1 **Combined effects of leaf litter inputs and a flood on nutrient retention in a Mediterranean**

2 **mountain stream during fall**

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22 **Abstract**

23   This study examined the effect of increasing in-channel leaf standing stocks on hydrologic

24 transient storage and nutrient retention in a Mediterranean mountain stream. A flood at the end

25 of the leaf fall period provided the opportunity to examine the effect of abrupt removal of much

26 of the leaf material. Twenty-one chloride additions were performed from October to December

27 2004. In 13 of these, we also added ammonium and phosphate to estimate nutrient uptake

28 lengths and uptake velocities to assess nutrient retention. The One-dimensional Transport

29 with Inflow and Storage (OTIS) model was used to estimate transient water storage

30 parameters. Although discharge remained constant during leaf fall, water residence time

31 increased because of in-channel litter accumulation, as did nutrient uptake velocity. Flooding

32 reduced leaf benthic standing stocks by 65% and dramatically altered hydraulic and nutrient

33 retention properties of the channel. Following recession, the stream rapidly recovered in

34 terms of nutrient retention, especially for phosphate. Abrupt changes in discharge under

35 flood conditions largely determined the variability in stream nutrient retention. However, leaf

36 litter inputs played an important role in nutrient dynamics during constant flow. Because

37 both the flood regime and the timing of leaf fall are being regionally altered by climate

38 change, our results have implications for stream nutrient dynamics under climate change

39 scenarios.

Introduction

Intense leaf fall from deciduous riparian vegetation is of major importance for both the community structure (Wallace et al. 1997) and metabolism (Crenshaw et al. 2002) of streams. Leaf litter inputs provide large quantities of energy to headwater streams that typically exhibit low levels of primary productivity (Fisher and Likens 1973). The ecological relevance of these inputs is well recognized, especially in temperate regions (Wallace et al. 1997). Streams in Mediterranean regions, in contrast to those from more humid climates, are characterized by high interannual variability in the intensity and frequency of floods as well as by periods of intermittent flow. In addition, in Northern Hemisphere Mediterranean regions higher leaf litter input coincides with periods of high flood frequency, low temperature, and low autotrophic activity (Gasith and Resh, 1999). Therefore, the residence time of the allochthonous matter in Mediterranean streams may be much shorter than in temperate streams because it enters shortly before or in conjunction with flooding. In consequence, the ecological relevance of this allochthonous energy source may depend on the timing of flood events relative to leaf inputs.

Mediterranean regions are among the most vulnerable to climate change (Schröter et al. 2005). In these regions, both a change in the frequency and intensity of rains and an increase in temperatures are expected (Christensen and Christensen 2004). Under this scenario, it is likely that alterations in the regimes of autumnal leaf inputs and flooding will have implications for stream metabolism and biogeochemistry. The effects of autumnal leaf litter inputs on stream biota (Maamri et al. 1997) and metabolism (Acuña et al. 2004) have been studied previously in Mediterranean streams, but little is known about their effect on nutrient retention. In addition, methodological constraints on measuring nutrient retention under flood conditions, together with the unpredictability and high rate of change of these episodic events,

64 have restricted the number of studies assessing flood effects on nutrient retention (but see

65 Martí et al. 1997).

66   Nutrient retention in stream ecosystems is a combination of hydrologic, biologic and

67 chemical retention (Valett et al. 1996). Hydrologic retention is influenced by discharge and

68 the hydraulic and morphologic properties of the stream channel, which determine the extent

69 of the transient water storage (i.e., water moving at slower velocity than the average velocity

70 in the channel, relative to the free flowing water). The magnitude of the transient water

71 storage can be relevant for nutrient retention, because the interaction between stream biota

72 and available nutrients is greater in transient storage zones than in the free flowing water

73 (Triska et al. 1989). Therefore, it has been hypothesized that the influence of in-stream

74 processes on stream nutrient concentrations increases with transient water storage. However,

75 literature results conflict (Mulholland et al. 1997, Hall et al. 2002, Ensign and Doyle 2005),

76 possibly because transient water storage can originate in a variety of channel structures that

77 delay water transport (e.g., eddies, back waters, side channels, streambed irregularities, pools,

78 mats of filamentous green algae, hyporheic zones, and organic debris dams), which may

79 contribute differently to nutrient retention across streams or within streams over time.

80   The presence of in-channel vegetation (Harvey et al. 2003), debris dams (Lautz et al.

81 2006), flow obstacles (Ensign and Doyle 2005), and complex stream morphology (Gücker

82 and Boëchat 2004) have been demonstrated to enlarge transient storage zones relative to main

83 channel cross-sectional area. In temperate streams with well-developed riparian forests,

84 autumnal litter inputs may naturally modify channel hydraulic properties, increasing transient

85 water storage (Haggard and Storm, 2003). Ecologically, leaf litter constitutes an external

86 input of energy and resources to stream communities, and provides new colonization substrata

87 for microbial communities. Therefore, an increase in transient water storage coupled to

88 enhanced microbial colonization during leaf fall can result in a hot nutrient retention moment

89   (sensu McClain et al. 2003). Mulholland et al. (1985) attributed temporal variation in

90   phosphate retention efficiency to the availability of benthic organic matter in streams,

91   showing that it was greatest during leaf fall. Nevertheless, several studies have also shown

92   that discharge is a key factor in controlling stream nutrient retention efficiency. In general,

93   rising discharge lowers nutrient retention, which may override or counterbalance other effects

94   such as the accumulation of benthic organic matter. This pattern is consistent both for

95   variation across streams (Peterson et al. 2001, Hall et al. 2002, Martí et al. 2004) and for

96   temporal variation within a stream (Butturini and Sabater 1998). Floods not only suddenly

97   increase discharge, but also dramatically affect stream biota and decrease stream nutrient

98   retention (Martí et al. 1997). Little is currently known about the subsequent recovery of

99   streams from high discharge events.

100   In this study we present insights into the combined effects of leaf litter inputs and

101   flooding on in-stream nutrient retention. The aims of this study were a) to examine how

102   autumnal accumulation of leaf litter modifies hydraulic properties of the channel, including

103   transient water storage, b) to evaluate nutrient retention response over this period, and c) to

104   examine its relationship with leaf accumulation and hydraulic properties. The occurrence of a

105   flood just after all trees had completely lost their leaves allowed us to examine flood effects

106   and subsequent responses of both hydraulic properties and in-stream nutrient retention to the

107   abrupt removal of much of the accumulated leaf litter.

108

109   **Methods**

110   *Study site*

111   The study was conducted in Riera de Santa Fe, a 2nd order tributary of La Tordera stream

112   in the natural protected area of Parc Natural del Montseny in the northeastern Iberian

113   Peninsula (50 km north of Barcelona, Spain; Fig. 1). At the study site (1180 m a.s.l.) the

114   stream drains a 2.15 km^2 catchment dominated by siliceous geology and forested primarily

115   with *Fagus sylvatica* at lower elevations and *Abies alba* at higher elevations. Mean annual

116   precipitation is 1200 mm and occurs mostly during autumn and spring. Precipitation

117   occasionally falls as snow during the coldest months (December and January). Stream flow is

118   permanent, with a mean discharge of 16.2 L s^{-1} (biweekly 2004-2005). During floods, which

119   occur mostly during spring and autumn, stream discharge can increase by more than two

120   orders of magnitude.

121   We selected a morphologically homogeneous 140 m reach, dominated by pools and

122   riffles and with a slope of 0.094 m m^{-1}. The streambed was composed of cobbles (47%),

123   boulders (25%), and pebbles (21%) with patches of gravel (5%) and sand (1%). The riparian

124   vegetation was well developed and dominated by trees (*Fagus sylvatica*) with some shrubs

125   (*Sambucus nigra*).

126

127   *Sampling strategy*

128   Between October-December 2004 we assessed the temporal variation in hydraulic and

129   nutrient retention parameters relative to variation in leaf benthic standing stocks and stream

130   discharge. The leaf fall period began in the first week of October and lasted through

131   November. We sampled benthic litter weekly in October, then at least twice weekly through

132   November until all the trees had lost their leaves. In the first week of December, a major

133   flood washed out 65% of the leaf biomass. To assess the temporal variation in hydraulic and

134   nutrient retention parameters as the flood receded, we then sampled three times a week

135   through December. In total, 21 samplings were completed during the study period (Oct-Dec

136   2004).

137   On each sampling date, we conducted a short-term conservative tracer (Cl$^-$ as NaCl)

138   addition at constant rate to estimate transient water storage parameters. In 13 additions we

139 also added NH_4-N (as NH_4Cl) and PO_4-P (as $Na(H_2PO_4)\cdot 2H_2O$) to estimate nutrient retention

140 metrics. Additions began at approximately 11:00 h and lasted until conductivity reached

141 plateau indicating complete mixing at the bottom of the reach (i.e., 2-3 h). Conductivity was

142 automatically recorded every 5 seconds using a conductivity meter (WTW®, model LF 340)

143 connected to a data logger (Campbell Scientific®) placed at the bottom of the reach. On the

144 dates of nutrient addition, we measured conductivity and collected water samples at eight

145 locations along the reach before the addition and once conductivity reached plateau. Water

146 samples for chemical analyses were collected using 50 mL syringes. At each location, two

147 replicates were collected for ambient concentrations and five for plateau concentrations.

148 Water samples were filtered in the field using Whatman® GF/F fiberglass filters (0.7 μm

149 pore diameter) and refrigerated until analysis. Ammonium (NH_4-N), nitrate (NO_3-N), nitrite

150 (NO_2-N) and soluble reactive phosphorus (SRP) concentrations were analyzed following

151 standard colorimetric methods (APHA 1998) using Bran+Luebbe® autoanalyzers (TRAACS

152 for NO_3-N, NO_2-N, and SRP, and Technicon for NH_4-N). On average, the nutrient additions

153 increased NH_4-N and SRP concentrations by 14.4±7.6 and 6.8±2.7 fold above ambient

154 concentrations, respectively. Despite this variability in enrichment levels, we did not find a

155 significant relationship between the degree of enrichment and uptake lengths or uptake

156 velocities.

157   Water temperature at each sampling station was determined several times over the course

158 of each addition and values were averaged. Discharge (Q, L s^{-1}) and average water velocity

159 (u, m s^{-1}) were measured using the time-curve conductivity data recorded at the bottom of the

160 reach. Calculation of u was done by dividing the reach length by the time needed to increase

161 the conductivity to one half of the plateau (i.e., nominal travel time). Calculation of Q was

162 based on a tracer mass balance approach.

163   Along the reach, we defined 29 channel transects at 5 m intervals. On each sampling date

164   at each transect we measured the channel wetted width (w, m), a cross-sectional profile

165   (every 20 cm) of water depth (h, m), and estimated the percentage coverage by different

166   kinds of substrata. A measure of channel roughness was calculated by solving the Darcy–

167   Weisbach equation:

168    $$f = (8gh\text{s})/u^2 \tag{1}$$

169   where f is the friction factor coefficient, g is the gravitational acceleration (9.8 m s^{-2}), and s

170   (m m^{-1}) is the streambed slope. This coefficient was used as an integrative measure of the

171   temporal changes in both discharge and leaf standing stocks.

172   Finally, on each sampling date we visually estimated the percentage of stream surface

173   that was covered by leaves and the percentage occupied by pools and riffles. These estimates

174   were made for each stream segment between every consecutive transect. Pools and riffles

175   were categorized according to flow types following River Habitat Survey guidelines (EA,

176   2003). Estimated percentages for each stream segment were then used to calculate the

177   surface area for each habitat type (i.e., pools or riffles). Leaf standing stock was determined

178   by sampling twenty-four 20 by 20 cm quadrats on each sampling date. Half of the samples

179   were collected in pools and half in riffles to account for differences in leaf accumulation

180   patterns associated with each habitat type. Leaf samples were dried and weighed to

181   determinate dry weight (g DW m^{-2}).

182

183   *Estimation of transient water storage parameters*

184   The magnitude of transient water storage zones was quantified using OTIS (One-

185   dimensional Transport model with Inflow and Storage, Runkel 1998) to obtain two

186   parameters: a) the transient water storage zone (A_s, m^2) and b) the water exchange coefficient

187   (k_1, s^{-1}) between the free flowing water and the transient storage zone.

188   The cross-sectional area of the stream channel (A) was calculated by dividing Q by u and

189   was used to obtain the ratio between the cross section of the transient water storage zone and

190   that of the surface stream channel (A_s:A). This was used to estimate k_2 (the water exchange

191   coefficient between the transient storage zone and the free flowing water) as:

192
$$\frac{A_s}{A} = \frac{k_1}{k_2}$$
(2)

193   Before applying the OTIS model to the conductivity time-series data, we calculated the

194   Damkohler number (DaI) to evaluate whether the selected reach length (L) was appropriate

195   (Wagner and Harvey 1997). DaI was estimated as:

196
$$DaI = \left((k_1 + k_2)L\right)/u$$
(3)

197   Although estimated hydraulic uncertainties are lowest at DaI values ~1.0, values of 0.5 to

198   5 have been considered acceptable (Hall et al. 2002, Ensign and Doyle 2005). If the reach

199   length is too short (DaI<0.5), not enough water enters the transient storage zone to estimate

200   transient water storage parameters properly. Conversely, DaI values >5 indicate that

201   dispersion dominates the shape of the solute concentration curve.

202   Relationships between hydraulic parameters (i.e., w, h, u, A_s, A_s:A, k_1, and k_2) and

203   discharge or leaf benthic standing stocks were examined using univariate regression analyses.

204   The level of significance considered was $p<0.05$.

205

206   *Calculation of nutrient retention metrics*

207   Two nutrient retention metrics were estimated from the short-term nutrient additions at

208   constant rate: nutrient uptake length (S_w, m) and nutrient uptake velocity (V_f, m s^{-1}), also

209   referred to as mass-transfer coefficient (Stream Solute Workshop 1990). S_w, the average

210   distance traveled by a nutrient molecule before being removed from the water column, was

211   calculated based on the variation in tracer nutrient concentrations along the reach at plateau

212   conditions (corrected for ambient levels) and by the variation in conductivity using the

213   following equation:

$$N_x = N_0 e^{-bx} \tag{4}$$

215   where N is the nutrient concentration at the first sampling station (N_0) and at the sampling

216   station located x m downstream (N_x), and b is the nutrient retention coefficient (m^{-1}). S_w is

217   the inverse of this coefficient (i.e., $S_w = -b^{-1}$) and is inversely proportional to stream nutrient

218   retention efficiency. Simple linear regression analysis was used to determine the degree of

219   significance of the S_w values (accepted significance level was $p<0.05$). The ratio between S_w

220   for N and P (i.e., S_w-NH_4:S_w-PO_4, Martí and Sabater 1996) was calculated to compare the

221   relative retention efficiency of the 2 nutrients among sampling dates.

222   We calculated V_f by dividing u times h by S_w. V_f indicates the rate at which a molecule

223   of a nutrient is removed from the water column, and is a good indicator of the stream nutrient

224   demand across variable flows (Hall et al. 2002).

225   Relationships between nutrient retention metrics (i.e., S_w and V_f) and hydrological and

226   hydraulic parameters or leaf benthic standing stocks were examined using univariate

227   regression analyses. The level of significance considered was $p<0.05$. All statistical analyses

228   were done using SPSS for Windows (version 12.0, SPSS Inc., Chicago).

229

230   **Results**

231   *Environmental characterization during the study period*

232   Over the leaf fall period (07 October to 02 December), Q remained almost constant at

233   around 8 L s^{-1}. However, just after defoliation was complete on 10 December, a large storm

234   increased Q from 7 to 124 L s^{-1} (Fig. 2A). After the flood, Q receded rapidly, but at the end of

235   the study the stream was still twice its pre-storm discharge. During the study water

236   temperature steadily declined from 12 to 3 ℃ (Fig. 2A) and was unaffected by changes in

237   discharge. The values of the friction factor f increased 3-fold during the leaf fall period from

238   205 to 657 (Fig. 2B), dramatically decreased just after the flood, and gradually increased

239   afterwards. By the end of the study, f was still 5-fold less than the pre-flood values.

240   Concentrations of SRP and NH_4-N remained low throughout the study (mean $\pm$ 1 SE were

241   14.4$\pm$8.2 μg P L^{-1} and 8.3$\pm$5.0 μg N L^{-1}, respectively; Fig. 2C). In contrast, NO_3-N

242   concentration decreased from 122 to 30 μg N L^{-1} during leaf fall, increased sharply after the

243   flood (to 252 μg N L^{-1}), and then decreased again. Due to the variation in NO_3-N

244   concentration, the DIN:P molar ratio varied from a mean of 11.3$\pm$4.0 before the flood to 45.4

245   just after the flood, after which it decreased gradually to 22.9 by the end of the study (Table

246   1). Leaves accumulated in the stream channel over the leaf fall period from 9.3 to 217.5 g DW

247   m^{-2} (Fig. 2D). After the flood, 65% of leaf benthic standing stocks were washed from the

248   reach, decreasing stocks to 77.1 g DW m^{-2}. Two weeks after the disturbance, in-channel leaf

249   standing stocks had recovered to pre-flood levels (Fig. 2D).

250

251   *Temporal variation of hydraulic parameters*

252   During leaf fall, the percentage of reach surface area dominated by pools increased from

253   51 to 67% (141 m^2 to 339 m^2; Fig. 3A). The decrease of leaf standing stocks after the flood

254   coincided with a sharp decrease in the proportion of reach surface area dominated by pools.

255   Once the flood receded, pool area increased again, but by the end of the study was still less

256   than before (Fig. 3A).

257   Because Q was relatively constant over the leaf fall period, the observed changes in the

258   relative proportion of habitat types resulted in a gradual increase of the average channel w

259   and h (Figs. 3B and 3C) and a concomitant decrease in average u (Fig. 3D). During this

260   period, the variation in these parameters was significantly related to the total biomass (g DW

261   m^{-2}) of leaves accumulated in the stream channel ($w=1.7\text{biomass}^{0.14}$, R^2=0.87, p<0.001,

262 df=12; $h=0.03\text{biomass}^{0.17}$, $R^2=0.58$, $p<0.005$, df=12; $u=0.04e^{-0.0013\text{biomass}}$, $R^2=0.53$, $p<0.005$,

263 df=12). During the flood mean w increased from 3.6 to 3.9 m, mean h decreased from 9 to 8

264 cm, and u increased 5-fold. Once the flood receded, all these parameters returned nearly to

265 pre-flood values.

266   The Damkohler number ranged between 1.7 and 4.3 (Table 2), and therefore hydraulic

267 parameters estimated with the OTIS model were considered reliable. A_s gradually increased

268 over the leaf fall period (Table 2) and positively correlated with leaf benthic standing stocks

269 ($A_s=0.4e^{0.002\text{biomass}}$, $R^2=0.46$, $p<0.050$, df=8). In contrast, k_1 and k_2 slightly decreased during

270 this period and were negatively correlated with leaf benthic standing stocks ($k_1=0.0004-5\times10^{-5}\ln(\text{biomass})$,

271 $R^2=0.59$, $p=0.010$, df=8 and $k_2=0.0008e^{-0.003\text{biomass}}$, $R^2=0.58$, $p<0.010$, df=8).

272 The flood had opposite effects on the hydraulic parameters (Table 2). After the flood, A_s

273 decreased 2.4-fold and k_1 and k_2 increased 4.2 and 10-fold, respectively. During discharge

274 recession, A_s tended to increase and k_1 and k_2 tended to decrease, but at the end of the

275 sampling period A_s had not fully recovered to pre-flood values and k_1 and k_2 were still 2

276 times greater than pre-flood values.

277   Combining all dates, A_s:A and A_s were negatively correlated with Q ($A_s:A=0.27e^{-0.03Q}$,

278 $R^2=0.63$, $p<0.001$, df=15; $A_s=0.05e^{-0.02Q}$, $R^2=0.36$, $p<0.050$, df=15), while k_1 and k_2 were

279 positively correlated to Q ($k_1=6.4\times10^{-5}+9.1\times10^{-6}Q$, $R^2=0.42$, $p=0.005$, df=15; and

280 $k_2=0.0003e^{0.07Q}$, $R^2=0.69$, $p<0.001$, df=15). No transient water storage parameter was

281 significantly related to litter accumulation when all the sampling dates were combined. Much

282 of the variability in A_s, k_1, and k_2 was explained by the friction factor coefficient, f ($A_s=0.013f^{0.219}$,

283 $R^2=0.74$, $p<0.001$, df=15; $k_1=0.001f^{-0.33}$, $R^2=0.69$, $p<0.001$, df=15; $k_2=0.009f^{-0.48}$,

284 $R^2=0.77$, $p<0.001$, df=15).

285

286 *Temporal variation of nutrient retention metrics*

287   During the leaf fall period, S_w did not show a clear temporal trend for either nutrient. On

288   average, S_w-PO_4 and S_w-NH_4 were relatively short (i.e., mean±1 SE were 219±57 m and

289   49±11 m, respectively). S_w-NH_4 was on average 4 times shorter than S_w-PO_4; thus, the S_w-

290   NH_4:S_w-PO_4 ratio was consistently <1 (Table 1). The flood caused a dramatic increase in S_w

291   for both nutrients (Fig. 4A). This effect was greater for S_w-NH_4 (8.0 times longer than pre-

292   flood values) than for S_w-PO_4 (6.7 times longer than pre-flood values). After the flood, S_w of

293   the two nutrients gradually shortened with stream discharge, almost returning to average pre-

294   flood values by the end of the study. The recovery rate, estimated from post-flood decrease in

295   S_w over time, for S_w-PO_4 (-1.01 d^{-1}) was significantly greater than that for S_w-NH_4 (-0.89 d^{-1};

296   *p*<0.05, Wilcoxon test for 2 related variables).

297   Values of V_f-NH_4 were on average 3.0±1.2 times greater than those of V_f-PO_4 (Table 1).

298   V_f tended to gradually increase as leaves accumulated in the channel (Fig. 4B). The flood

299   decreased both V_f-PO_4 and V_f-NH_4 (1.2 times and 1.4 times, respectively). Post-flood, V_f-

300   PO_4 increased gradually, reaching slightly greater values than pre-flood. V_f-NH_4 remained

301   low after the flood, gradually increasing as discharge receded (Fig. 4B). Regression analyses

302   showed that V_f-PO_4 was related to leaf benthic standing stocks and temperature (Table 3). V_f

303   -NH_4 was negatively correlated to DIN concentration and the DIN:P molar ratio (Table 3).

304   No significant relationship was found between V_f and SRP concentration. Both V_f-PO_4 and

305   V_f-NH_4 were positively related to A_s (Fig. 5).

306

307   **Discussion**

308   *Influence of leaf litter inputs and the flood on hydraulic parameters*

309   The large quantity of accumulated leaves over the leaf fall period, coinciding with low

310   and stable discharge, affected the relative dominance of habitat type and hydraulic

311   characteristics of the reach. Leaf inputs tended to accumulate at the head of the riffles

14

312   favoring the formation of small leaf-debris dams, which increased the upstream pool surface

313   area. Shifting proportions of habitat types presumably induced the observed change in

314   hydraulic properties. As leaves accumulated on the stream channel, it became wider and

315   deeper, water velocity decreased, and channel roughness increased. These changes caused a

316   gradual change in transient water storage parameters. The increase in A_s indicates an

317   increased volume of water in transient storage zones, consistent with previous findings on the

318   physical effect of leaf litter accumulation (Hart et al. 1999, Haggard and Storm 2003, Jin and

319   Ward 2005). In addition, the gradual decrease in k_1 and k_2 during the leaf fall period indicates

320   weakened connectivity between the slow and fast flowing hydrologic compartments.

321   Together, these changes in the hydraulic template, mostly driven by litter inputs, increased the

322   water residence time and enhanced the opportunity for nutrient uptake by microbial

323   communities.

324   Flooding greatly reduced the influence of litter accumulation on channel hydraulics.

325   While changes driven by leaf litter inputs were gradual (weeks), changes due to the flood

326   were abrupt (days). The abrupt increase in discharge significantly increased water velocity,

327   decreased relative transient water storage (i.e., reduced A_s and A_s:A) and increased

328   connectivity between low and high flow hydrologic compartments (i.e., greater k_1 and k_2).

329   These findings are similar to those of Martí et al. (1997) for a Sonoran Desert stream

330   (Arizona, USA). The changes observed in the study stream just after the flood could be the

331   result of both the washout of a high proportion of leaves from the channel, which reduced

332   surface obstructions, as well as an increase in the cross-sectional area (A) of the channel.

333   These changes likely reduced the influence of streambed topography on surface water flow,

334   decreasing the relative importance of A_s. Conversely, following recession, transient water

335   storage parameters returned to pre-flood values faster than discharge. This was probably due

336   to lateral leaf litter inputs from adjacent riparian soil, which created zones of slow moving

337   water in the stream channel. These results suggest that most variation in transient water

338   storage was associated with surface water compartments rather than modification of

339   subchannel flow paths in the hyporheic zone.

340   Considering all sampling dates, stream discharge accounted for the largest proportion of

341   the variability in the hydraulic parameters. However, when we focus on low flow conditions,

342   our results indicate that leaf standing stocks primarily influenced stream hydraulics. Variation

343   in transient water storage parameters was related to leaf benthic standing stocks only during

344   leaf fall, when discharge was low; however, this relationship was not significant for the whole

345   study period. In contrast, we found a negative relationship between A_s:A and discharge using

346   the complete data set. In a study with similar results, D'Angelo et al. (1993) argued that at

347   high discharge transiently stored water is more quickly incorporated into the main flow, but at

348   low discharge is stored more independently of the main flow. Results from previous studies

349   relating A_s and Q are inconsistent. While no relationship has been found for some streams

350   (e.g., Hart et al. 1999), others agree with the present study (Valett et al. 1996, Martí et al.

351   1997, and Butturini and Sabater 1999). Similarly, the positive relationship between k_1 and k_2

352   and discharge found in this study agrees with some previous studies (Hart et al. 1999), but

353   contrasts with others who either found no relationship between exchange coefficient and

354   discharge (Butturini and Sabater 1999, Hall et al. 2002, Jin and Ward 2005) or found an

355   inverse relationship (D'Angelo et al. 1993, Martí et al. 1997).

356   In order to test if our results obey a general pattern, we compiled data from 17 studies

357   done across several streams worldwide (*n*=187) to see if a significant relation between

358   transient water storage parameters and discharge emerged. Results from this analysis revealed

359   significant relationships between these parameters and streamflow across all the streams

360   considered (Fig. 6) supporting results from our study. Nevertheless, the percentage of

361   variation of transient water storage parameters explained by discharge considering the

362   compiled data was less than that obtained considering only data from the present study,

363   probably reflecting the variable location and nature of the transient water storage zones in

364   each particular stream.

365

366   *Combined effects of leaf litter inputs and the flood on nutrient retention*

367   The two nutrient retention metrics (S_w and V_f) helped to determine the relative influence

368   of both leaf inputs and flooding on stream nutrient retention. Leaf litter inputs played an

369   important role in PO_4 and NH_4 retention during stable Q although abrupt flooding and

370   subsequent flood recession largely controlled the overall variability in nutrient retention. To

371   our knowledge, this study is the first of its kind with sufficiently intensive sampling to

372   evaluate stream nutrient retention to gradual and abrupt changes over a short-time scale.

373   The observed nutrient retention responses (both S_w and V_f) for PO_4 and NH_4 were in line

374   with headwater streams elsewhere (e.g., see Peterson et al. 2001, Hall et al. 2002, Webster et

375   al. 2003). Retention of both nutrients was relatively high during leaf fall. In addition, the S_w-

376   NH_4:S_w-PO_4 ratios, which were consistently <1, indicate greater efficiency in retaining NH_4

377   than PO_4 regardless of leaf benthic standing stocks or stream discharge. A similar pattern has

378   previously been reported from another stream in the same region (Martí and Sabater, 1996).

379   In contrast to our expectations, PO_4 and NH_4 retention efficiencies (i.e., S_w) remained

380   relatively constant over the leaf fall period, when discharge was relatively constant and low,

381   despite the clear increase in the additional energy resource from the leaf inputs and in

382   transient water storage size. The lack of relationship between S_w-PO_4 and leaf litter

383   accumulation agrees with D'Angelo et al. (1991), but contrasts with other studies, showing

384   greater P retention efficiency during periods of benthic organic matter accumulation

385   (Mulholland et al. 1985, Haggard and Storm 2003). Differences could be explained in part by

386   the temporal scale of each study. While previous studies were temporally extensive (annual),

387　the present study was temporally intensive (seasonal). Moreover, the relationship between

388　NH_4 retention efficiency and temporal shifts in benthic organic matter has seldom been

389　addressed.

390　　　Nutrient retention efficiency is affected by both hydromorphologic factors and

391　biogeochemical processes. V_f corrects S_w for depth and velocity (Stream Solute Workshop

392　1990), and was more sensitive to benthic leaf accumulation and its influence on transient

393　water storage parameters than S_w. The variation in V_f for both nutrients followed the increase

394　in transient water storage (A_s) both before and after the flood. At these two moments

395　transient water storage increased and there was a greater decoupling between fast and slow

396　hydrologic compartments (i.e. reduced k_1 and k_2). These conditions may have favored the

397　interaction between stream communities and available nutrients, and thus increased stream

398　nutrient demand. In addition, because leaf inputs increased the availability of energy-rich

399　substrata, increased nutrient demand could also be directly associated with the development

400　of microbial communities. Ensign and Doyle (2005) similarly observed a greater nutrient

401　demand as superficial transient storage increased after baffles were installed in a channel.

402　Other studies have found no significant relationships between transient storage parameters

403　and V_f (e.g., Hall et al. 2002, Webster et al. 2003). In those studies, however, relationships

404　were compared between different streams; therefore, the lack of relationships could be

405　attributed to differences in the nature of the transient water storage and the associated

406　biogeochemical processes.

407　　　The same arguments presented above could also explain the subtle differences in

408　temporal patterns observed between PO_4 and NH_4 uptake velocities. For instance, temporal

409　variation in V_f-NH_4 was influenced by the increase in transient storage volume just like V_f-

410　PO_4, but it was also negatively influenced by the availability of dissolved inorganic nitrogen

411 (mostly in the form of NO_3). Hall et al. (2002) found similar results and suggested that high

412 NO_3 concentration may alleviate microbial demand for NH_4, lowering V_f-NH_4.

413   The greatest temporal variability in nutrient retention metrics was related to the flood and

414 its subsequent recession. Nutrient retention efficiency of PO_4 and NH_4 was significantly

415 reduced after the flood. The increased discharge would be partly responsible (Martí et al.

416 1997). The flood also flushed out a high percentage of leaves, removing channel obstructions

417 and exporting part of the microbial community. These effects likely contributed to the

418 decreased post-flood nutrient demand. Therefore, the combination of physical factors (i.e.,

419 increase in water depth and velocity, and reduction in transient water storage) and biological

420 consequences (i.e., decrease in nutrient demand) resulted in reduced post-flood retention

421 efficiency. The stream recovered relatively fast from disturbance. Based on the estimated

422 recovery rates, average pre-flood S_w values for PO_4 and NH_4 were reached 22 and 47 days

423 after the flood, respectively. Theses values are within the range of those reported for S_w-NO_3

424 in Sycamore Creek (Martí et al. 1997). In that study, the recovery in nutrient retention was

425 attributed to a fast post-flood growth of algal communities. In the present study, S_w recovery

426 could be associated with a significant increase in NH_4 and PO_4 demand as discharge declined

427 and leaves reaccumulated. Return to base flow stream discharge took 64 days, much longer

428 than for S_w. This indicates that biogeochemical processes significantly contributed to the

429 high resiliency (i.e., fast recovery capacity) in nutrient retention, presumably enhanced by the

430 lateral leaf input.

431   In summary, the seasonal litter input not only modified the physical template of the

432 stream reach, but also increased PO_4 and NH_4 demand, either directly through microbial

433 demand or through increasing transient storage. The flood altered channel hydraulic

434 properties and nutrient retention in the stream. However, once the flood receded, the stream

435 exhibited fast recovery in nutrient retention, especially for PO_4, probably enhanced by the

436   lateral input of riparian leaf litter. Therefore, the net contribution of leaf inputs to headwater

437   stream metabolism over the leaf fall period appears to depend on the timing of floods relative

438   to leaf fall. This has implications in the context of climate change because both the timing of

439   leaf fall and flood regimes are expected to be influenced by climate change (Christensen and

440   Christensen 2004). For example, Peñuelas et al. (2002) have reported that leaf fall has been

441   delayed an average of 13 days relative to 1952 in the study area. Stream hydrologic regimes

442   are also expected to change (McCarthy et al. 2001), with projections for the study region

443   indicating an increase in extreme episodic storms and droughts. These changes may alter the

444   timing of leaf fall and floods, with varying impacts on nutrient retention. Less flooding during

445   the season of leaf fall would increase the residence time of leaves in the stream channel,

446   enhancing nutrient retention. Conversely, an increase in flood frequency during leaf fall

447   would result in leaf litter being periodically flushed from the headwaters and exported

448   downstream to zones of higher flow and lower nutrient retention capacity.

449

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Table 1. Temporal variation in nutrient uptake length (S_w), uptake length ratio (S_w NH$_4$-N:S_w PO$_4$-P), nutrient uptake velocity (V_f), uptake velocity ratio (V_f NH$_4$-N:V_f PO$_4$-P), and DIN:P molar ratio during the study period.

Date	S_w (m)		S_w ratio	V_f (mm min^{-1})		V_f ratio	DIN:P molar ratio
	PO$_4$-P	NH$_4$-N		PO$_4$-P	NH$_4$-N		
Leaf fall period							
07 Oct 04	287.3	60.5	0.21	0.40	1.89	4.75	14.8
21 Oct 04	135.8	51.3	0.38	0.71	1.87	2.65	6.6
04 Nov 04	223.1	44.4	0.20	0.71	3.56	5.03	9.3
11 Nov 04	251.0	55.7	0.22	0.49	2.22	4.51	14.9
26 Nov 04	196.6	51.9	0.26	0.66	2.49	3.79	11.5
30 Nov 04	-	30.0	-	-	5.70	-	10.3
Post-flood period							
13 Dec 04	1312.2	416.4	0.32	0.55	1.73	3.15	45.4
15 Dec 04	825.2	551.5	0.67	0.68	1.01	1.50	32.9
17 Dec 04	665.6	299.9	0.45	0.68	1.50	2.22	24.0
19 Dec 04	585.2	240.8	0.41	0.55	1.34	2.43	24.0
21 Dec 04	429.3	227.6	0.53	0.61	1.15	1.89	22.8
23 Dec 04	287.2	148.6	0.52	0.88	1.70	1.93	21.0
29 Dec 04	202.5	92.5	0.46	1.16	2.54	2.19	22.9

Table 2. Temporal variation of hydraulic parameters during the study period. Discharge (Q), dispersion (D), cross-sectional area of the transient storage (A_s), transient storage exchange rates (k_1, from channel to transient storage and k_2, from transient storage to main channel), ratio of the cross-sectional area of the transient storage zone to the cross-sectional area of the stream (A_s:A), and Damkohler number (DaI).

Date	Q (L s^{-1})	D (m^2 s^{-1})	A_s (m^2)	k_1x10^{-3} (s^{-1})	k_2x10^{-3} (s^{-1})	A_s:A	DaI
Leaf fall period							
14 Oct 04	6.53	0.07	0.036	0.25	0.88	0.29	3.96
18 Oct 04	8.90	0.08	0.045	0.14	0.61	0.23	2.58
21 Oct 04	6.19	0.09	0.039	0.14	0.54	0.26	2.79
28 Oct 04	20.76	0.14	0.042	0.08	0.54	0.07	2.28
02 Nov 04	9.70	0.08	0.036	0.14	0.82	0.17	3.33
04 Nov 04	8.18	0.10	0.041	0.12	0.56	0.22	2.55
16 Nov 04	8.34	0.08	0.050	0.10	0.43	0.23	2.44
19 Nov 04	8.55	0.07	0.063	0.12	0.42	0.29	2.44
23 Nov 04	7.76	0.08	0.054	0.10	0.39	0.26	2.20
30 Nov 04	6.69	0.07	0.053	0.12	0.40	0.30	2.31
Post-flood period							
13 Dec 04	28.72	0.22	0.022	0.50	4.05	0.12	4.27
15 Dec 04	23.65	0.23	0.029	0.22	1.48	0.15	2.00
17 Dec 04	18.94	0.20	0.032	0.20	1.08	0.18	1.74
19 Dec 04	15.34	0.18	0.033	0.21	1.02	0.21	1.95
21 Dec 04	14.25	0.17	0.030	0.21	1.11	0.19	2.30
23 Dec 04	15.47	0.17	0.041	0.20	0.93	0.22	2.13
29 Dec 04	11.61	0.15	0.043	0.19	0.75	0.25	2.18

Table 3. Regressions of uptake velocities on environmental variables (leaf biomass as dry weight, water temperature, dissolved inorganic nitrogen concentration (DIN) and DIN:P molar ratio) during the study period period. no sign. = no significant relationship.

	V_f-PO_4 (mm min^{-1})	V_f-NH_4 (mm min^{-1})
biomass (g DW m^{-2})	V_f-PO_4=0.42biomass-0.002 R^2=0.55, $p<0.010$, df=10	no sign.
temperature (ºC)	V_f-PO_4=1.40-0.38ln(temp) R^2=0.47, $p<0.050$, df=10	no sign.
[DIN] (ppb)	no sign.	V_f-NH_4=14.75-2.73ln[DIN] R^2=0.75, $p<0.001$, df=11
DIN:P	no sign.	V_f-NH_4=8.82[DIN:P]$^{-0,52}$ R^2=0.37, $p<0.050$, df=11

568   Fig. 1. Map showing general location of Riera de Santa Fe in Europe and in the La Tordera

569   catchment.

570   Fig. 2. Temporal variation of (A) stream discharge and water temperature, (B) Darcy–

571   Weisbach friction factor, (C) ambient nutrient concentrations, and (D) leaf standing stocks in

572   the stream channel during the study period. The break in the lines corresponds to the onset of

573   flooding.

574   Fig. 3. (A) Surface area of the stream channel dominated by pools, (B) average channel

575   wetted width, (C) average water depth, and (D) average water velocity during the study

576   period. The break in the lines corresponds to the onset of flooding.

577   Fig. 4. (A) Temporal variation of uptake length (S_w) and (B) uptake velocity (V_f) over the

578   study period for PO_4-P (squares) and NH_4-N (circles). The abrupt increases in nutrient uptake

579   lengths coincided with the onset of flooding.

580   Fig. 5. Relationships between transient storage and nutrient uptake velocities (V_f-

581    $PO_4=0.29e^{25.93As}$, $R^2=0.59$, $p<0.050$, df=7; V_f-$NH_4=0.33e^{48.37As}$, $R^2=0.65$, $p=0.005$, df=8) for

582   PO_4-P (squares) and NH_4-N (circles).

583   Fig. 6. Relationships between stream discharge and transient storage parameters: (A) transient

584   storage ratio, A_s:A=0.51Q-0.28, $R^2=0.14$, $p<0.001$, df=185, (B) exchange ratio from transient

585   storage to main channel, $k_1=0.0002e^{-0.0013Q}$, $R^2=0.05$, $p=0.002$, df=175, and (C) exchange ratio

586   from main channel to transient storage, $k_2=-0.0003+0.001lnQ$, $R^2=0.17$, $p<0.001$, df=170.

587   Closed circles are data from the present study and open circles are data from: Bencala and

588   Walters (1983), Bencala et al. (1984), Bencala et al. (1990), Broshears et al. (1993),

589   D'Angelo et al. (1993), Martí et al. (1997), Morrice et al. (1997), Mulholland et al. (1997),

590   Butturini and Sabater (1999), Hart et al. (1999), Hall et al (2002), Haggard and Storm (2003),

591   Harvey et al. (2003), Webster et al. (2003), Ensign and Doyle (2005), Jin and Ward (2005),
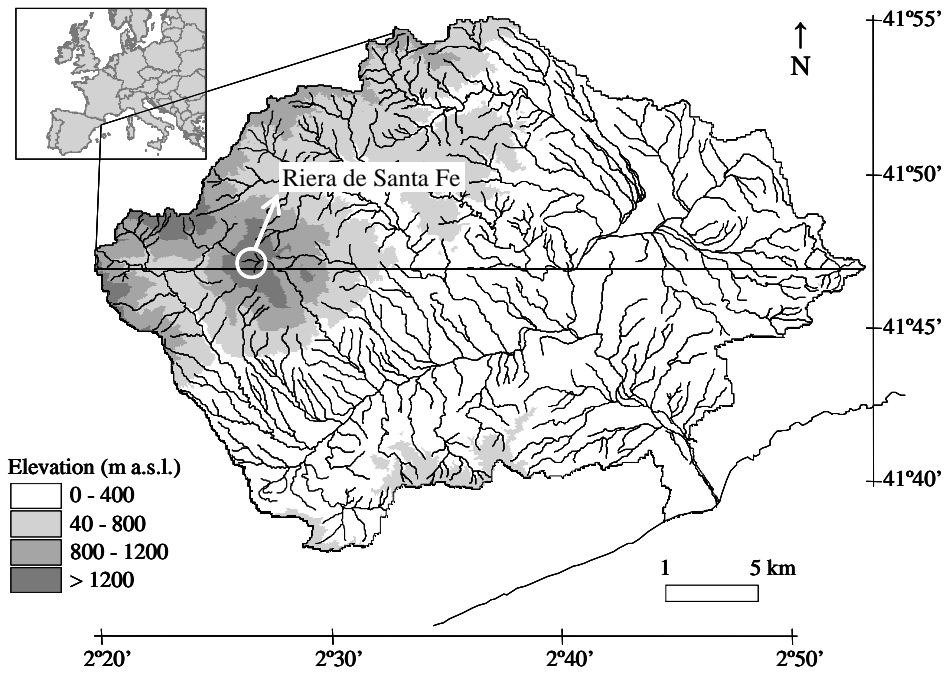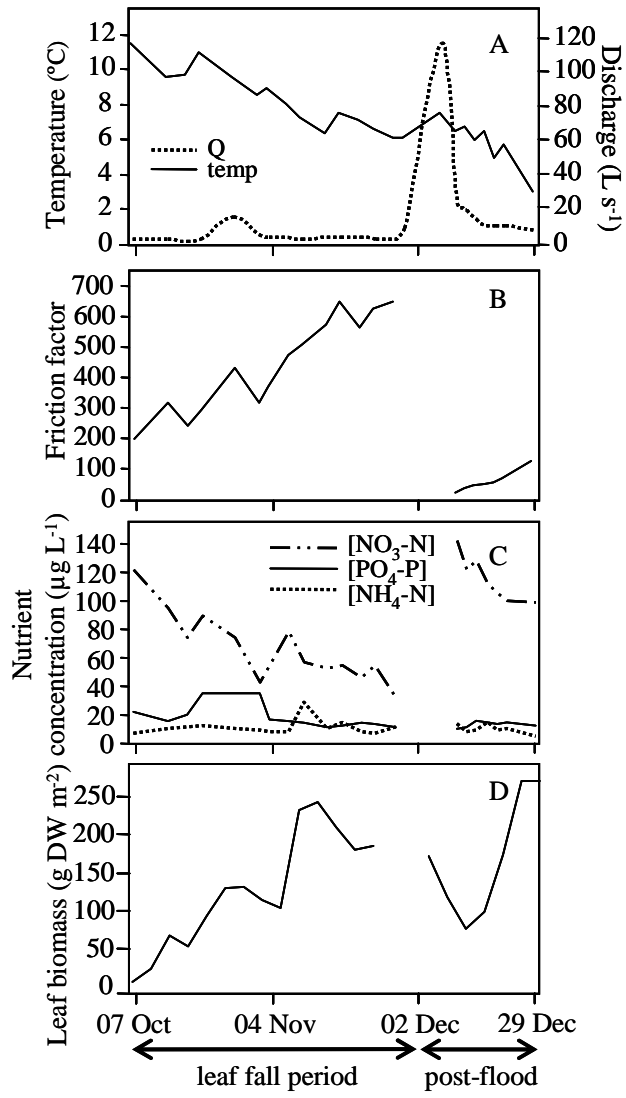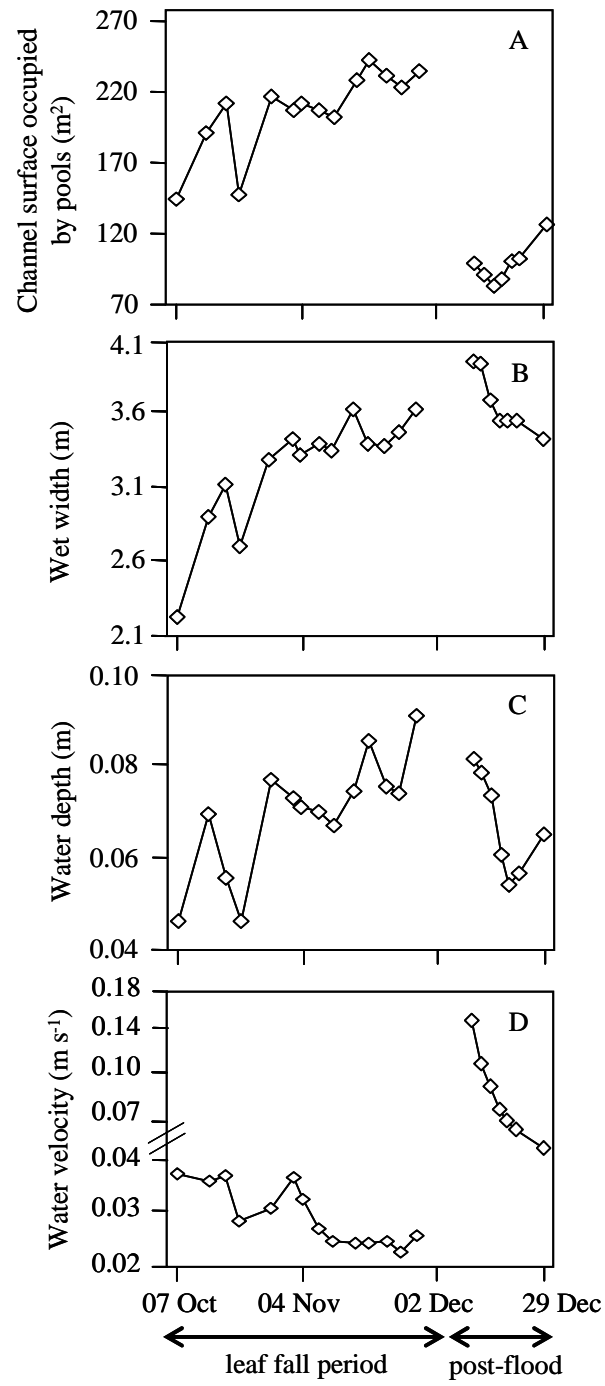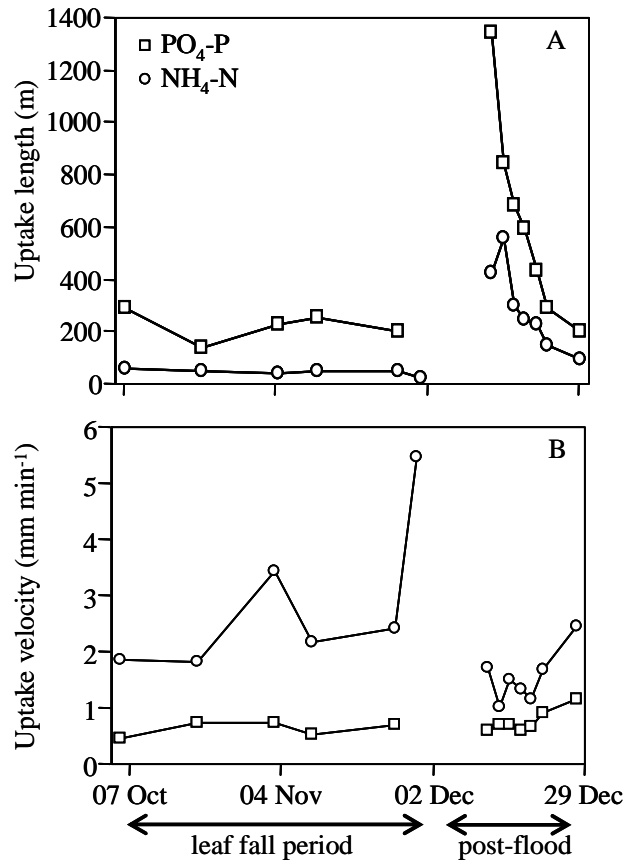
592   and Lautz et al. (2006).

Fig. 1

Fig. 2

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Fig. 3

Fig. 4

Fig. 5

Fig. 6