (e.g., elevated temperature and concentration of C dioxide, altered precipitation, and flow regimes), land use change or habitat fragmentation, is shifting the composition

of riparian plant communities, increasing deciduous, drought-tolerant, and plantation species (Kominoski et al. 2013). Global change is also expected to modify leaf litter inputs quantity and quality (Carpenter et al. 1992). These changes will influence as well leaf litter processing and storage within streams. However, few long-term studies of natural variation in riparian organic matter (OM) dynamics exist to serve as a baseline to better understand the effects of these global changes.

Inputs are determined by riparian forest properties (i.e., forest structure, composition, and phenology). The dynamics of riparian inputs are different in deciduous vs. perennial forests (Pozo et al. 1997; Hoover et al. 2011), and phenology of leaf fall is directly related to air temperature and photoperiod (Menzel 2002). Finally, litter retention in the stream is related to stream morphology, the physical properties of the materials, and hydrology (Hoover et al. 2006; Richardson et al. 2009). Therefore, it is important to extend the study of OM dynamics to different climatic regions. Abiotic factors have the capacity to modulate litter quantity and quality. For instance, annual riparian inputs are related to precipitation (Benfield 1997), and autumn frost or summer drought can cause an incomplete nutrient remobilization and an increase

Additional Supporting Information may be found in the online version of this article.

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in the quality of litter inputs (Keskitalo et al. 2005; Marchin et al. 2010). Surface flow permanence jointly with interannual ground water level fluctuation were also the hydrologic variables that explained most of the variance in riparian species abundances (Lite and Stromberg 2005) and leaf litter production (Follstad Shah and Dahm 2008). In addition to local variables, global processes can exert an influence at the reach scale. In parts of the western Iberian Peninsula, the climate during the winter is under the influence of the North Atlantic Oscillation; however, in the eastern region, interannual climate oscillations are strongly linked to El Niño Southern Oscillation (ENSO) (Rodó et al. 1997). El Niño Southern Oscillation is an air–sea coupled phenomenon that originates in the Pacific Ocean and affects global climate (D'Aleo et al. 2007). This phenomenon is the largest mode of interannual variability of the global climate system, with El Niño and La Niña events typically occurring every 3–5 yr and the interval between events varying from 2 yr to 7 yr, and is accompanied by a teleconnection pattern that extends outward from the Pacific region (Nyenzi and Lefale 2006). El Niño Southern Oscillation has teleconnections in the eastern Iberian Peninsula with effects on precipitation patterns (Rodó et al. 1997), stream nitrate concentrations (Vegas-Vilarrúbia et al. 2012), and streamflow and oxygen content in reservoirs (Marcé et al. 2010). El Niño Southern Oscillation may also determine vegetation responses, notably via shifts in major controls such as temperature, precipitation, and snow cover (Fischlin et al. 2007).

Mediterranean regions are predicted to be highly affected by global change (Sabater and Tockner 2010). Mediterranean streams are ecosystems with high intra-annual and interannual hydrological variability. Thus, heavy precipitation events in spring and autumn might cause floods, whereas high temperatures together with low precipitation (high evapotranspiration) create summer droughts in streams (Gasith and Resh 1999). This temporal variability affects a wide range of stream components and processes. Hydric stress during summer drought can anticipate leaf abscission from riparian forests (Acuña et al. 2007), leading to an accumulation of benthic OM (BOM) in the dry stream bed or in stagnant pools. When flow resume in autumn high concentrations of dissolved organic C (DOC) flush during the rewetting, although their origin is not well solved yet (Vázquez et al. 2007). Moreover, BOM dynamics affect detritus availability for consumers and consequently detritivores abundance and trophic complexity (Muñoz 2003; Vázquez et al. 2007; Gaudes et al. 2010; Power et al. 2013).

Riparian inputs in Mediterranean streams extend over time and are related to hydric stress in contrast to temperate streams, where inputs occur solely in autumn (e.g., Abelho and Graça 1998; Richardson et al. 2009). Despite the importance of interannual variations, the studies performed on the dynamics of OM inputs in these particular streams are mid-term (maximum of 3 yr; Maamri et al. 1994; Bernal et al. 2003; Acuña et al. 2007). Thus, there is a need to collect data at larger temporal scales to analyze the potential impact of climatic

phenomena and to explore in greater depth the impact of drought severity, on OM inputs in headwaters.

The goal of this study was to analyze a long-term (~10 yr) series of OM dynamics in a Mediterranean stream to (i) assess the quantity and quality of these OM inputs and (ii) determine which global and local (out- and in-stream) factors control these dynamics. Our working hypotheses were that (i) inputs of OM would be influenced by meteorological variables (such as precipitation or temperature) and modified, in turn, by ENSO teleconnections; (ii) droughts would increase the quantity of inputs due to hydric stress affecting riparian trees and floods would scour the stream channel reducing the retention of OM in the stream; and (iii) the quality of the inputs would decrease (C : nitrogen [N] molar ratio increase) in a gradient from the beginning of the summer/drought periods to the end of autumn due to rapid leaf death caused by drought vs. nutrient translocation to the tree before leaf abscission in autumn.

Materials and methods

Study site

This study was performed on the Fuirosos stream, which is situated in the north-eastern Iberian Peninsula (41° 42' N, 02° 34' E) in an area with a Mediterranean climate, characterized by mild winters and warm springs and summers, in addition to seasonality and variability in precipitation. The stream drains a catchment of 15.6 km² located in the Montnegre-Corredor Natural Park, where there is no marked anthropogenic pressure. Fuirosos is a forested, intermittent, third-order stream with oligotrophic waters and a basal discharge ranging from 0 L s⁻¹ to 25 L s⁻¹; its hydrology is characterized by extreme events, i.e., floods and droughts (Butturini et al. 2008). The flow is usually interrupted by a long drought period (1–3 months) in summer. The drought is followed by an abrupt short rewetting period in late summer-early autumn, which in turn, is followed by a long wet period that lasts until late spring.

Data for this study were collected in the main stem of the stream from a reach 50 m long and 2 m wide (on average) with a channel slope of 0.019 and draining an area of 12.3 km². The stream banks were steep with a well-developed riparian forest, mainly composed of *Platanus acerifolia* Willd. (exotic), *Alnus glutinosa* (L.) Gaertn., *Populus nigra* L., and *Corylus avellana* L., all of which are deciduous species and formed a closed canopy (except during the leafless periods). The streambed was composed of riffles dominated by boulders and cobbles and pools with accumulated gravel and sand. The study period lasted from January 2001 to September 2010 (see Supporting Information Table S1 for details on data availability and frequency).

Climatic, meteorological and hydrological variables

El Niño Southern Oscillation was characterized through the Southern Oscillation Index (SOI), calculated as the series of standardized differences in monthly standardized sea level

pressure between Tahiti and Darwin (Ropelewski and Jones 1987). Monthly SOI values were obtained (<http://www.cru.uea.ac.uk/cru/data/soi/>, 2012) and 5-month running mean values were calculated to smooth out short-term fluctuations and to determine El Niño and La Niña phases. Five-month running mean values of the SOI remaining below -0.5 standard deviations (SD) for 5 months or longer indicate El Niño phases, whereas those over $+0.5$ SD for 5 months or longer indicate La Niña events (Ropelewski and Jones 1987; Ropelewski and Halpert 1996).

Daily values of meteorological data (Supporting Information Table S1) were provided by the Diputació de Barcelona from two weather stations within the natural park. Vapor pressure deficit (VPD) was calculated as the difference between the saturation vapor pressure (following Buck 1981) and the actual vapor pressure (relative humidity \times saturation vapor pressure). Photoperiod was calculated as the difference between the sunrise and sunset times (http://www.fomento.gob.es/MFOM/LANG_CASTELLANO/DIRECCIONES_GENERALES/INSTITUTO_GEOGRAFICO/Astronomia/publico/efemerides/salida_puesta_sol.htm, 2012). The ratio of potential evapotranspiration (PET) to precipitation (PET/Prec ratio) was calculated to indicate the degree of hydric stress. Water level was monitored continuously during the sampling period with a pressure transducer (PDCR 1830, Druck limited, Leicester, UK) connected to a logger. Stream discharge was determined every 2 weeks using the slug-injection method with NaCl as a conservative tracer (Gordon et al. 1992). These measurements were used to determine a state-discharge relationship; in this way, the stream discharge during the entire study period was calculated. In this stream, discharges of between 250 L s^{-1} and 1012 L s^{-1} are considered to create moderate floods (sediment motion) and higher than 1012 L s^{-1} create large floods (streambed disruption) (Sabater et al. 2008).

From the long-term hydrological daily data, we defined two drought-severity parameters:

- a. The nonflow period of the year X (NF_x): the number of consecutive days without superficial runoff during the drought summer episode of that year.
- b. The cumulative nonflow period of the year X (ΣNF_x): the backward accumulated sum of days without superficial runoff observed during the previous consecutive years with summer drought episodes. The calculation of ΣNF_x resets to zero when a permanent summer flow was monitored.

Organic matter

All the OM fractions were collected monthly (see Supporting Information Table S1 for details on data availability and frequency). The OM entering into the stream from the riparian forest (riparian inputs; RI) was collected separately as vertical (VI) and lateral inputs (LI). Vertical inputs were collected using vertical traps measuring 1 m^2 ($1 \times 1 \text{ m}$) and

suspended above the stream surface ($n = 5$), whereas LI were collected with traps (0.55 m long) installed at ground level on the stream sides ($n = 10$; 5 on each side). All traps were fitted with 1 mm mesh size (Coarse Particulate OM [CPOM]) and were situated every 10 m along the reach.

Total annual RI were calculated for calendar years (January to December year X) to analyze interannual variability. Total VI were calculated for phenological years (April year X to March Year X + 1) to analyze the effects of the environment on the tree phenology from the moment of leaf emergence and for hydrological years (October year X to September year X + 1) to test for the effects of summer drought periods.

Benthic OM was measured by collecting the OM from a corer (14 cm diameter) randomly situated in detritus-covered areas ($n = 3$). The streambed coverage (%) by OM (leaves, branches and fine detritus) was obtained through visual estimation of transects along the reach every 8 m ($n = 5$). Transported CPOM (particles $> 1 \text{ mm}$) was measured with a net of 1 mm mesh size, and transported fine POM (FPOM; particles $0.05\text{--}1 \text{ mm}$) was measured with a net of 0.05 mm mesh size. The two drift nets ($20 \times 20 \text{ cm}$ opening at the mouth) were installed in the reach for intervals of 45 min to 90 min (upstream and downstream; $n = 2$). Transported ultrafine POM (UFPOM; particles $0.7 \mu\text{m}\text{--}0.05 \text{ mm}$) was measured by filtration through pre-weighed GF/F filters ($0.7 \mu\text{m}$ pore size; Whatman, Maidstone, UK) of a certain stream water volume (previously filtered by 0.05 mm net; $n = 3$).

All the OM fractions collected were oven-dried at 60°C , and dry mass (DM) was determined. Filters (UFPOM) were oven-dried and combusted at 450°C for 4 h to obtain the ash-free DM. Total RI were calculated as the sum of LI rate ($\text{g DM m}^{-1} \text{ d}^{-1}$) divided by the stream width and VI rate ($\text{g DM m}^{-2} \text{ d}^{-1}$); BOM as OM per reach surface (g DM m^{-2}); and concentrations of POM fractions were obtained by dividing the DM by the volume of filtered water (mg DM L^{-1}). The C and N content of OM was determined with an elemental analyzer (EA 1108, Thermo Fisher Scientific, Milano, Italy) using vanadium pentoxide as the oxidation catalyst, and the C : N molar ratio was calculated.

Dissolved OM content in stream water was estimated in terms of C content (DOC). Samples were refrigerated and transported to the laboratory, filtered through precombusted GF/F filters, acidified with 2 M HCl (2%), and preserved at 4°C until analysis. The concentrations of DOC were determined by oxidative combustion-infrared analysis using a total organic C analyzer (TOC-V_{CS}, Shimadzu, Kyoto, Japan).

Data analysis

Results are given as mean \pm standard error, if not the case, SD is indicated. Variables referring to RI rates were averaged values that took into account the OM found in the traps on the sampling date and the days between samplings, and it was assumed that input rates remained constant between samplings. Two-way ANOVA was used to test the effect of

season and drought (years with or without NF), as well as their interaction, on VI and LI (seasonal averages for each year). The normality of residuals (Kolmogorov–Smirnov [with Lilliefors correction] and Shapiro–Wilks tests) and homoscedasticity (Levene’s test) were tested, and a post hoc Tukey HSD test was conducted for the season factor. Daily meteorological and hydrological data were averaged for the periods between each sampling of OM. Due to a gap in the data from 2009 to 2010 period, the precipitation of the phenological year 2009–2010 was estimated using the available data combined with the data of the other weather station, transformed using a regression equation between the data from the two stations. Correlations between OM variables and climatic, meteorological, and hydrological variables were tested using nonparametric correlation analyses (Spearman’s rank correlation coefficient, r_s). When two or more variables were correlated with the dependent variable but showed co-linearity ($r_s > 0.95$), only the variable explaining the highest variability of the dependent variable was kept. The significance level (α) was set at 0.05 and all analyses were performed with PASW (Version 18, IBM, Armonk, U.S.A.).

Results

Climatic, meteorological and hydrological description

From 2001 to 2010, several El Niño and La Niña events occurred based on the SOI values (Fig. 1a). El Niño was recorded for the years 2002–2003, 2004–2005, 2006–2007, and 2009–2010, and La Niña was recorded at the beginning of 2001 (end of 2000–2001 event), from 2007 to 2009 and the last event started in mid-2010. During the study period, years varied widely in terms of meteorological and hydrological features (Table 1; Fig. 1b). For example, 2003 was a very hot year, with the highest mean temperature of all the studied summers (21.6°C vs. 19.6°C on average) and the highest absolute maximum temperature (36.6°C vs. 32.7°C on average). That year, PET and VPD were the highest and the PET/Prec ratio daily mean was 107.3 in summer vs. 4.1 on average. In contrast, 2005 was a cold year with the lowest daily mean temperature and the lowest absolute minimum (−7.3°C vs. −3°C on average). 2002 was a very humid year, with the highest annual precipitation, mainly concentrated in spring (5.76 mm d^{−1} vs. 2.59 mm d^{−1} on average), and the lowest PET/Prec ratio daily mean (0.62 vs. 4.1 on average). Accordingly, that year, the stream discharge was the highest and there were 20 d of moderate and large floods. A seasonal NF around summer occurred in the stream nearly every year (Fig. 1b). Flow cessation fluctuated from the beginning of June to mid-July and flow return from the end of August to the end of October, with the longest NF (>100 d) in 2001, 2008, and 2009. The average NF was 87 d (from June 28 to September 23). According to our data set, the exact estimation of the Σ NF was possible from 2002 onward.

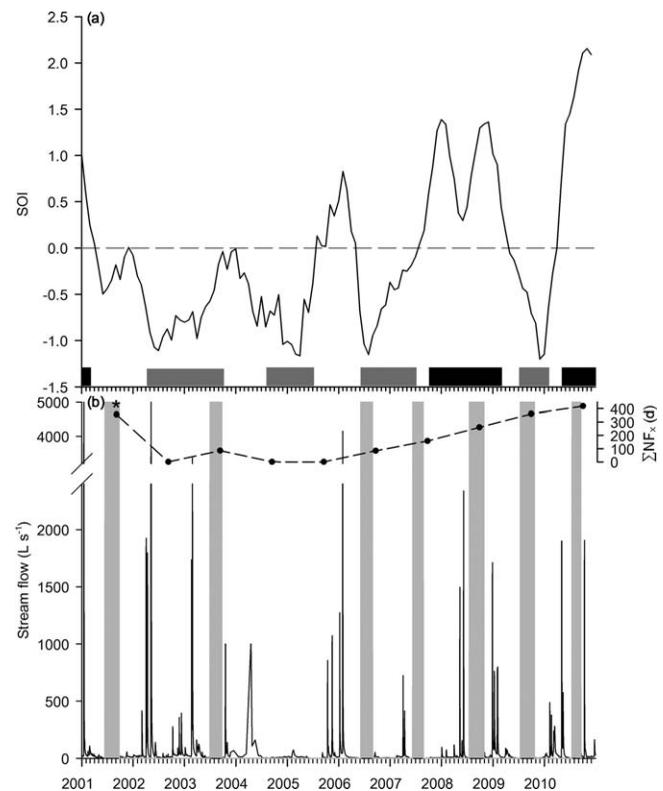


Fig. 1. (a) Southern Oscillation Index (SOI) values (5-month running mean) used to characterize El Niño Southern Oscillation during the studied period. On the X axis, El Niño events are marked in dark gray and La Niña events in black. (b) Stream discharge during the study period. Gray areas represent nonflow periods (NF) and the dashed line represents cumulative nonflow periods (Σ NF). *This value may be underestimated, due to the lack of hydrological data before 1998.

Three summers with permanent flow (2002, 2004, and 2005) were reported; therefore, Σ NF₂₀₀₂ = Σ NF₂₀₀₄ = Σ NF₂₀₀₅ = 0. The largest Σ NF was estimated for 2010 (Σ NF₂₀₁₀ = 418 d) because it reflected the concatenation of four years with summer NF. Photoperiod, solar radiation, and wind velocity did not exhibit important interannual differences. Photoperiod had the lowest average length during autumn (10.3 h d^{−1}) and an annual mean of 12.2 h d^{−1}, and solar radiation ranged from 12.9 MJ m^{−2} d^{−1} to 13.9 MJ m^{−2} d^{−1}. Wind velocity was 1.9 (±0.9) m s^{−1} on a daily average, with a maximum velocity reaching 28.8 m s^{−1}.

Riparian organic matter inputs

Total RI to the stream were 911.67 (± 55.80; $n = 9$) g DM m^{−2} yr^{−1} on average (Fig. 2), representing 356.63 (± 24.70; $n = 7$) g C m^{−2} yr^{−1}. The annual inputs in 2003 and 2006 were the highest, and 2008 showed the lowest value. The C : N molar ratio of RI was on average 59.12 (± 14.48 SD; Supporting Information Fig. S1). The C content (%) was positively related to temperature and VPD and negatively related to humidity, and N content (%) was, in part, explained by the photoperiod. As C : N was mainly determined by the N

Table 1. Main hydrological and meteorological features of the studied years in the Fuirosos catchment; daily mean values of temperature (°C), potential evapotranspiration (PET; mm) and vapor pressure deficit (VPD; kPa), median values of discharge (L s⁻¹), annual values of discharge (L s⁻¹), annual mean of precipitation (mm yr⁻¹), annual nonflow period (NF_x; d), and floods (d).

Year	Temperature		Precipitation		Discharge		PET		VPD		NF _x		Floods	
	Mean	SD	Mean	SD	Median	SD	Mean	SD	Mean	SD	M	L	M	L
2001	13.0	6.3	631.0	2706.3	8.97	276.60	1.90	1.23	0.48	0.42	102	2	2	3
2002	12.7	5.2	1015.4	3643.1	18.62	370.85	1.72	1.12	0.40	0.34	0	13	7	7
2003	13.1	7.2	795.4	2833.2	15.78	259.59	2.47	1.87	0.54	0.57	84	10	4	4
2004	12.2	6.2	732.7	2899.7	5.39	164.13	2.16	1.37	0.36	0.28	0	2	2	0
2005	11.7	6.9	674.9	2482.6	18.05	148.04	2.23	1.54	0.39	0.36	0	5	5	1
2006	13.3	6.5	479.4	2398.1	3.14	312.46	2.28	1.42	0.44	0.40	83	5	5	3
2007	12.4	5.5	561.1	2184.8	3.06	48.68	2.23	1.31	0.37	0.30	74	3	3	0
2008	11.9	5.6	886.3	3104.9	7.91	214.47	2.10	1.51	0.29	0.29	103	5	5	4
2009	NA	NA	NA	NA	2.80	101.16	NA	NA	NA	NA	101	7	7	0
2010	NA	NA	NA	NA	13.80	190.86	1.74	1.32	NA	NA	57	12	12	3

M = moderate floods (250 L s⁻¹–1012 L s⁻¹); L = large floods (> 1012 L s⁻¹); NA = unavailable data.

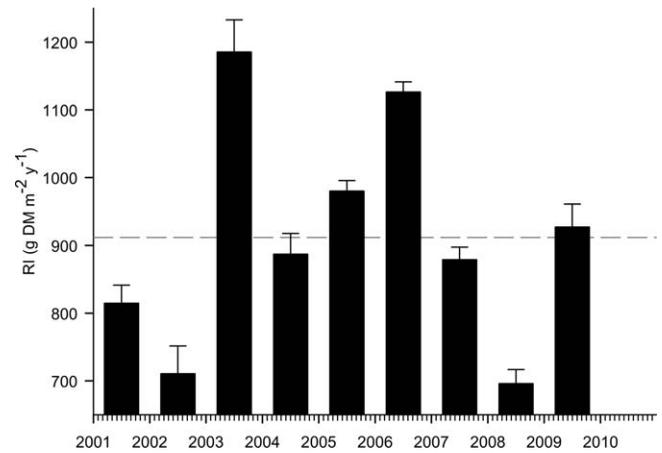


Fig. 2. Total annual riparian inputs (RI) of calendar years (from January to December each year) into the stream during the study period. The dashed line represents the average value for all the years, and error bars represent + standard error. Note that the Y axis does not start at zero.

Table 2. Significant Spearman correlations between the riparian organic matter inputs and the hydrological and meteorological variables.

Dependent Variable	Independent variable	r _s	p	n
RI C (%)	Maximal temperature (°C)	0.303	0.028	53
	Maximal relative humidity (%)	-0.477	0.001	48
	VPD (kPa)	0.375	0.009	48
RI N (%)	Photoperiod (h)	0.270	0.042	57
RI C : N (molar ratio)	Photoperiod (h)	-0.268	0.043	57
VI (g DM m ⁻² d ⁻¹)	Discharge (L s ⁻¹)	-0.363	0.002	73
	Prec (mm)	-0.292	0.015	69
	Minimal temperature (°C)	0.353	0.003	69
	NF (d)	0.246	0.036	73
	PET/Prec ratio	0.344	0.004	68
	VPD (kPa)	-0.249	0.042	57

RI = total riparian inputs; VI = vertical inputs; LI = lateral inputs; VPD = vapor pressure deficit; Prec = precipitation; NF = nonflow period; PET = potential evapotranspiration.

content ($r_s = -0.919$; $p < 0.001$; $n = 57$), C : N was also negatively correlated with photoperiod (Table 2).

Riparian inputs were 60.5 (± 0.4)% from VI and 39.5 (± 0.4)% from LI (Supporting Information Fig. S2). The inter-annual variability in the quantity of VI was substantially explained by ENSO. Vertical inputs from phenological years were related to the SOI of September (i.e., the mean value of the SOI from July to November; $r_s = -0.900$; $p = 0.001$; $n = 9$; Fig. 3a). This correlation was the most explanatory and significant (highest r_s and p value, respectively) of the tested correlations between VI and SOI values. The local

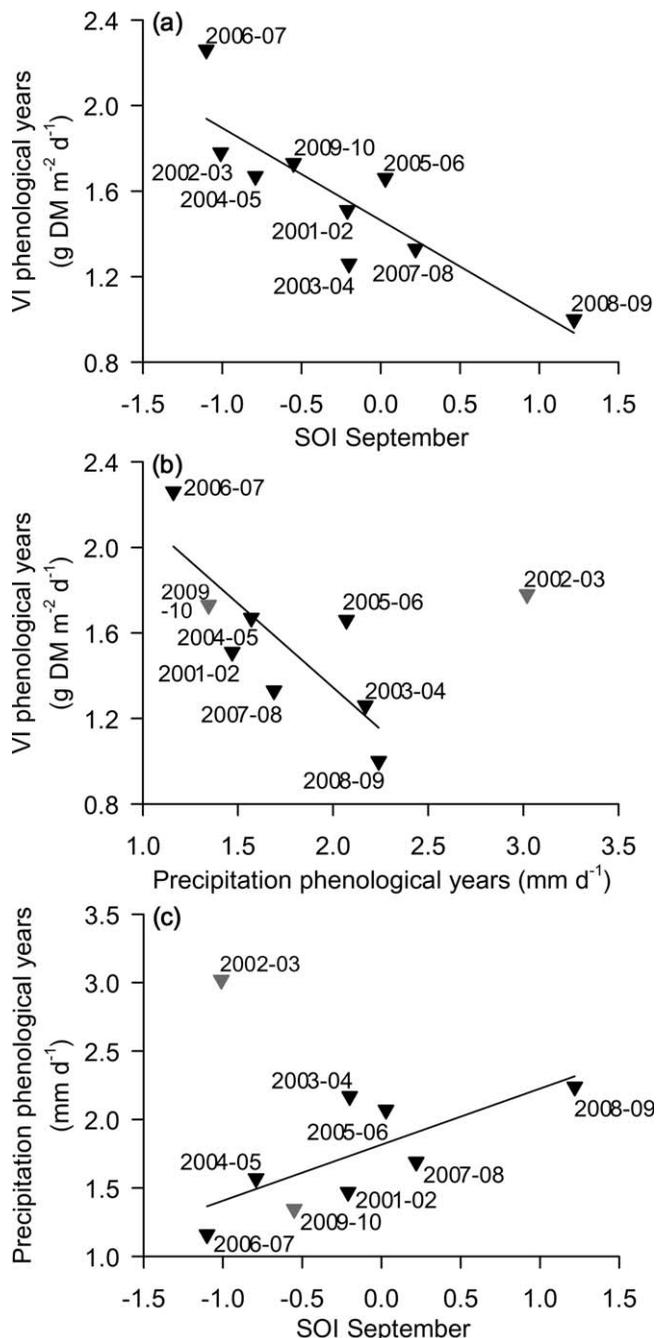


Fig. 3. Correlations between (a) riparian vertical inputs (VI) in phenological years and Southern Oscillation Index (SOI) for September ($r_s = -0.900$; $p = 0.001$; $n = 9$), (b) VI and precipitation in phenological years ($r_s = -0.821$; $p = 0.023$; $n = 7$) and (c) precipitation in phenological years and SOI for September ($r_s = 0.821$; $p = 0.023$; $n = 7$). Phenological years account for the average values from April year X to March year X+1, and SOI is from September year X. In (b) and (c), gray triangles indicate data not included in the correlation (see text for explanation and Supporting Information Table S2 for the results of the correlations adding these data). Note that the axes do not start at zero.

variable relating VI and ENSO was precipitation (VI vs. Precipitation: $r_s = -0.821$; $p = 0.023$; $n = 7$; Fig. 3b; Precipitation vs. SOI Sept: $r_s = 0.821$; $p = 0.023$; $n = 7$; Fig. 3c). Two phenological years were situated at both extremes of these correlations: 2008–2009 with a strong La Niña period and lower-than-mean VI and 2006–2007 with a strong El Niño period and higher-than-mean VI. These correlations did not include 2002–2003 or 2009–2010. 2002–2003, which included a long El Niño period and was a particularly humid year, fell outside the correlation. The higher precipitation during that period was likely not related to ENSO and did not explain the quantity of VI. In contrast, the estimation of the precipitation value for the phenological year 2009–2010 reinforced these correlations (Supporting Information Table S2). Southern Oscillation Index was not significantly correlated with LI ($p = 0.406$) or total RI ($p = 0.139$) in phenological years.

Vertical inputs were positively related to minimum temperature, NF duration, and the PET/Prec ratio and negatively related to discharge and precipitation (Table 2), indicating that high VI were related to warm temperatures with low flow and precipitation, thus, mainly in drought periods, when riparian trees would have high evapotranspiration rates. The VI distribution throughout the year depended both on the season and the occurrence of NF (Season: $F_{3,31} = 14.04$, $p < 0.001$; NF: $F_{1,31} = 0.27$, $p = 0.607$; Season \times NF: $F_{3,31} = 6.54$, $p = 0.001$). Years with NF (Fig. 4a) showed the highest values in summer (representing 36% of annual VI), whereas years with permanent flow (Fig. 4b) showed the highest values in autumn (52% of annual VI). The autumn peak in years with NF represented 31% of the annual VI. Further, VI in hydrological years decreased with longer Σ NF ($r_s = -0.898$; $p = 0.001$; $n = 9$; Fig. 5), while the relationship between VI and NF was barely significant ($r_s = -0.678$; $p = 0.045$; $n = 9$).

Lateral inputs were only negatively related to the VPD (Table 2), indicating that high LI were related to periods with high humidity and low temperatures. The LI distribution throughout the year was not significantly affected by the season or by the occurrence of NF ($p > 0.500$).

Benthic and transported organic matter

Benthic OM was on average $182.31 (\pm 33.92; n = 38)$ g DM m^{-2} (Supporting Information Fig. S3a), representing $99.20 (\pm 21.14; n = 26)$ g C m^{-2} . The quantity of BOM was not directly related to discharge (averaged for sampling periods; $p = 0.105$), to RI ($p > 0.776$), or to transported POM ($p > 0.227$), but depended mainly on the time since the last flood, whether the floods were moderate or large, as well as the BOM coverage (%; Table 3). The average C : N molar ratio of BOM was $50.01 (\pm 11.56 \text{ SD})$, and the C content was higher with longer NF periods (Table 3). The quality of BOM was not related to its quantity ($p > 0.681$) or to the quality of RI ($p > 0.143$).

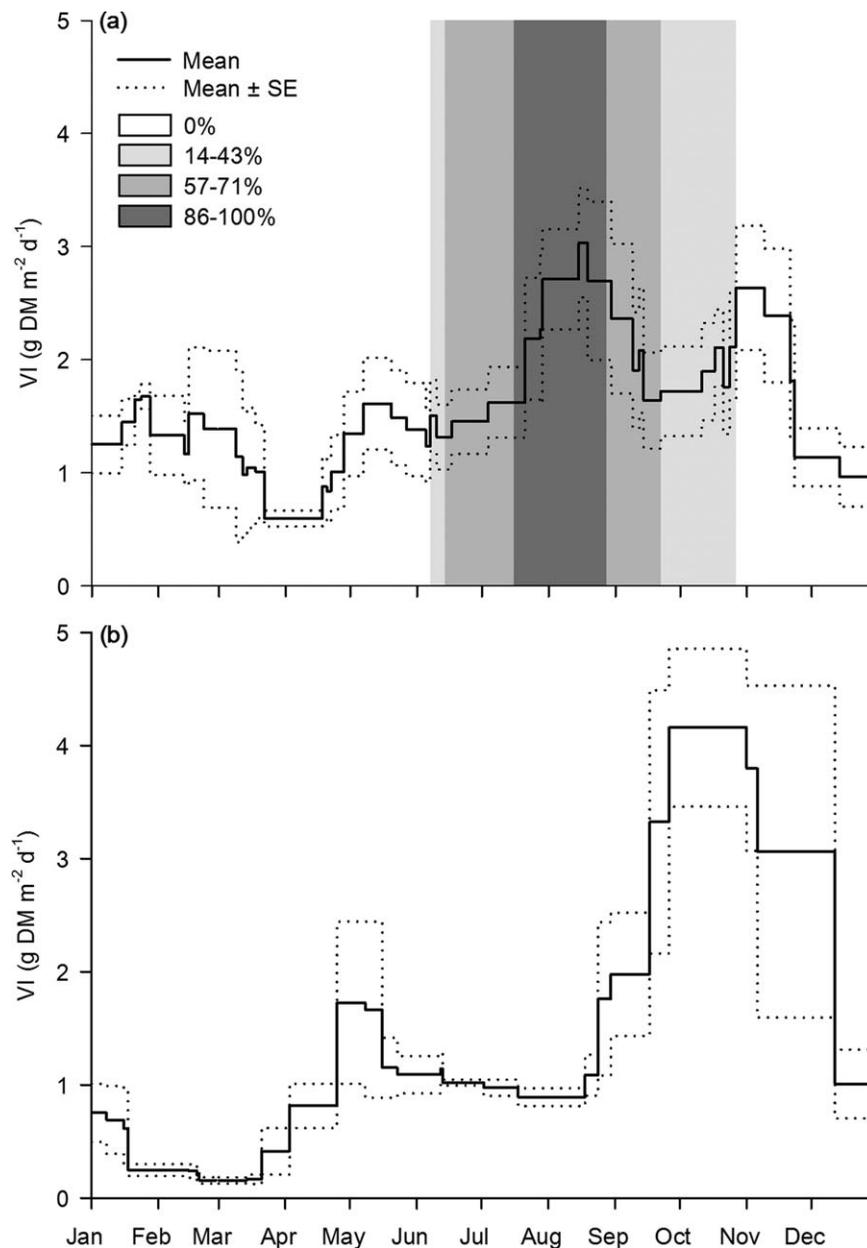


Fig. 4. Vertical input (VI) mean values (\pm standard error) for (a) years with nonflow periods ($n = 7$; 2001, 2003, 2006, 2007, 2008, 2009, 2010) and (b) years with permanent flow ($n = 3$; 2002, 2004, 2005). Gray shading indicates the percentage of years during which that period the stream was dry.

Transported CPOM was on average $0.26 (\pm 0.11; n = 33)$ mg DM L^{-1} , representing $0.07 (\pm 0.03; n = 18)$ mg C L^{-1} ; FPOM was on average $0.22 (\pm 0.06; n = 33)$ mg DM L^{-1} , representing $0.04 (\pm 0.02; n = 18)$ mg C L^{-1} ; and UFPOM was $2.26 (\pm 0.43; n = 24)$ mg DM L^{-1} , representing $0.02 (\pm 0.01; n = 21)$ mg C L^{-1} (Supporting Information Fig. S3b-d). Coarse POM and FPOM followed parallel dynamics, and their concentration in water increased with floods, whereas UFPOM concentration was negatively related to punctual discharge. Fine POM and moderate floods showed the strongest relationship (Table 3).

The average C : N molar ratio of the transported CPOM was $38.64 (\pm 9.71 \text{ SD})$, which was higher than the C : N of FPOM ($22.01 \pm 6.69 \text{ SD}$) and UFPOM ($14.66 \pm 5.72 \text{ SD}$). Higher discharge and flood frequency were related to a lower C content and C : N ratio of CPOM but a higher C content and C : N ratio of FPOM (Table 3).

Dissolved organic C exhibited high peaks after drought periods (Supporting Information Fig. S4). The DOC concentration during the rewetting period was positively related to the quantity of VI accumulated during the “summer” period ($r_s = 0.667, p = 0.050, n = 9$; Supporting Information Fig. S5).

Discussion

Climate is the strongest controller of OM dynamics through its effect on vegetation (Webster and Meyer 1997). This study strongly suggests that the dynamics of riparian VI were driven by ENSO, a global scale phenomenon, through precipitation and by an inter-year carryover effect of drought at a more local scale.

Although 10 yr might be considered a relatively short period over which to observe the effects of global climate processes, this study detected that the annual VI of phenological years were affected by ENSO through changes in precipitation in the studied stream. The SOI value of September (i.e., the mean value of the SOI from July to November), which integrates the drought and autumn peak periods, was significantly correlated with VI because VI respond directly to the physiology of the riparian trees. Vertical inputs were higher with lower precipitation during El Niño periods, likely related to hydric stress of riparian trees, which increases leaf abscission (Tabacchi et al. 2000; Acuña et al. 2007). In the same direction, an increase in defoliation in southern Europe forests, related to increased water deficit, had been observed from 1987 to 2007 (Carnicer et al. 2011). In contrast, during La Niña periods, precipitation was higher than at other times, leading to decreased VI. Atmospheric teleconnections of ENSO with precipitation (and drought) patterns have been observed in the Iberian Peninsula, in general, and the north-eastern region (where this study was performed), in particular (Muñoz-Díaz and Rodrigo 2005; Vicente-Serrano 2005).

The inter-year carryover effect of drought on the RI consisted of a reduction in the VI correlated with the duration of the ΣNF. Riparian annual VI were reduced on average by 45% (from 1.8 g DM m⁻² d⁻¹ to 1.0 g DM m⁻² d⁻¹) in years with permanent flow (e.g., 2005–2006) in comparison to years with a ΣNF of approximately 400 d (e.g., 2009–2010). To our knowledge, the cumulative effect of drought on RI found in this study has not been observed before; however, Follstad Shah and Dahm (2008) found a decrease in leaf litter production and inputs over 4 yr in semiarid riparian forests attributed to drought-induced recession of ground water, and a similar pattern referred to as “drying memory” by Datry et al. (2011) consisted of observations of a decrease in the leaf litter breakdown with increased drying average duration and frequency in a temporary stream, which was observed for a 24-yr period. These results suggest that temporary streams remain affected by drying events over the long term, highlighting the importance of drought both in the short and the long term. The cause of the observed effect on the VI in this study was most likely that soil drying induces a decrease in nutrients, in particular N, with strong effects on plant growth and function (McDonald and Davies 1996). In addition, the low decomposition of OM on the riparian forest floor of the studied stream, which is even lower in drought years, causes a N impoverishment of the soil (Bernal

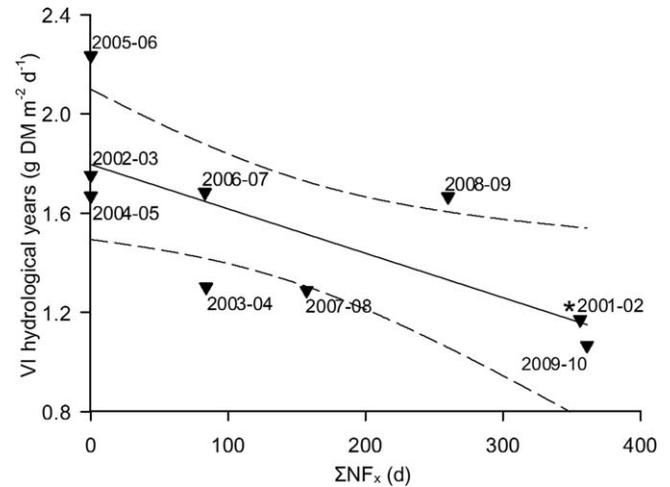


Fig. 5. Correlation between the average vertical inputs (VI) in hydrological years (October year X to September year X+1) and cumulative nonflow period for year X (ΣNF_x; $r_s = -0.898$; $p = 0.001$; $n = 9$). The dashed lines represent the 95% confidence intervals of the regression line. *This value may be underestimated because of the lack of hydrological data before 1998. Note that the Y axis does not start at zero.

Table 3. Significant Spearman correlations between the benthic and transported organic matter (OM) and the hydrological and meteorological variables.

Dependent Variable	Independent variable	r_s	p	n
BOM (g DM m ⁻²)	Time from M (d)	0.447	0.005	38
	Time from L (d)	0.404	0.012	38
BOM coverage (%)	Time from M (d)	0.504	0.003	32
	Time from L (d)	0.774	<0.001	32
BOM C (%)	NF (d)	0.435	0.030	25
CPOM (mg DM L ⁻¹)	Time from M (d)	-0.359	0.040	33
FPOM (mg DM L ⁻¹)	Time from M (d)	-0.559	0.001	33
	Time from L (d)	-0.511	0.002	33
	CPOM (mg L ⁻¹)	0.570	0.001	33
UFPOM (mg ash-free DM L ⁻¹)	Discharge (L s ⁻¹ , punctual)	-0.525	0.008	24
CPOM C (%)	Discharge (L s ⁻¹ , punctual)	-0.488	0.034	19
CPOM N (%)	CPOM (mg DM L ⁻¹)	-0.513	0.030	18
CPOM C : N (molar ratio)	Time from L (d)	0.565	0.012	19
FPOM C (%)	Time from L (d)	-0.553	0.014	19
FPOM C : N (molar ratio)	Discharge (L s ⁻¹ , punctual)	0.598	0.007	19
	Time from M (d)	-0.512	0.025	19
	Time from L (d)	-0.506	0.027	19

BOM = benthic OM; CPOM = coarse particulate OM; FPOM = fine particulate OM; UFPOM = ultrafine particulate OM; M = moderate floods (250 L s⁻¹–1012 L s⁻¹); L = large floods (>1012 L s⁻¹); NF = nonflow period.

et al. 2003), affecting tree growth and leaf production in the subsequent years. This mechanism was also observed in semiarid streams with a negative feedback between leaf litter production and soil inorganic N (Follstad Shah and Dahm 2008). Other factors related to drought and soil N, such as water table level (Burt et al. 2002), temperature and soil moisture could be also affecting these results.

Vertical inputs were related to drought but not to any of the variables that could indicate the phenological autumn peak (e.g., photoperiod). This pattern indicated the primary importance of hydric stress peak vs. a phenological effect in this stream. Drought also shaped the dynamics of these inputs throughout the year. In the years in which summer NF occurred, VI in Fuirosos were characterized by a two-peak annual cycle, one coinciding with the NF and the other in autumn. This dynamic has been reported in the study site by Acuña et al. (2007) and Bernal et al. (2003) and the summer peak has been described as a response of riparian vegetation to hydric stress (Larned 2000; Tabacchi et al. 2000). The autumn peak (52% of the total VI) in years with permanent flow is comparable to the values reported for temperate streams (Fisher and Likens 1973; Richardson 1992), whereas it was lower in the years with NF (31%). Hence, the immediate effect of NF is that riparian trees release before the leaves, which generates the summer peak, while it does barely affect the quantity of leaf litter inputs, which is probably more related to leaf production of the trees (Follstad Shah and Dahm 2008). In turn, leaf production by the trees would be affected by the conditions in the riparian soil in spring, which would be affected by the quantity of N in the soil and other factors. In this study, leaf production of trees was not measured, but it should be considered in future studies.

Total annual RI ranged from 695.83 g DM m⁻² yr⁻¹ to 1185.38 g DM m⁻² yr⁻¹, showing the high interannual variability in this stream compared to other streams with a similar amount of litter inputs among years (Richardson 1992). The average of total annual inputs during the 10 yr of the study period (911.67 g DM m⁻² yr⁻¹) is approximately double that of other Mediterranean streams (King et al. 1987; Stewart and Davies 1990; Maamri et al. 1994) but is similar to the values reported for temperate streams (e.g., Treadwell et al. 1997; Wallace et al. 1997a; Molinero and Pozo 2004) because of the deciduous nature of the riparian forests.

The C content of OM increased related to drought conditions (high temperatures and VPD and low relative humidity), whereas N was related to photoperiod, which increases through the spring and reaches its maximum in summer, resulting in the lower molar C : N ratios in summer. These results support our initial hypothesis of a C : N increase from summer to autumn. Bernal et al. (2003) found that N content was higher in plane trees during the summer peak (1.65 ± 0.04%) than in autumn (0.76 ± 0.03%), which is related to the

physiology of riparian trees and the nutrient translocation process that occurs before autumn leaf abscission.

The average quantity of BOM stored in the streambed is comparable to values found in other temperate streams with deciduous forests (table 4.1 in Pozo and Elosegi 2005), and its dynamics were mainly explained by the time since the last large flood; however, BOM was not directly related to RI or OM transport. González and Pozo (1996) and Pozo et al. (1997) found that the timing of inputs and the hydrologic regime act together to influence temporal dynamics of BOM, with accumulation in periods with high RI and low transport (low flow). The transport of CPOM and FPOM in Fuirosos, was highly related to the occurrence of floods. Large exports of POM (and dissolved OM) during storms have also been observed by Wallace et al. (1995), Newbold et al. (1997), and Neatrou et al. (2004). Although it has long been recognized that OM transport in streams is dominated by high-flow events, measurements of transport in most studies are limited to base flow conditions (Tank et al. 2010). This problem is difficult to solve because of the complexity of measuring these variables continuously (Elosegi and Pozo 2005). Carbon : N gradually decreased from RI, followed by BOM and transported materials because of the degree of conditioning and processing of the different particles, which causes N enrichment (Triska et al. 1975; King et al. 1987). The quality of CPOM was higher (lower C : N ratio) when discharge and flood frequency were high, perhaps because the CPOM quality was imported from upstream, whereas the quality of FPOM was higher with lower discharge and flood frequency, most likely because of the higher OM processing time in the reach. Finally, the significant positive link between the VI accumulated during the summer period and DOC flushed in the successive rewetting period revealed the potential importance of OM stored on the dry streambed for regulating the availability of DOC in the stream through OM lixiviates (Meyer et al. 1998; Romani et al. 2006).

Conclusions and implications

In this long-term study, we demonstrated that the riparian OM inputs to a Mediterranean stream were driven by both global scale phenomena, such as ENSO, and local scale events, mainly drought. The interannual variability of VI was substantially explained by ENSO through changes in precipitation. An interesting and not previously described cumulative effect of drought consisted on a decrease in annual VI caused by successive years in which the stream dried up in summer, most likely through a decrease on the nutrient content of the riparian soil. In years with permanent flow, autumnal peaks occurred because of phenological leaf abscission, whereas a two-peak annual cycle was observed in years with summer NF, with the first peak from hydric stress and the second corresponding to the phenological peak.

Thus, drought has both immediate and long-term effects on the dynamics of allochthonous OM.

The importance of allochthonous resources for food webs in forested headwater streams is widely recognized (Polis et al. 1997; Wallace et al. 1997b), and the timing of these pulsed resources is important in determining the strength of trophic cascades (Leroux and Loreau 2012); therefore, the effects of ENSO and drought on the allochthonous OM inputs to the stream will have effects on OM availability timing for decomposers.

The frequency of ENSO events has increased over the past few decades (Huntington 2006) and following the same trend, the correlation between ENSO and Iberian precipitation increased toward the end of the past century (Rodó et al. 1997). Although changes in ENSO intensity for the 21st century are uncertain, there is high confidence that ENSO will remain the dominant mode of the natural climate variability, and due to changes in moisture availability ENSO-induced rainfall variability on regional scales, will intensify (Christensen et al. 2013). Further, climate change might influence the frequency and severity of ENSO events (Nyenzi and Lefale 2006). Thus, it is still difficult to predict how riparian dynamics will be affected by ENSO.

Hydrology is affected by several components of global change. Extreme events, mainly droughts, will generally increase in frequency and magnitude (Hartmann et al. 2013) and result in increased intermittency of stream flow (Acuña et al. 2014). Hence, based on our results, we can predict that an increase in the frequency of droughts in the near future will lead to a more frequent bimodal temporal distribution of riparian inputs and a decrease in the quantity and quality of available allochthonous resources in forested Mediterranean streams. This will decrease the quantity of C that enters from riparian systems to streams and its processing, which should be taken into account in the contribution of inland waters to global C fluxes. The present study is a long-term study on the natural variation in riparian OM dynamics, contributes to understand the mechanisms driving the effects of climate on these dynamics and will serve as a baseline to understand the effects of global changes.

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