

Spatial analysis of plant detritus processing in a Mediterranean River type: the case of the River Tirso Basin, Sardinia, Italy

Maurizio Pinna, Franca Sangiorgio, Alessio Fonnesu, Alberto Basset

(Department of Biological and Environmental Sciences and Technologies, University of Lecce, 73100 Lecce, Italy. E-mail: maurizio.pinna@unile.it)

Abstract: The river continuum concept represents the most general framework addressing the spatial variation of both structure and function in river ecosystems. In the Mediterranean ecoregion, summer drought events and dams constitute the main sources of local disturbance to the structure and functioning of river ecosystems occurring in the river basin. In this study, we analysed patterns of spatial variation of detritus processing in a 7th order river of the Mediterranean ecoregion (River Tirso, Sardinia-Italy) and in three 4th order sub-basins which were exposed to different summer drought pressures. The study was carried out on *Phragmites australis* and *Alnus glutinosa* leaf detritus at 31 field sites in seasonal field experiment. Detritus processing rates were higher for *Alnus glutinosa* than for *Phragmites australis* plant detritus. Processing rates of *Alnus glutinosa* leaves varied among seasons and study sites from 0.006 d^{-1} to 0.189 d^{-1} and those of *Phragmites australis* leaves ranged from 0.0008 d^{-1} to 0.102 d^{-1} , with the lowest values occurring at sites exposed to summer drought. Seasons and sites accounted for a significant proportion of such variability. Alder detritus decay rates generally decreased with increasing stream order, while reed detritus decay rates generally increased on the same spatial gradient. Summer drought events affected these spatial patterns of variation by influencing significantly the decay rates of both plant detritus. The comparisons among and within sub-basins showed strong negative influence of summer drought on detritus processing rates. Similarly, in the entire River Tirso basin decay rates were always lower at disturbed than at undisturbed sites for each stream order; decay rates of reed detritus remained lower at those sites even after the end of the disturbance events, while alder decay rates recovered rapidly from the summer drought perturbations. The different recovery of the processing rates of the two leaves could also explain the different patterns of spatial variation observed between the two leaves.

Keywords: ecosystem processes; spatial patterns; disturbance; Mediterranean ecosystem type

Introduction

Spatial variations of the main structural and functional features of the river ecosystems are addressed *a priori* by the “river continuum concept” (Vannote, 1980) in relation to the directional variation of the stream order from the river source to the river mouth. The “river continuum concept” and its corollaries (Elwood, 1983; Ward, 1983) treat the stream-river profile as a continuum of physical gradients and associated biotic adjustments. Streams are envisioned as longitudinally linked systems where ecosystem processes in downstream areas are linked to those in upstream areas by the unidirectional flow of water and materials. Therefore, the original concept and the subsequent modifications (Minshall, 1985; Statzner, 1985) provide a strong theoretical base for developing a holistic perspective for lotic ecosystems. On the other hand, there is also an experimental basis for examining river ecosystems as a series of patches where community and processes vary locally, rather than on a gradient or along a continuum (Frissell, 1986; Hawkins, 1985; Huet, 1949; Illies, 1961) and the boundaries between these patches are readily detected on various spatial and temporal scales (Forman, 1986; Frissell, 1986; Wiens, 1985). Detritus dynamics support up to 95% of stream energetics (Fisher, 1973). Nevertheless, the variations in detritus input, availability and processing rates on the longitudinal gradient in streams along the river continuum are not yet clear. Natural perturbations or anthropogenic pressure are also likely to disrupt locally the river continuum (Hynes, 1970; Baxter, 1977; Petts, 1984; Resh, 1988; Gasith, 1999).

The allochthonous input to the river ecosystems has generally been found by the latitude and by annual precipitation occurring in the catchments area rather than by the stream order on a river continuum (Benfield, 1997). However, a gradual reduction of the litterfall input with increasing stream order has

been observed inside regional areas (Conners, 1984) due both to direct allochthonous detritus and to lateral inputs (Naiman, 1987). Consistently, the availability of allochthonous detritus seems to be higher in low order than in higher order streams (Cummins, 1988) partly because lower order streams have greater retentiveness for the plant material derived from riparian vegetation (Jones, 1991; Snaddon, 1992).

Most of the studies dealing with the plant detritus dynamics in streams ecosystems have focused on detritus processing rates (Graca, 1993). The influence of many factors, including temperature (Reice, 1974; Guthrie, 1982), acidification (Friberg, 1980; Carpenter, 1983), water chemistry (Rounick, 1983; Newbold, 1983; Brock, 1985; Burton, 1985; Chauvet, 1988; Thompson, 1989), biotic factors (Anderson, 1979; Rossi, 1985; Taylor, 1989; Blair, 1990; Cummins, 1989), pollution (Kaushik, 1971) and disturbance (Resh, 1988; Richardson, 1990; Gurtz, 1988) on the detritus processing rate has been addressed and analyzed at local scale.

Much less attention has been paid to describing the spatial variation of processing rates along the river continuum and available studies report contrasting results, i.e. inverse relationships between decay rates and stream order (Naiman, 1987), direct relationships (Horton, 1991) and unclear relationships (Hill, 1992). On the other hand, the spatial distribution of benthic detritivore functional groups along the river continuum (Cummins, 1989) would lead one to expect an inverse relationship between processing rates and stream order.

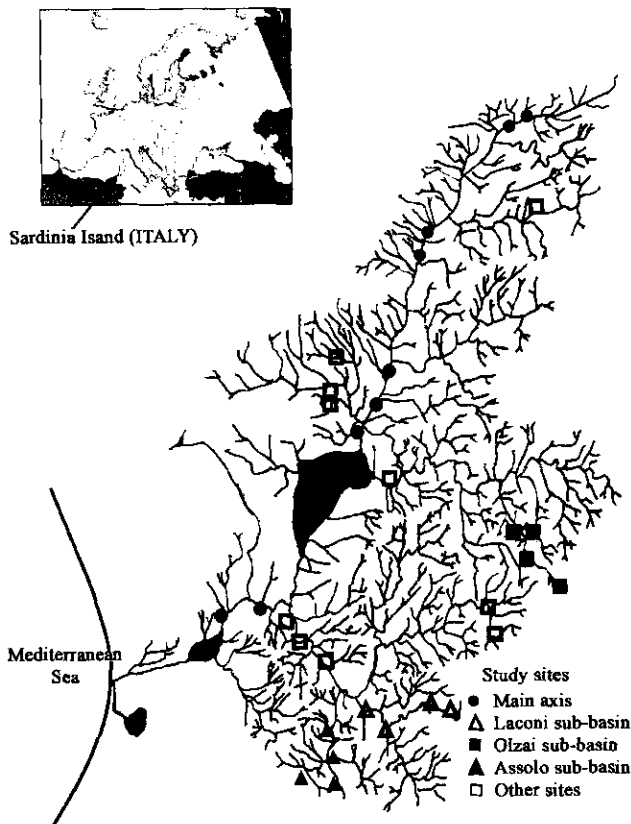


Fig. 1 The River Tirso basin and location of the study sites

Local or regional disturbance pressures may constitute a major source of observed variability of these relationships but the available data are insufficient to show general patterns in relation to disturbance. In

the Mediterranean climate regions, the streams are physically, chemically, and biologically dependent on sequential, predictable, seasonal events that affect the water flow, temporally drying up large areas of the river basin over an annual cycle (Gasith, 1999). These events can affect the longitudinal patterns of variation of the ecosystem processes in the river basin and community structure.

In this study, we analyzed the pattern of spatial variation of the detritus processing rates in a river basin in a Mediterranean ecoregion, along a river continuum and within a gradient of desiccation. Since summer drought is known to be a relevant disturbance factor in these ecosystems (Gasith, 1999), the role of summer drought events was specifically tested on three small 4th order sub-basins, with different hydrology and stream discharge rates. The aim of this study was to test the relevance of the river continuum concept for detritus processing in Mediterranean climate type river ecosystems. To this aim we analyzed the decomposition processes of two leaf species, *Alnus glutinosa* (L.) Gaertner and *Phragmites australis* (Cav.) Trin. ex Steudel, along a spatial gradient of variation in the river Tirso basin. The two plant species have a different distribution in the basin along the stream banks.

1 Site description

This study was carried on the River Tirso Basin. The River Tirso is the most important river on the island of Sardinia (Italy). The main axis of the river is 159 km long, with a catchment area of 3376 km² (Sanna, 1989) (Fig.1).

The River Tirso has its main source at 880m a. s. l., flows in the mid-west of Sardinia, over Paleozoic granites and basalt, and flows into the Oristano Gulf (Fassò, 1986). Rock permeability within the basin is typically medium-low and is related mainly to superficial alteration and, locally, to cracking. Average precipitation in the basin over the last 30 years has been close to 800 mm rain per year. The distribution of rainfall is generally heterogeneous during the year with a period of summer drought; 74% of rainfall occurs during the late autumn-winter period (Fig.2). This rainfall distribution is typical of the Mediterranean climatic zone. The scarce rainfall in the summer-early fall season results in the complete

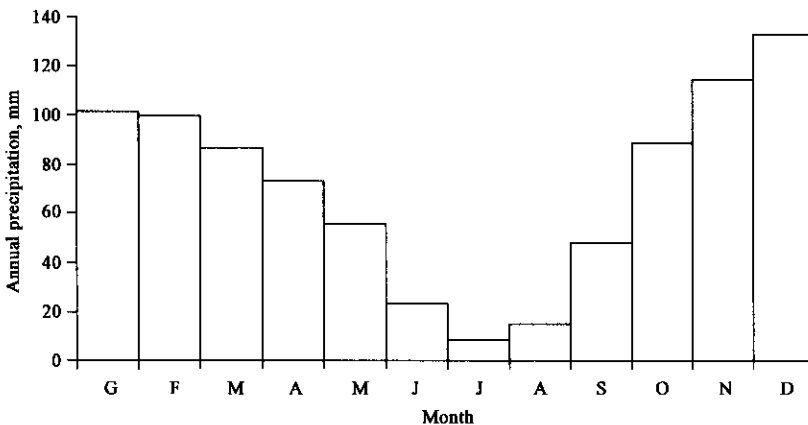


Fig.2 Annual distribution of water precipitation in the River Tirso catchment area

desiccation of the lower order branches in the River Tirso basin, particularly of the streams flowing across the mountains.

The hydrographic analysis of the River Tirso was carried out using maps of the Geographic Military Institute (I.G.M.) on a scale of 1:100000. At this scale, the River Tirso reaches the 7th order at its mouth. The main axis is divided into three different geo-morphological stretches: the first stretch starts at the source, is about 60 km long, is sinuous and has an average slope of 12%; the next 30 km stretch

flows linearly with an average slope of 30% , and the last stretch of 50 km flows over the Oristano plain with an average slope of 1% (Fassò, 1986) .

2 Materials and methods

The study was carried out seasonally using the leaf pack technique (Petersen, 1974) at 31 study sites (Table 1) distributed along the main axis and its tributaries. The study sites were divided into five main groups: (1) 9 sites on the main River Tirso axis, on river branches ranging from the 3rd to the 7th order; (2) 4 study sites in the Olzai sub-basin, one per order on stream branches ranging from the 1st to the 4th stream order; (3) 4 study sites in the Laconi sub-basin, one per order on stream branches ranging from the 1st to the 4th stream order; (4) 4 study sites in the Assolo sub-basin, one per order on stream branches ranging from the 1st to the 4th stream order; and (5) 10 study sites on other tributaries of the River Tirso were included, grouping sites distributed among different order tributaries. The spatial distribution of the study sites in each group was defined according to a random sampling design. Geographic location, stream order, altitude and distance from the source and from the mouth were assessed at each study site, as reported in Table 1.

Table 1 Sampling sites in the River Tirso Basin. In the table, the main physical features of field sites are reported: Acronym of field site (A); Topographic co-ordinates (B); Stream order (C); Altitude (m. a.s.l.) (D); Distance from source (km) (E); Distance from mouth (km) (F). The asterisks indicate the sub-sample of the study sites where we studied the *Alnus glutinosa* decay rate contemporary at *Phragmites australis* decay rate. The study sites are divided into 5 groups: main axis of the River Tirso indicate as Tirso; three sub-basins indicate as Assolo, Olzai, Laconi and the last group comprising all study sites selected randomly in remaining branches of basin

A	B		C	D	E	F		
Assolo 1	39	9°35'N	8	0°53'E	1	250	1.0	61.6
Assolo 2	39	8°22'N	8	2°16'E	2	230	5.0	61.4
Assolo 3	39	1°40'N	8	3°08'E	3	210	1.5	61.2
Assolo 4	39	9°32'N	8	4°23'E	4	200	3.5	61.0
* Olzal 1	40	9°50'N	9	8°00'E	1	350	0.3	69.9
* Olzal 2	40	0°18'N	9	8°05'E	2	350	2.9	71.7
* Olzal 3	40	0°25'N	9	7°13'E	3	325	4.7	69.1
* Olzal 4	40	0°35'N	9	6°43'E	4	192	7.1	65.7
* Laconi 1	39	1°50'N	9	4°13'E	1	793	0.2	82.6
* Laconi 2	39	2°15'N	9	5°11'E	2	760	1.3	81.4
* Laconi 3	39	2°40'N	9	4°28'E	3	720	5.4	89.7
* Laconi 4	39	3°28'N	9	1°58'E	4	500	19.1	76.1
Atzara	40	3°30'N	9	3°23'E	2	583	4.0	95.2
Borore	40	0°50'N	8	7°38'E	2	349	10.7	72.6
Dualchi	40	5°10'N	8	4°48'E	3	249	8.8	84.2
Anela	40	5°48'N	9	1°23'E	3	359	18.7	118.2
Siamanna	39	5°30'N	8	9°40'E	3	28	18.8	23.2
Sorgono	40	3°40'N	8	2°38'E	3	513	4.0	91.4
* Tirso A	40	1°42'N	9	3°58'E	3	550	14.2	146.2
* Tirso B	40	1°52'N	9	2°38'E	3	520	16.3	144.1
Murtazzolu	40	1°38'N	8	4°40'E	4	183	14.8	77.8
Villaurbana	39	3°50'N	8	8°23'E	4	79	7.6	33.4
Tirso C	40	5°44'N	9	1°10'E	4	280	29.8	129.4
* Tirso D	40	5°48'N	9	1°14'E	4	296	29.5	129.7
* Tirso E	40	0°23'N	9	1°46'E	5	192	61.8	98.9
* Tirso F	40	5°15'N	9	1°28'E	5	163	76.1	84.4
* Mannu	39	8°12'N	8	1°38'E	6	50	53.1	46.8
* Tirso G	40	1°27'N	8	6°15'E	6	160	82.3	77.7
* Taloro	40	7°50'N	9	1°43'E	6	150	17.8	62.7
* Tirso I	39	9°27'N	8	8°58'E	7	24	119.3	40.9
* Tirso L	39	7°10'N	8	1°38'E	7	13	138.5	21.6

Decay rates of reed leaves, *Phragmites australis* (Cav.) Trin. ex Steudel, were studied at all study sites. Decay rates of alder, *Alnus glutinosa* (L.) Gaertner were also studied at a sub-sample of 17 sites indicated by an asterisk in Table 1. Reed swamps occurred at 13 study sites, mainly in the downstream section of the river basin; alder trees occurred the stream channel at 12 study sites, located mainly in the upstream section of the basin. Both plant species occurred at 2 sites and none of them at 8 sites. The study was carried out seasonally using the leaf pack technique (Petersen, 1974), with 3g leaf packs. Alder and reed leaves were collected in autumn, immediately before abscission, from the banks of the Tirso at two different sites. We used 3 grams of leaf enclosed in net bags with a mesh size of 5 mm. Leaf pack weight was assessed as dry weight after air desiccation and successive desiccation in the oven for 72h at 60°C. We also assessed the ash content of leaf packs after combustion in a muffle furnace for 6h at 500°C. All data were reported as ash free dry weight (AFDW). Average AFDW for each start leaf pack was 2.68g for reed and 2.81g for alder leaf pack.

Seasonally, 20 leaf packs of two species were placed in each study site, fixed to the stream bottom with a nylon cord. Reed leaf packs were placed in 31 study sites and collected after 30 and 90 days of submersion in the stream; alder leaf packs were placed in 17 study sites contemporary with reed leaf packs and collected after 15 and 30 days of submersion. Seasonally, on a sample of leaf packs the weight loss was assessed given leaching after 8h and 72h of submersion; therefore all leaf pack decomposition data were expressed clean from leaching.

At the start of the experiments and at each time of sampling, we recorded the main physico-chemical features of each study site such as: air and water temperature, pH, dissolved oxygen, width of wet channel between banks and stream depth. Field equipment was used to assess physico-chemical parameters (WTW 340 oxymeter-A/SET-2 pH meter).

Leaf packs sampled were placed individually in plastic bags and were then brought to the laboratory, where the leaves were gently washed to remove the attached sediments and the macro-invertebrate colonizers. Leaves of each pack were dried in an oven at 60°C for 72h, weighed, burned in a muffle furnace at 500°C for 6h and then weighed again. Data are expressed as ash-free dry weight (AFDW).

Determination of decomposition rate: The decomposition rate coefficients were obtained for each level of investigation by fitting the relationship between time of immersion and average percentage of AFDW remaining of the leaf packs; we used days and degree-days as a measure of time. The model that describes the decomposition process was the negative exponential regression model.

The decomposition rate of each reed and alder leaf pack was computed from the exponential decay equation as follows

$$k = -\ln(W_t/W_0) \cdot 1/t,$$

where t is the time, W_t is the ash-free dry weight of the pack at time t , W_0 is the ash-free dry weight of the pack at time 0. As a measure of the time, we used both days, obtaining a $k \cdot d \cdot s^{-1}$ measure of decomposition rate, and degree-days (i.e., days of immersion multiplied by the average water temperature during the immersion period), obtaining a $k \cdot (^\circ C \cdot d \cdot s^{-1})$ as a measure of decomposition rate, according to MacArthur *et al.* (MacArthur, 1988). Using the k values, we calculated the half-life of reed detritus as $t_{50} = 0.693/k$, the turnover time as $T = 1/k$ and the % daily loss as $(1 - e^{-k}) \cdot 100$. For numerical analysis, the decay rate data were normalized per leaf and per collection date as follows: $K_{norm} = (K_i - K)/\sigma$. In this way the decay rates of all leaves had at all collection times and seasons a general mean equal to 0 and variance equal to 1.

In other cases, as a decomposition value for each study sites we used the exponent value (k) of negative exponential regression model:

$$W_t = W_0 \cdot e^{-kt}$$

where t is the time, W_t is the ash-free dry weight of the pack at time t , W_0 is the ash-free dry weight of the pack at time 0. As a measure of time, we used both days, obtaining a $k \cdot d \cdot s^{-1}$ by fitting the time of immersion (days or degree days) with the average of percentage of detritus biomass remaining at each time of immersion.

3 Results

In the River Tirso, leaf species, seasons, and sampling sites were found to be significant sources of variation of the detritus processing rates (three-way ANOVA, Table 2).

Table 2 Three-way analysis of variance of the average decay rate at alder and reed leaf packs in the entire study. Leaf species, seasons and sampling sites as potential sources of variation (* * * = highly significant, $P < 0.001$)

Source of variation	SS	d. f.	MS	F	P
Leaf species	0.077	1	0.077	126.39	* * *
Season	0.139	3	0.046	75.86	* * *
Sampling sites	0.269	16	0.017	27.48	* * *
Leaf species * seasons	0.013	3	0.004	7.01	* * *
Leaf species * sampling sites	0.072	16	0.005	7.39	* * *
Seasons * sampling sites	0.332	48	0.007	11.29	* * *
Leaf species * seasons * sampling sites	0.168	48	0.003	5.71	* * *
Error	0.926	1511			

3.1 Summer drought events and discharge variation

Drought events occurred at a number of study sites, mainly during summer, and the water level varied greatly at all sites. The minimum width of the wet stream channel and the coefficient of variation of the average width for each study site over the entire study period were used here to quantify the variability of the water level and the occurrence of drought periods on a continuous scale instead of on a binary one (Fig. 3).

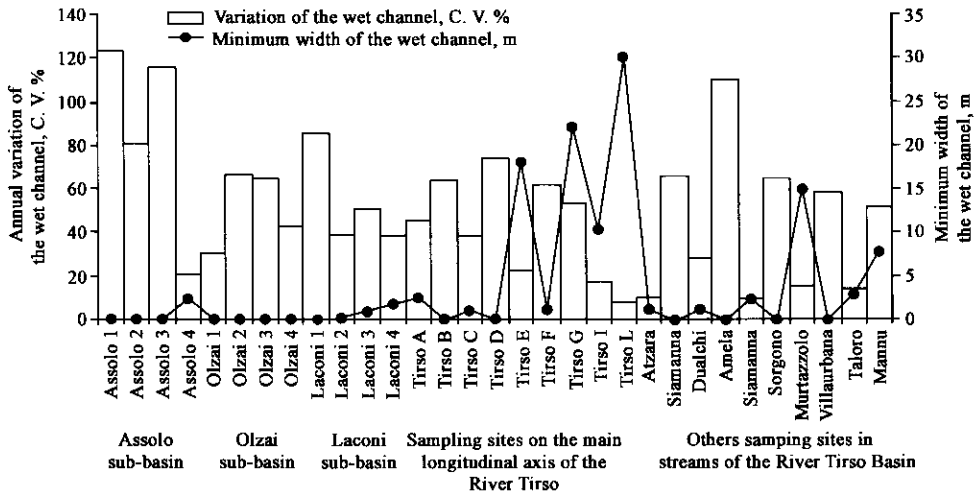


Fig.3 Seasonal variability of the width of the wet stream channel at the study sites expressed as minimum percentage of coefficient of variation of the animal measure. The study sites are grouped into the five main groups considered in this study

Here, we considered the sites with a minimum wet channel width of 0 (expressed as percentage of the maximum) as disturbed sites. Disturbed sites occurred only on 1st, 2nd, 3rd and 4th order stream

branches. Globally, in field sites where reed decomposition was studied, 67% of the 1st order sites, 40% of the 2nd order, 44% of the 3rd order and 29% of the 4th order sites were disturbed. Concerning the sample of field sites where alder decomposition was studied 50% of the 1st, 2nd, and 3rd order sites and 66.7% of the 4th order sites were disturbed. Disturbance pressure was different for the three sub-basins studied; only the 1st order site was disturbed in the Laconi sub-basin, 2nd, 3rd and 4th order sites were disturbed in the Olzai sub-basin and 1st, 2nd and 3rd sites were disturbed in the Assolo sub-basin.

3.2 Detritus processing

3.2.1 Differences among substrates

As a general mean among seasons and sites the decay rate of *Alnus glutinosa* leaf packs ($K = 0.029 \text{ d}^{-1}$) was more than twice the decay rate of *Phragmites australis* leaf packs ($K = 0.013 \text{ d}^{-1}$) (Fig.4).

Alder leaves decayed faster than reed leaves at the 88% of the study sites. This difference between leaves was due to biological decomposition; leaching rates of reed leaves were in fact higher than those of alder leaves both after 0.33 days of immersion (t -Student test = 16.59; $d.f. = 54$; $P < 0.001$) and 3 days of immersion (t -Student test = 7.66; $d.f. = 75$; $P < 0.001$), while biological decay rates of alder leaves were much higher than those of reed leaves (t -Student test = 14.96; $d.f. = 1254$; $P < 0.01$) (Fig.5).

The decay rates of *P. australis* and *A. glutinosa* leaf packs varied greatly among seasons and study sites. *P. australis* decay rates ranged from 0.0008 d^{-1} to 0.102 d^{-1} and *A. glutinosa* decay rates ranged from 0.006 d^{-1} to 0.189 d^{-1} .

3.2.2 Temporal variations

The decay rate of both *Alnus glutinosa* and *Phragmites australis* leaf packs showed a pattern of temporal variation with low rates during fall and high rates during spring (Fig. 6a). The same pattern was observed even when only unperturbed sites were taken into account (Fig. 6b), being decay rates always higher at unperturbed sites. Since the fastest decay rates occurred during spring, decay rates varied seasonally with water temperature only as regards *Phragmites australis* (*P. australis*: $y = 0.0011x + 0.005$, $d.f. = 99$, $r = 0.28$, $P < 0.05$; *A. glutinosa*: $y = 0.0017x + 0.0174$, $d.f. = 63$, $r = 0.22$, $n.s.$).

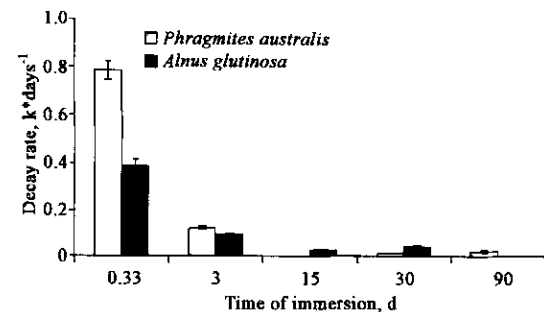


Fig.5 Variation of the average decay rate of alder and reed leaf packs during decomposition. Vertical bars represent $\pm 2^*$ standard error

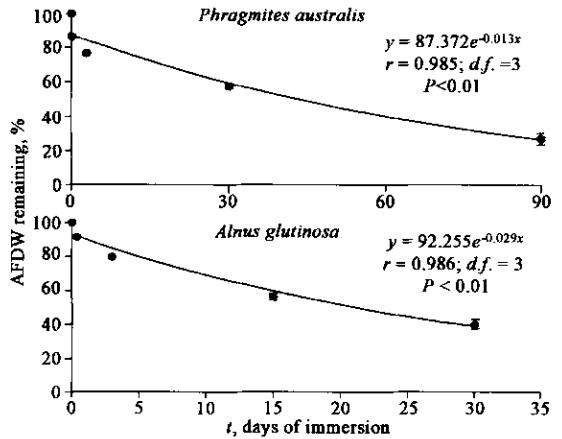


Fig.4 Analysis of regression between sampling times and ash free dry weight remaining of *Phragmites australis* and *Alnus glutinosa* leaf packs

Decay rates of alder leaf packs were always higher than the decay rates of reed packs in each season, considering both all study sites or only the undisturbed sites. In both cases, the largest differences between leaves occurred during summer, when alder packs decayed 2.44 times and 2.29 times faster than reed packs at all sites or only at undisturbed sites, respectively.

3.2.3 Spatial variations

Decay rates of both *A. glutinosa* and *P.*

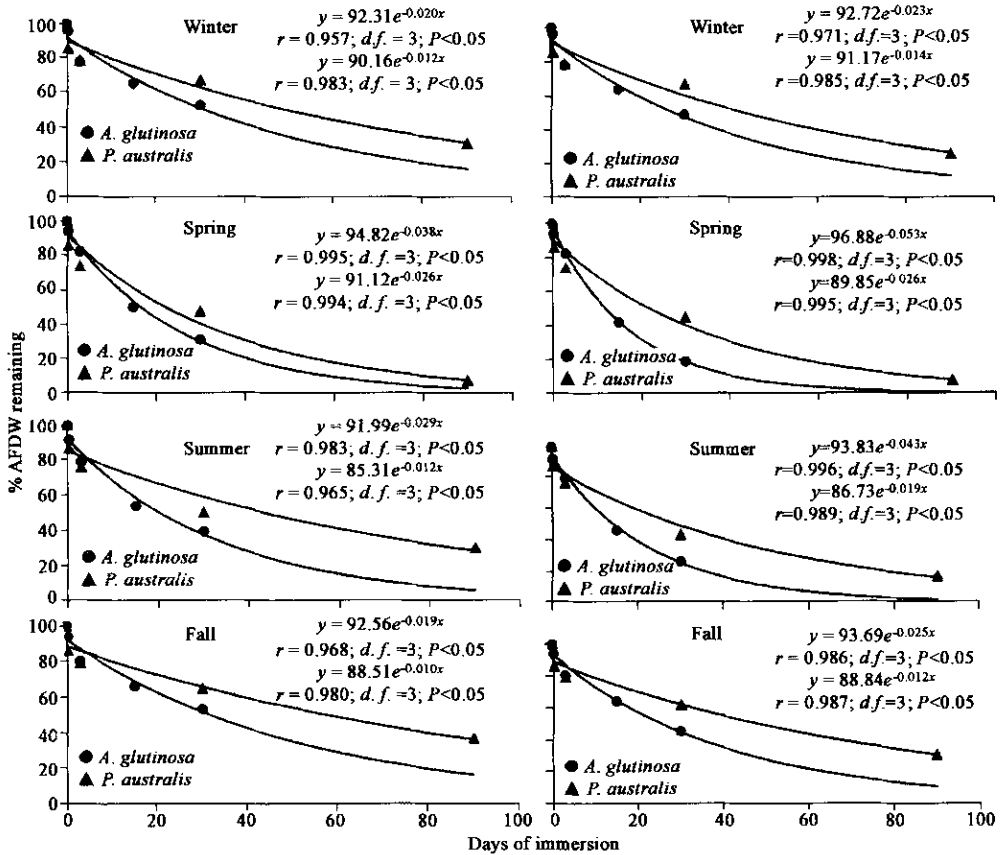


Fig. 6 Regression analysis between sampling times and alder and reed weight remaining in each seasonal period (a) All sites and leaf packs included; (b) only undisturbed sites and leaf packs are included

australis varied significantly among sites in the river Tirso basin (Table 2). We analyzed the co-variation between decay rates and some major structural abiotic features of the study sites, such as stream order altitude, distance from the river source and from the mouth. Decay rates showed regular pattern of variation only with the stream order.

Alder decay rates decreased with increasing stream order up to the 6th or 7th order during fall, winter and spring, while during summer decay rates decreased from the first to the third order study sites and then increased up to the seventh order. Reed decay rates increased with the stream order during summer and fall up to the 6th order. During winter and spring there were no clear patterns of variation of decay rates. Fig. 7 shows the spatial variation of the decay rates of reed and alder leaves in relationship to order taking together all leaf packs in all sites.

3.2.4 Role of perturbation

In Table 3, decay rates of *Phragmites australis* in unperturbed and perturbed study sites along stream order are reported seasonally. In the River Tirso, perturbation due to the dry period affected only stream branches 1st to 4th stream orders. In all seasons unperturbed study sites showed higher decay rates than perturbed study sites and only in one case did the contrary happen (spring, 4th stream order). Globally, reed decay rates were inversely related to the coefficient of variation of the wet streambed at each study site ($y = -26.77 \ln[x] - 62.88$; $r = 0.581$; $d.f. = 29$; $P < 0.01$). Alder decay rates were also slower at disturbed than at undisturbed sites, but only during the season when the perturbation occurred (Table 4).

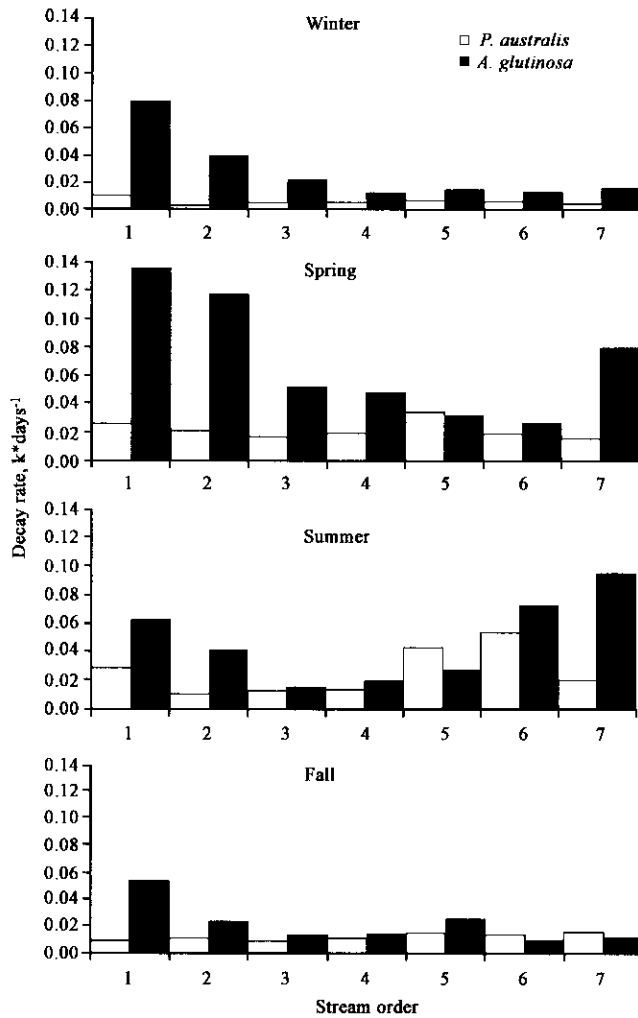


Fig.7 Seasonal models of spatial variation between stream orders or the alder and reed decay rates in the River Tirso Basin

Globally, alder decay rates were also inversely and significantly related to the coefficient of variation of the wet stream bed ($y = 22.94\ln[x] - 29.87$; $r = 0.542$; $d.f. = 15$; $P < 0.05$).

In Figs.8a and 8b we report seasonally the relationship between decay rates and annual variations of stream bed (percentage of coefficient of variation) both reed and alder leaves. Significant relations were observed only for *Phragmites australis* leaves in spring and fall, cases where we widened the sampling set with a strongly perturbed sub-basin.

Summer drought events affected the spatial patterns of variation by influencing significantly the decay rates of plant detritus. The comparisons among and within sub-basins showed strong negative influence of summer drought on detritus processing rates(three way ANOVA, Table 5; Fig.9).

Table 3 Average decay rates of *Phragmites australis* leaf packs in unperturbed and perturbed study sites, according to stream order and season. Within brackets ± 2 standard error are reported

Stream order		I	II	III	IV	V	VI	VII
Total study sites		3	5	9	7	2	3	2
Annual dry sites, %		67	40	44	29	0	0	0
<i>P. australis</i> decayrate, $k \cdot d \cdot s^{-1}$								
Winter	Unperturbed	0.087 (± 0.000)	0.011 (± 0.003)	0.011 (± 0.003)	0.019 (± 0.018)	0.011 (± 0.003)	0.008 (± 0.006)	0.008 (± 0.001)
	Perturbed	0.008 (± 0.000)	0.010 (± 0.000)	0.012 (± 0.007)	0.012 (± 0.004)	—	—	—
Spring	Unperturbed	0.093 (± 0.000)	0.029 (± 0.030)	0.023 (± 0.010)	0.025 (± 0.013)	0.039 (± 0.008)	0.052 (± 0.042)	0.015 (± 0.014)
	Perturbed	0.008 (± 0.014)	0.016 (± 0.018)	0.014 (± 0.005)	0.036 (± 0.022)	—	—	—
Summer	Unperturbed	0.038 (± 0.000)	0.015 (± 0.011)	0.016 (± 0.011)	0.017 (± 0.004)	0.036 (± 0.022)	0.062 (± 0.043)	0.022 (± 0.013)
	Perturbed	0.011 (± 0.000)	0.010 (± 0.000)	0.010 (± 0.007)	0.004 (± 0.003)	—	—	—
Fall	Unperturbed	0.024 (± 0.000)	0.012 (± 0.002)	0.012 (± 0.003)	0.014 (± 0.002)	0.017 (± 0.010)	0.014 (± 0.011)	0.018 (± 0.000)
	Perturbed	0.004 (± 0.003)	0.007 (± 0.003)	0.006 (± 0.001)	0.008 (± 0.005)	—	—	—

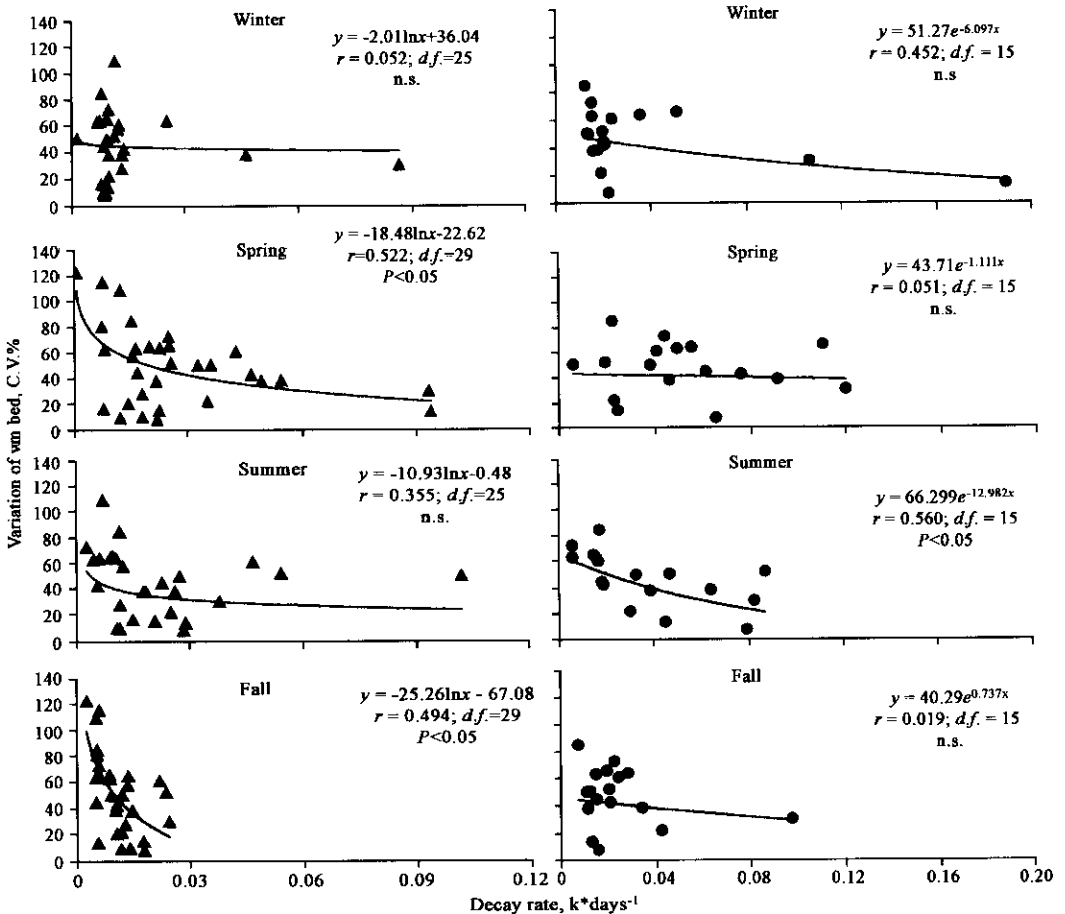


Fig. 8 Correlation analysis between plant detritus decay rates and the coefficient of variation of the wet streambed, in the River Tirso Basin (a) reed leaves; (b) alder leaves

Table 4 Average decay rates of *Phragmites australis* leaf packs in unperturbed and perturbed study sites according to stream order and season. Within brackets ± 2 standard error are reported

Stream order		I	II	III	IV	V	VI	VII
Total study sites		2	2	4	3	2	3	1
Annual dry sites, %		50	50	50	67	0	0	0
<i>A. glutinosa</i> decayrate, $k^* d^{-1} s^{-1}$								
Winter	Unperturbed	0.017	0.017	0.017	0.016	0.021	0.074	0.022
	Perturbed	—	—	(± 0.006)	(± 0.000)	(± 0.005)	(± 0.115)	(± 0.000)
Spring	Unperturbed	0.012	0.051	0.025	0.018	—	—	—
	Perturbed	—	—	(± 0.020)	(± 0.006)	—	—	—
Summer	Unperturbed	0.120	0.092	0.050	0.046	0.032	0.017	0.066
	Perturbed	—	—	(± 0.023)	(± 0.000)	(± 0.018)	(± 0.011)	(± 0.000)
Fall	Unperturbed	0.022	0.111	0.053	0.060	—	—	—
	Perturbed	—	—	(± 0.006)	(± 0.032)	—	—	—
Winter	Unperturbed	0.083	0.064	0.026	0.039	0.024	0.060	0.079
	Perturbed	—	—	(± 0.014)	(± 0.000)	(± 0.013)	(± 0.027)	(± 0.000)
Spring	Unperturbed	0.017	0.015	0.011	0.013	—	—	—
	Perturbed	—	—	(± 0.010)	(± 0.013)	—	—	—
Summer	Unperturbed	0.097	0.034	0.013	0.011	0.033	0.015	0.015
	Perturbed	—	—	(± 0.004)	(± 0.000)	(± 0.018)	(± 0.005)	(± 0.000)
Fall	Unperturbed	0.007	0.019	0.021	0.021	—	—	—
	Perturbed	—	—	(± 0.014)	(± 0.002)	—	—	—

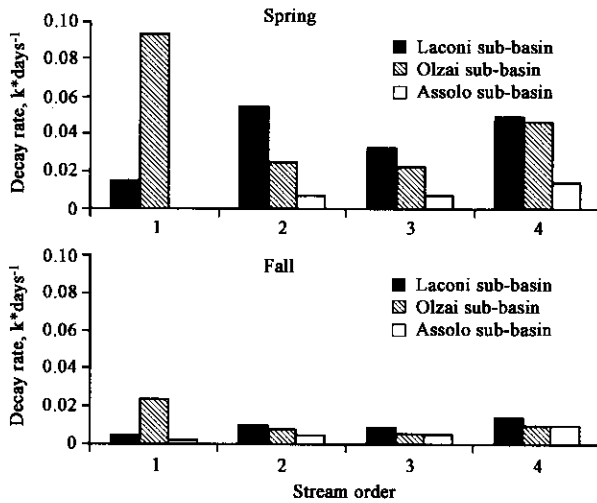


Fig.9 Spatial variation of reed leaf pack decay rates in three sub-basins exposed at different levels of perturbation during spring and fall

Table 5 Three-way ANOVA of reed leaf decay rates in three sub-basins within River Tirso Basin (*Laconi* sub-basin, *Olzai* sub-basin, *Assolo* sub-basin) (* * * = highly significant; n. s. = not significant)

Source of variation	SS	d.f.	MS	F	P
Seasons	0.007	1	0.007	113.25	* * *
Sbu-basins	0.006	2	0.003	47.95	* * *
Stream order	0.000	3	0.000	2.62	n. s.
Seasons * sub-basins	0.004	2	0.002	35.53	* * *
Seasons * stream orders	0.000	3	0.000	2.57	n. s.
Sub-basins * stream orders	0.003	6	0.001	9.19	* * *
Seasons * sub-basins * stream orders	0.003	6	0.000	7.01	* * *
Error	0.010	146			

4 Discussions

The results of this paper emphasize three main points: (1) Detritus processing rates, globally, have species-specific patterns of spatial variation along the river continuum in the River Tirso Basin; (2) Summer drought events represent a significant source of perturbation for detritus processing, in respect to which alder leaves are more resilient than reed leaves; (3) The resilience from perturbation can explain the different pattern of spatial variation of the two leaves along the river continuum in the Tirso Basin.

Alder and reed leaves can be classified as fast leaves in the River Tirso Basin. The decay rates observed in the Tirso basin agree with those observed in other aquatic ecosystems of the Mediterranean ecoregions (Rossi, 1987; Dadea, 1996; Fazi, 1994). The difference observed between the two leaves are consistent with the bibliographic studies showing that alder leaves decay at a faster rate than reed leaves (Rossi, 1987).

The difference between the two leaves could also be affected by the fact that reed leaves seem to start their decomposition when still on the plant, before their abscission and their entrance into the aquatic environment (Gessner, 1994). The occurrence of decomposition of reed leaves directly on the plants can affect the quantification of the reed decay rate in the River Tirso Basin but does not seem to be relevant to the spatial pattern of decay rate variation, which represents the main result of this study.

The first point of this discussion is supported by the observation that the decay rates of alder leaf packs globally decreased with increasing stream order in the range from 1st to 6th, while decay rates of reed leaf packs globally increased with increasing stream order, within the same range. Decay rates of both leaves did not follow this pattern in the 7th order branches or in summer.

Perturbation of the water flow seems likely to be a major cause of these alterations to the observed spatial patterns. In fact the 7th order sites are downstream from Lake Omodeo, one of largest European reservoirs, which interrupts the River Tirso continuum, representing a source of disturbance for ecosystem structure and processes. Similarly, summer was the season when drought events were more frequent and severe.

Summer drought events had a relevant negative influence on detritus decomposition in the River Tirso Basin. The influence of summer drought events represents the second part of this discussion. It is supported by the evidence regarding both the basin as a whole and the three sub-basins differentially affected by the drought events.

In this study we considered as perturbed field sites those exposed to complete desiccation according to Gurtz and Tate (Gurtz, 1988) and Richardson (Richardson, 1990). Richardson (Richardson, 1990) compared only one unperturbed and one perturbed stream and he found that both *fraxinus* and alder leaf packs showed lower decay rates in perturbed than unperturbed streams. In the River Tirso, the same pattern was observed on larger spatio-temporal scales. It is relevant to observe that this was true for a period of time longer than the drought event for both leaves.

The different resilience of the processing rates of the two leaves seems likely to be related to their quality as a growth substratum for micro-organisms and as a food resource for benthic invertebrates. Alder leaves are much softer and richer in nitrogen than reed leaves and the former decay faster than the latter. Therefore, at the end of the disturbance events, when leaves were abundant but consumers were rare, consumption is likely to be concentrated on the best quality leaves while less optimal leaf substrata may remain unused.

This explanation seems to be consistent with the evidence that the only case of recovery of *Phragmites australis* decay rates occurred in the 4th order stream branches, where the perturbation event was less intense than the lower orders in terms of temporal duration.

Also the comparison between sub-basins showed that decay rates of *Phragmites australis* decrease with pressure of perturbation in the Laconi and Assolo sub-basins in almost all stream orders (the 1st stream order study site in the Olzai sub-basin seems to be a case where decay rate is site-specific). Inside sub-basin decay rates of *Phragmites australis* tend to increase with stream order particularly in the more perturbed sub-basin.

The different resilience of the two leaves to the perturbation events can supply an explanation for the different spatial patterns observed for the two plant species. Alder decay rates followed the expected pattern

along the river continuum, with high processing rates in lower order streams where shredders are expected to be abundant, and low processing rates in higher order streams where shredder diversity is expected to be low (Vannote, 1980; Cummins, 1989).

The decomposition rate of *Phragmites australis* leaves had a spatial pattern of variation in the River Tirso Basin, which was in contrast with that predicted by the river continuum concept. However, the higher resilience of faster leaves in lower order disturbed streams can explain the low decay rates of the reed leaf detritus in these streams. This is supported by the evidence that lower order stream branches in the River Tirso Basin are generally invasion-structured; particularly those exposed to summer drought events [CoDePASs Project N° ENVA-CT97-0584, Final Technical Report, 2001]. In invasion-structured, resource-unlimited communities, a switching behavior of benthic invertebrates, with disproportionately high pressure on fast decaying high quality substrata and disproportionately low pressure on relatively slow decaying, low-quality substrata, is an expected result.

The results collected in the River Tirso Basin therefore supported the extension of the “river continuum concept” to the processing rates. Perturbation events and species-specific resilience to these perturbations interfere with the driving force related to the river continuum and contribute to determinate the actual pattern of spatial variation of decay rates of different plant substrata within a river basin.

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