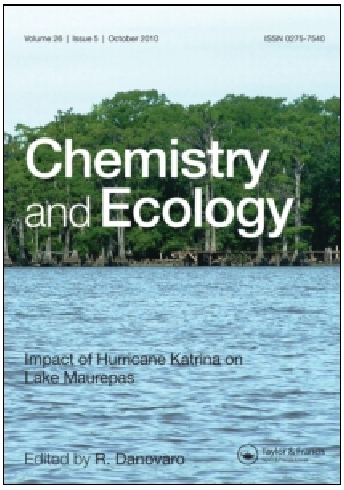

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Inter- and intra-habitat variability of plant detritus decomposition in a transitional environment (Lake Alimini, Adriatic Sea)

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INTER- AND INTRA-HABITAT VARIABILITY OF PLANT DETRITUS DECOMPOSITION IN A TRANSITIONAL ENVIRONMENT (LAKE ALIMINI, ADRIATIC SEA)

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A comparative analysis of inter- and intra-habitat variations of detritus decay rates across ecosystem types was carried out in the Lake Alimini complex (Italy) to assess the relevance of major structural ecosystem features on detritus processing rates. Reed (*Phragmites australis*) detritus decomposition was studied in a stream, a freshwater lake and a salt marsh on a seasonal basis at a total of 20 sampling stations using the leaf pack technique. Overall, the spatial variability of leaf decomposition rates was more pronounced than the temporal variability, decomposition rates in the stream being 3.6 and 5.2 times faster than in the freshwater lake and salt marsh, respectively. The intra-habitat spatial variability of leaf decay rates in the stream was also higher than in the other systems. Environmental features were relevant factors affecting intra- and inter-habitat variation of reed decay rates, and their relevance to leaf detritus decomposition showed a strong seasonal variation.

Keywords: Decomposition; *Phragmites australis*; Intra-habitat heterogeneity; Inter-habitat heterogeneity; Niche

1 INTRODUCTION

The decomposition processes of plant detritus in aquatic ecosystems have received increasing attention in the last three decades. Most of these studies have been based on three major approaches, focusing on the influence of detritus decomposition on water chemistry (Gupta *et al.*, 1996), the chemical and biochemical changes in leaf detritus during processing (Suberkropp *et al.*, 1976; Robertson, 1987; Bärlocher *et al.*, 1995) and the energetic aspects of detritus processing (Petersen and Cummins, 1974; Akanil and Middleton, 1997). The third approach was developed mainly utilizing detritus breakdown rates as descriptors of detritus processing (Gessner, 1991; 2000; Cortes *et al.*, 1995).

Plant breakdown rates have been found to be affected by internal factors, *i.e.* leaf species and chemical–physical characteristics of the leaves themselves (Kok *et al.*, 1990; Canhoto and Graça, 1996), and by external environmental factors (Webster and Benfield, 1986), including both structural and physical–chemical features of the ecosystems, such as stream typology and order (Cortes *et al.*, 1995), temperature (Carpenter and Adams, 1979), pH (Carpenter *et al.*, 1983; Thompson and Bärlocher, 1989), climate (Murphy *et al.*, 1998),

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solar radiation (Denward and Tranvik, 1998) and nutrients (Elwood *et al.*, 1981; Sharma and Gopal, 1982). It has also been observed that plant detritus decomposition rates are affected by biotic agents of decomposition, such as fungal communities and macroinvertebrate guilds that colonize dead organic matter (Rossi, 1985; Gessner and Chauvet, 1994).

Most of the literature dealing with leaf detritus processing in aquatic ecosystems describes the decomposition of leaves in freshwater ecosystems, such as rivers and streams (Akanil and Middleton, 1997; Abelho and Graça, 1998) and lakes (Gessner *et al.*, 1996; Gupta *et al.*, 1996). Studies of leaf detritus breakdown in transitional ecosystems, as salt-marsh ecosystems or coastal lagoons, are much less common in the ecological literature (Samiaji and Bärlocher, 1996; Rossi and Costantini, 2000).

Transitional aquatic ecosystems are ecotones, functionally connecting the land and its rivers on one side and the sea on the other (Wiegert and Pomeroy, 1981). They are characterized by a high spatial and temporal heterogeneity, even on a small spatial scale, and they have temporally variable spatial boundaries, sometimes not easily identifiable (Abbiati and Basset, 2001).

In this framework, the aim of the present work is to contribute to the comprehension of leaf detritus decomposition processes by a comparative field experiment of leaf litter decomposition in lentic and lotic, freshwater and transitional ecosystems.

The aims of this study were: (1) to analyse the intra-habitat variation of decomposition processes in a Mediterranean lagoon (Lake Alimini Grande); (2) to compare inter-habitat variation of detritus decomposition among aquatic ecosystems of different typologies, *i.e.* lotic freshwater, lentic freshwater and lentic salt-marsh ecosystems; and (3) to infer the relevance of major structural ecosystem features on plant detritus decay rates in transitional aquatic ecosystems from the comparative analysis of inter-habitat variation among ecosystems and intra-habitat variation within each ecosystem studied.

To address these aims, decomposition processes and major structural, morphological, physical and chemical features of the ecosystems were studied in the Lake Alimini drainage basin, which is made up of three ecosystems of different types: a freshwater stream, a freshwater lake and a salt-marsh lake.

2 MATERIALS AND METHODS

2.1 Study Area

The study was carried out in the drainage basin of Lake Alimini Grande, located in southern Italy on the Adriatic coast, 40 km south of Lecce (geographic coordinates: 40° 10′ 00″ N to 40° 12′ 15″ N and 18° 26′ 25″ E to 18° 27′ 35″ E; Fig. 1). This basin includes three aquatic ecosystems of different type: a salt-marsh lake (Alimini Grande), a freshwater channel (the Zuddeo) and a freshwater lake (Alimini Piccolo or Fontanelle).

Lake Alimini Grande covers an area of 1.37 km^2 and measures 2.86 km by 1.54 km. The total length of the shoreline is 9.53 km with a sinuosity index of 2.29, indicating a very irregular shape. The mean depth of the lake is 1.50 m, but the water level varies depending on marine and freshwater inputs. The lake receives three main freshwater inputs: one from Alimini Piccolo, a second from a small stream (the Zuddeo) and another from three small channels entering the north side of the lake, carrying water from the Traugnano Swamp. The lake receives seawater input from the Adriatic Sea, to the east, through a canal 150 m long and 10 m wide. In Alimini Grande, the water salinity values vary from 2.2 to 34.8.

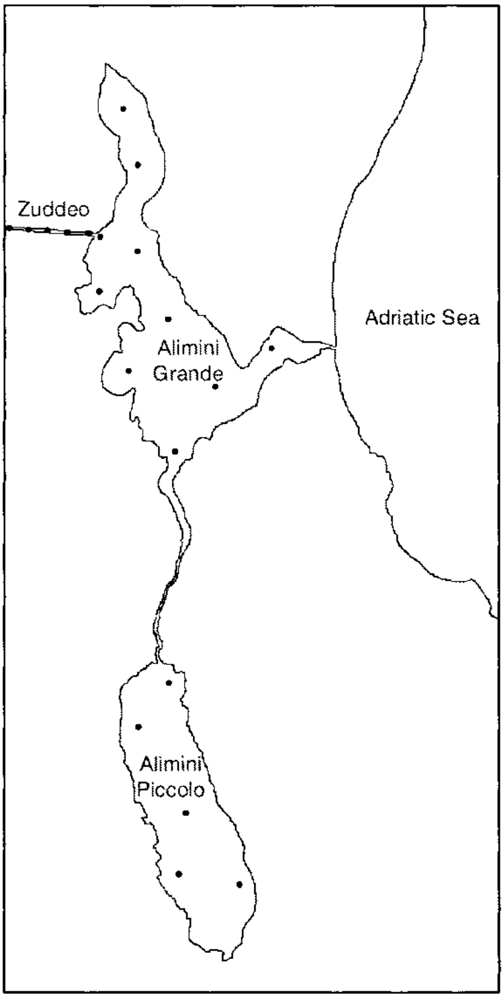


FIGURE 1 Map of the basin including Lake Alimini Grande, Lake Alimini Piccolo and Zuddeo Channel. Sampling stations are reported for each ecosystem.

Lake Alimini Piccolo covers an area of 0.50 km^2; its mean depth is 0.70 m. This lake is fed by groundwater through many springs, called 'fonti' (in Italian), from which the lake's nickname 'Fontanelle' is derived. The lake is connected to Alimini Grande through a major channel, 1300 m long, called Strittu. In Alimini Piccolo, the water salinity remains constant at around 0.4.

The Zuddeo stream is a drainage channel originating from underground springs in the north-east of Alimini Grande; water flow here is temporally variable depending on rainfall. It has a winding course and an underground section, 800 m long, and flows into the western side of Alimini Grande. The average depth of this channel is 0.2 m.

The vegetation in the hydrographic basin of the Alimini Lakes consists mainly of Mediterranean maquis, dominated by *Pistacea lentiscus* L., *Quercus calliprinos* Webb. and *Mirtus communis* L. (Marchiori *et al.*, 1999). In both lakes and in the stream there are dense swamps of emergent macrophytes, which are dominated by a single species: *P. australis* (Cav) Trin. ex Steudel.

2.2 Sampling

The study was performed using leaves of *P. australis* (Cav) Trin. ex Steudel, and was carried out at a total of 20 sampling sites: nine in Alimini Grande, five in Alimini Piccolo and six in the Zuddeo channel. The fieldwork was carried out over a year from autumn 1998 to summer 1999; the experiments were performed in four seasonal periods, and data sets on detritus decomposition were collected at four times from the start of the experiments in each season. Detritus processing of *P. australis* leaves was studied using the leaf pack technique (Bocock and Gilbert, 1957; Petersen and Cummins, 1974; Melillo *et al.*, 1983), based on the estimate of mass loss from litterbags of reed leaves. Leaves of *P. australis* were collected at the beginning of autumn, air-dried and stored in a dark room at standard temperature and low humidity until needed. Before use, leaves were cut into 8-cm-long fragments and oven-dried to constant weight (60 °C for 72 h), and then lots of 3 ± 0.005 dry weight were placed in 5 mm mesh bags. The ash-free dry weight (AFDW) of leaf packs was determined on a sub-sample of 15 leaf packs to obtain an estimate of the biomass of leaf packs at the beginning of the experiment. The leaf packs were submersed at each sampling station and collected at four sampling times: after 1, 3, 30 and 90 d from the beginning of the experiment. At each sampling time, eight leaf packs were sampled at each sampling station, placed in a plastic container separately, and rapidly brought to the laboratory. Here, leaves were gently washed to remove sediments and macroinvertebrate colonizers. Leaves from each pack were dried in an oven at 60 °C for 72 h, weighed, burned in a muffle furnace at 500 °C for 6 h and weighed again. Therefore, the data are expressed as AFDW. Reed decay rates were calculated from a negative exponential model (Olson, 1963; Ando, 1970).

At each sampling station, a set of physical–chemical water variables and parameters was also measured monthly. We determined water salinity, temperature, dissolved oxygen, nitrite, nitrate, ammonia, phosphate and chlorophyll *a* concentrations. In the freshwater lotic ecosystem, the distance of the sampling stations from the Zuddeo channel mouth in the salt-marsh lake was also determined. Water salinity (expressed as PSU) and temperature were measured *in situ* with field instruments (LF 340-A/SET-2 conductibility-meter); chlorophyll *a* and nutrient concentrations were determined in the laboratory on water samples collected with a 5 l Niskin bottle, using standard techniques (American Public Health Association, American Water Works Association, Water Environmental Federation, 1995).

2.3 Statistical Analysis

Mass-loss data were processed using non-linear regression analysis of the exponential model (Olson, 1963):

$$M_t = M_0 \mathrm{e}^{-kt},$$

where M_t is the mass remaining at time t, M_0 the initial mass and k the breakdown coefficient expressed (d^{-1}). k values are used as a measure of reed processing rates. Analysis of variance (ANOVA) was used to test for temporal (*i.e.* among seasons) and spatial (*i.e.* among and within ecosystems) differences in leaf decay rates; the slopes of regression equations on the mass-loss data from each ecosystem were compared by analysis of covariance (ANCOVA).

The relevance of potential sources of leaf decay rate variation such as water temperature, salinity, dissolved oxygen, nutrient concentrations (*i.e.* nitrite, nitrate, ammonia, phosphate) and chlorophyll *a* concentrations was analysed using multiple regression analysis. Furthermore, in the freshwater stream, the distance of the sampling stations from the channel mouth in the salt-marsh lake was also considered. A stepwise multiregression analysis was performed using Systat 9 software on normalized data $[\bar{x}_{\text{norm}} = (x_i - x)/s]$.

3 RESULTS

3.1 Inter-Habitat Variation

Overall, *P. australis* processing in the Alimini complex fits with a negative exponential model ($y = 89.6e^{-0.018x}$; $r = 0.700$; d.f. = 16; $P < 0.05$). Accounting for all sampling stations, in both lotic and lentic ecosystems, we have calculated an average daily percentage of reed detritus weight loss equal to 1.75% and a reed detritus half-life equal to 39 d.

On the entire data set, considering ecosystem types and seasons as sources of heterogeneity, spatial variation of reed decay rates among ecosystem types was significantly more important than temporal variation (two-way ANOVA, $P < 0.001$) (Tab. I), even though the processing rates of *P. australis* leaf packs tended to vary significantly among seasons (one-way ANOVA; $F(3, 708) = 20.5$, $P < 0.001$).

Reed leaves decayed faster in the Zuddeo channel ($k = 0.036$) than in the two lentic ecosystems, Alimini Piccolo ($k = 0.010$) and Alimini Grande ($k = 0.007$) (ANCOVA, $F(2,12) = 5.9$, $P < 0.05$). The remaining leaf pack biomass at the end of the field experiments (day 90) was 5.6% ± 8.1 in the lotic ecosystem, Zuddeo, 39.5% ± 2.5 in Alimini Piccolo and 47.2% ± 4.7 in Alimini Grande.

A similar pattern of variation among ecosystem types was observed for each seasonal period (Fig. 2). Reed decomposition rates ranged from a minimum winter value ($k = 0.005$) in Alimini Grande to a maximum spring value ($k = 0.038$) in the Zuddeo. Comparisons of the slopes of linear regression of the remaining leaf detritus biomass over time in the four seasons showed significant differences between lotic and lentic ecosystems in 75% of the analysed cases (ANCOVA test, $P < 0.05$), decay rates being faster in the warm season than in the cold season, while reed processing rates were similar in all seasons in the two lentic ecosystems (Fig. 2; ANCOVA test, n.s.).

On a temporal scale, the processing rates of *P. australis* leaves varied significantly among seasons in both lentic ecosystems, Alimini Grande and Alimini Piccolo (one-way ANOVA, $P < 0.001$), while in the lotic ecosystem, processing rates of *P. australis* leaves were not affected by seasonal differences (Tab. II). In Lake Alimini Piccolo and Lake Alimini Grande, the reed leaf decomposition was 1.3–1.5 times faster in summer than in the other seasons, respectively.

The reed decay-rate variation among ecosystem types and seasons was also shown by the analysis of the distribution of detritus leaf pack decay coefficients into three processing categories (Petersen and Cummins, 1974). Most of the reed leaf packs had fast decay rates (*i.e.* $k > 0.010$), 28% of reed packs had medium decay rates (*i.e.* 0.005–0.010), and only

TABLE I Two-way ANOVA results for ecosystems and seasonal periods of decay-rate data in the drainage basin of Alimini.

Source	*Sum of squares*	*d.f.*	*Mean squares*	*F*
Systems	0.070	2	0.035	59.904**
Time	0.001	3	0.000	0.850
Systems × Time	0.006	6	0.001	1.582
Error	0.040	68	0.001	

**$P < 0.001$.

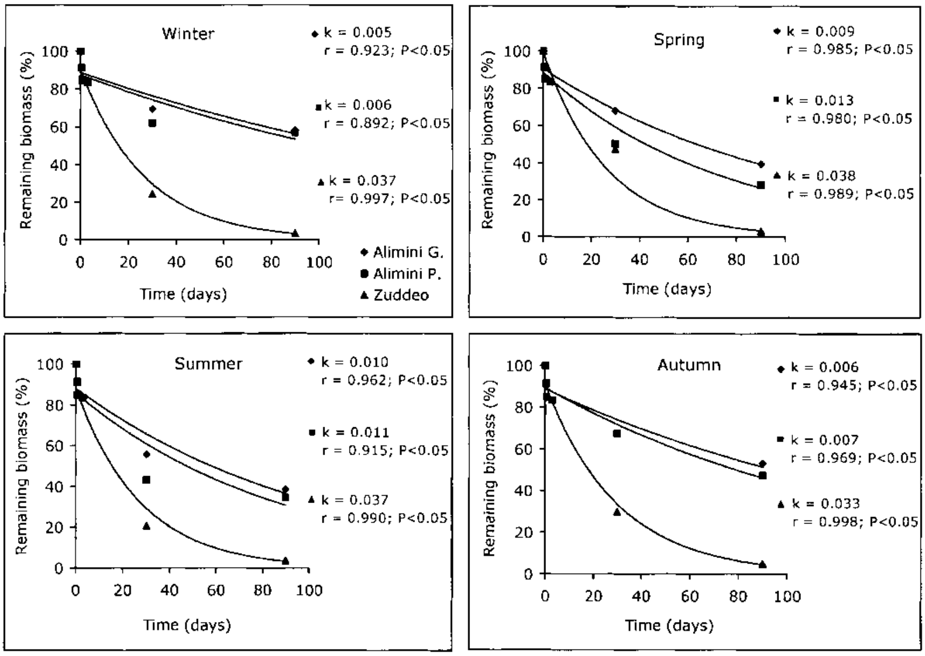


FIGURE 2 Statistical patterns of temporal variation of reed leaf pack ash-free dry weight in the three aquatic ecosystems for the four seasons.

10% had slow decay rates (*i.e.* $k < 0.005$). More than 50% of fast-decaying leaves were from the freshwater stream (Fig. 3), and most of them were sampled during the warm season.

3.2 Intra-Habitat Variation

Detritus reed decay rates also showed patterns of spatial variation within each ecosystem type. Temporal variance of reed decay rates explained 65% of the overall variance in Alimini Grande, 79% in Alimini Piccolo but only 14% in Zuddeo.

Spatial heterogeneity of reed decomposition rates, expressed as the coefficient of variation among sampling stations, was higher in the freshwater stream (c.v. = 61%) than in the freshwater lake (38%) and the salt-marsh lake (33%).

TABLE II One-way ANOVA results from the sampling stations for the remaining leaf pack biomass data in each ecosystem.

		Sum of squares	*d.f.*	*Mean squares*	*F*
Alimini Grande	Between	1.47E-04	3	4.91E-05	20.17**
	Within	7.79E-05	32	2.44E-06	
	Error	2.3E-04	35		
Alimini Piccolo	Between	1.96E-04	3	6.52E-05	20.50**
	Within	5.09E-05	16	3.18E-06	
	Error	2.50E-04	19		
Zuddeo	Between	6.50E-03	3	2.17E-03	1.09
	Within	3.97E-02	20	1.99E-03	
	Error	4.62E-02	23		

**$P < 0.001$.

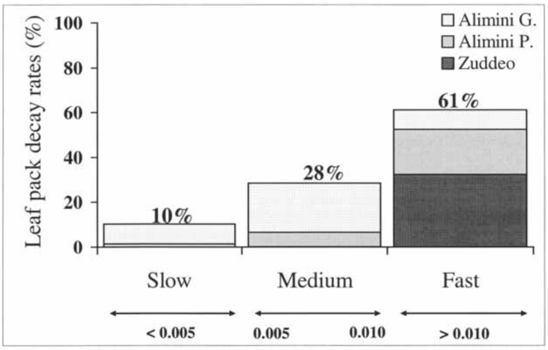


FIGURE 3 Distribution of *Phragmites australis* leaf packs, collected from the three ecosystems, grouped into decay-rate categories.

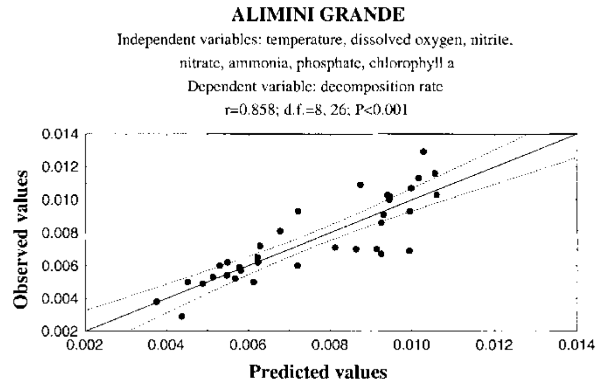
Intra-habitat variation of reed decomposition processes was analysed taking account of several structural features and abiotic characteristics of the ecosystems (Tab. III). In the two lentic ecosystems, environmental variables explained 74% of variance of leaf decay rates in Lake Alimini Grande ($r = 0.858$; d.f. = 8,26; $P < 0.001$) and 93% in Lake Alimini Piccolo ($r = 0.963$; d.f. = 7,12; $P < 0.001$; Fig. 4, Tab. IV).

When the data were pooled on an annual basis, most of the decay rate variation was found to be due to physical features both in Lake Alimini Piccolo (77%) and in Lake Alimini Grande (45%), with water temperature accounting for more than 80 and 30% of decay rate variation in Alimini Piccolo and Alimini Grande, respectively. When the data were analysed on a seasonal basis most of the decay rate variation was due to chemical factors which accounted for up to 93% and 85% of decay rate variance in Alimini Grande and Alimini Piccolo, respectively, during the autumn.

TABLE III Physical–chemical parameters measured at each sampling station in the three ecosystems.

Station	*Temperature (°C)*	*Salinity (PSU)*	*DO* ($mg\,l^{-1}$)	NH_3 (μM)	NO_2 (μM)	NO_3 (μM)	PO_4 (μM)	*Chlorophyll a* ($\mu g\,l^{-1}$)
1*	18	29.4	8.2	8.03	0.61	55.76	0.13	2.60
2*	18	28.3	8.1	8.61	0.63	47.51	1.49	3.53
3*	19	21.0	7.5	14.01	0.88	55.28	0.10	2.57
4*	14	10.0	7.6	14.90	1.25	70.69	0.15	3.24
5*	19	30.6	7.5	6.99	0.61	50.06	0.10	3.36
6*	18	30.2	7.7	8.82	0.67	49.34	0.05	3.62
7*	19	29.0	7.1	10.46	0.65	56.10	0.12	4.09
8*	19	28.0	9.8	10.50	0.65	78.27	0.06	3.83
9*	18	31.0	9.3	9.68	0.70	49.54	0.03	3.73
10†	18	0.3	7.7	2.23	0.16	38.89	0.10	20.84
11†	18	0.4	7.7	0.55	0.14	27.29	0.16	32.66
12†	18	0.5	8.3	7.89	0.47	58.07	0.08	13.40
13†	18	0.4	7.7	1.95	0.23	29.94	0.14	33.04
14†	16	0.5	8.3	1.88	0.23	38.28	0.10	32.52
15‡	17	0.2	9.1	1.18	0.26	168.4	0.13	–
16‡	17	0.2	8.3	1.16	0.41	193.0	0.13	–
17‡	18	0.2	7.5	0.72	0.32	226.1	0.14	–
18‡	18	0.3	6.5	0.75	0.23	229.0	0.14	–
19‡	17	0.2	4.8	0.37	0.20	237.0	0.14	–
20‡	17	0.2	4.2	1.14	0.21	211.1	0.09	–

*Alimini Grande; †Alimini Piccolo; ‡Zuddeo.



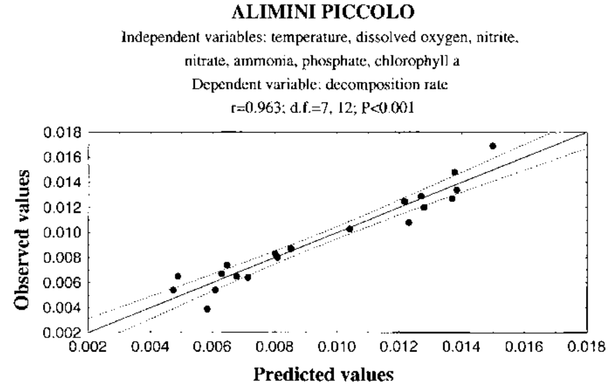


FIGURE 4 Relationships between predicted and observed values of leaf pack decay rates in the two lentic ecosystems: Lake Alimini Grande and Lake Alimini Piccolo.

In the lotic ecosystem, Zuddeo, the distance of each sampling station from the channel mouth in the salt-marsh lake, physical features and nutrients together accounted for 56% of decay rate variance ($r = 0.745$; d.f. = 7,16; $P < 0.05$; Fig. 5, Tab. IV). On an annual basis, a similar percentage (30%) of decay rate variation was due to structural

TABLE IV Multiple regression analysis of litter breakdown rate in relation to abiotic factors in the lentic and lotic ecosystems.

	r	r^2	*d.f.*	*P*	*S.E.*
Alimini Grande					
All features	0.858	0.736	8, 26	**	0.001
Nutrients	0.809	0.654	5, 29	**	0.001
Physical features	0.668	0.446	3, 31	**	0.002
Alimini Piccolo					
All features	0.963	0.927	7, 12	**	0.001
Nutrients	0.372	0.139	5, 14	n.s.	0.004
Physical features	0.876	0.771	2, 17	**	0.002
Zuddeo					
All features	0.745	0.555	7, 16	*	0.799
Nutrients	0.319	0.102	4, 19	n.s.	1.043
Physical features	0.544	0.296	2, 21	*	0.878
Structural features	0.543	0.295	1, 22	**	0.858

$^*P < 0.05$; $^{**}P < 0.001$.

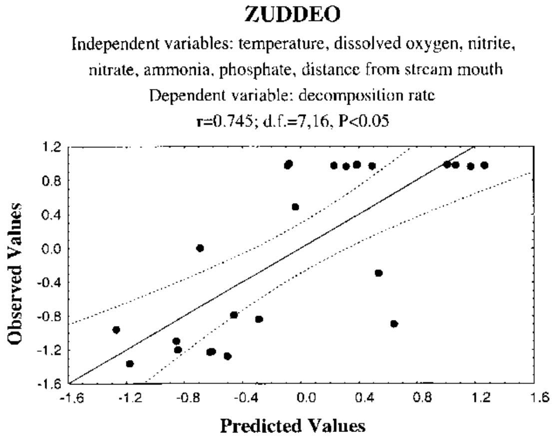


FIGURE 5 Relationships between predicted and observed values of leaf pack decay rates in the Zuddeo stream. Data are normalized by average values and standard deviation.

characteristic and physical factors. On a seasonal basis, a pattern was identified only for the physical features, which explained 98% of decay-rate variance in the summer–autumn period and 45% in the winter–spring period.

4 DISCUSSION

4.1 Decomposition Rates and Decay Patterns of *P. australis* in the Lake Alimini Complex

Litter breakdown has been widely studied in aquatic ecosystems, including rivers, lakes and salt marshes (Polunin, 1984; Newell, 1993). The common reed, *P. australis*, has received considerable attention in this context because it is an important primary producer in those ecosystems (Akanil and Middleton, 1997; Wrubleski *et al.*, 1997; Denward and Tranvik, 1998; Rossi and Costantini, 2000). Decomposition processes of reed leaves have been investigated in different ecosystem types in which reed decay rates ranged from slow to fast, according to Petersen and Cummins (1974) depending on different factors, including the climatic features of the geographical area of each ecosystem. Low reed decay rates were found in colder regions, as in central and northern European lakes ([$k = 0.002$] Meulemans and Roos, 1987; [$k = 0.001$] Hietz, 1992; [$k = 0.004$] Gessner *et al.*, 1996) and in mountain streams at higher altitudes than the Zuddeo stream ([$k = 0.006$] Akanil and Middleton, 1997). Therefore, the decay rates of reed leaf packs obtained in the present study in the Lake Alimini complex are faster than those observed in colder regions and accord with those observed in previous studies carried out in the Mediterranean area in coastal lagoons (Fazi and Rossi, 1996; Rossi and Costantini, 2000) and rivers (Pinna *et al.*, 2003).

P. australis leaf detritus showed a seasonal pattern of decomposition with decay rates significantly higher during spring–summer than during autumn–winter. This seasonal pattern of leaf-detritus breakdown is consistent with the temporal trend of decomposition processes observed for plant detritus in other aquatic ecosystems (Reice, 1974; Suberkropp *et al.*, 1976; Short *et al.*, 1980). However, the seasonal heterogeneity of reed detritus decomposition processes in the Alimni complex was not the same for all ecosystem types. In the two lenthic ecosystems, reed leaf breakdown rates were higher in the warmer periods than in the other periods, reflecting the high seasonal variation of the water temperature (8–29 °C over the year), while they were almost constant in the stream.

The temporal and spatial patterns described for *P. australis* decay rates in the Lake Alimini complex are unlikely to be due to methodological biases arising from the experimental treatment of the leaf material (Newell, 1996), the timing of leaf collection (Gessner, 1991), the use of oven-dried leaves instead of fresh leaves or air-dried leaves (Bärlocher, 1991; 1992; Gessner, 1991) and the use of different parts of the reed plants (Kufel and Kufel, 1988; Gessner, 2000). For this study, we collected all leaves at the same time and from the same area at the beginning of autumn, we cut off the basal and apical parts of all leaves, and we used only the central leaf sections for the leaf packs. Therefore, eventual bias as a result of the procedures used in this study may have affected the absolute value of decay rates, as a systematic bias, rather than the spatial and temporal patterns of reed decay rates, the analysis of which represents a major objective of this study.

4.2 Inter-Habitat *vs.* Intra-Habitat Differences in Decomposition Rates

The analysis of the results concerning the spatial variability of reed detritus decomposition rates in the Lake Alimini complex highlights two important points:

(1) The decomposition processes of *P. australis* leaves show both inter-habitat and intra-habitat heterogeneity in the Lake Alimini complex.
(2) The structural features and physical–chemical parameters of each ecosystem are factors which influence the spatial heterogeneity of reed processing rates in the Lake Alimini complex.

The first point is supported, first of all, by evidence that reed decomposition processes are faster in the stream than in the two lakes, and faster in the freshwater than in the brackish lake, in every seasonal period. These results are in agreement with those obtained in studies comparing plant detritus decay rates in lotic and lentic ecosystems. Lower decomposition rates have been observed in lakes than in streams (Hodkinson, 1975; Gasith and Lawacz, 1976; Webster and Simmonds, 1978; Cortes *et al.*, 1995). Basset and Rossi (1985) found lower decomposition rates in a central Italian freshwater lake than in its tributary. The most interesting difference between other investigations of the spatial patterns of plant detritus decomposition processes and the present investigation is the comparative analysis in this paper of reed decomposition processes carried out among different ecosystem types located in the same geographical area. Here, the three ecosystems investigated have the same climate and natural rock substrate and do not have permanent physical barriers to the dispersion of either invertebrates or micro-fungi, at least between the two freshwater ecosystems. The salinity barrier is broken in the winter period when the water salinity of Lake Alimini Grande remains very low along the shoreline between the freshwater stream mouth and the freshwater lake (Basset, 2000). Accounting for these structural and physical–chemical features of the Alimini complex, it can be used profitably as a natural mesocosm in which there is experimental evidence of the differences between detritus decomposition processes in lentic and lotic ecosytems, and freshwater and brackish ecosystems.

Differences in leaf mass decay rates were also observed in the Alimini complex within each ecosystem type. The intra-habitat spatial variability of litter breakdown is more significant in the stream than in the lakes, and more significant in the brackish than in the freshwater lake. In the lotic ecosystem, differences in *P. australis* decay rates were observed between sampling stations located in the northern part of the stream, where the stream bed is artificial, and the other stations. Reed decay rates in the Zuddeo are always faster where the stream bed is artificial than where it is natural. However, spatially homogeneous litter breakdown was observed among sampling stations in the southern section of the stream. In the brackish lake, reed leaves decompose more rapidly in the northern than in the southern area, and in the areas in which freshwater comes into the lake than in the central area. In the freshwater lake, where structural features and physical parameters are more constant in space and time, reed decay rates were almost homogeneous among sampling stations.

The second point concerns the identification of factors limiting reed processing rates in the two lakes compared with the stream. The results highlight the different relevance of structural features and physico-chemical parameters to reed leaf decomposition processes among different ecosystem types. A higher percentage variation of reed decay rate‘ is accounted for by abiotic factors in the two lakes than in the stream. In addition, a seasonal pattern of physico-chemical features and litter breakdown was observed in each ecosystem.

The most important difference between lotic and lentic ecosystems is current velocity, which can affect processing rates directly, through leaf fragmentation (Witkamp and Frank, 1969; Hodkinson, 1975; Gurtz and Tate, 1988), and indirectly, by renewing oxygen and favouring microbial activity (Reice, 1974; Godshalk and Wetzel, 1978). The spatial heterogeneity of litter breakdown observed in the Alimini complex cannot be due to the direct influence of current velocity, since freshwater inflow was low on average in the Zuddeo ($6.2 \times 10^3\,\mathrm{m}^3\,\mathrm{g}^{-1}$), and the leaf packs were protected from fragmentation by the net. Moreover, superficial sediments in both lakes are generally in oxygenated conditions throughout the year, and the stream water is always well oxygenated (Basset, 2000). Taking these characteristics into account, the indirect influence of the temperature on microbial and invertebrate activity, via differential oxygen renewal rates, should be limited to the summer season and thus would not explain the differences observed throughout the year.

Some authors (Howarth and Fisher, 1976; Elwood *et al.*, 1981) have found that leaf breakdown rates increased under conditions of nitrogen and phosphorus enrichment, while in experimental channels, large-scale nitrate addition did not accelerate weight losses from leaf packs (Triska and Sedell, 1976). In this work, nutrient concentrations played a role in the intra-habitat heterogeneity in the two lake ecosystems, as well as in the inter-habitat differences between freshwater and salt-marsh ecosystems; however, they cannot account for the differences observed between processing rates in the two freshwater ecosystems. Moreover, the fact that intra-habitat processing rates co-varied with nutrient concentrations only in the lake ecosystems strongly suggests that micro-organisms play a more important role in the two lakes than in the stream, as has been suggested (Basset and Rossi, 1985). The differences among ecosystems and sampling sites in the decay rates of single leaf substrates are commonly attributed to differences between the activity of micro-organisms and benthic invertebrates (Saunders, 1976). However, their activity is only the proximate cause of decomposition rates; it is factors affecting their activity that should be considered the ultimate causes. In the Lake Alimini complex, the comparisons of inter- and intra-habitat reed decomposition rates indicate that the structural features and physical–chemical parameters (ultimate causes) of each ecosystem are the factors which determine the spatial heterogeneity of reed processing rates, by affecting the abundance and metabolic activity on leaf packs of the actual agents (proximate cause) of reed decomposition.

The results for the spatial heterogeneity of detritus processing suggest that the inter- and intra-habitat differences in reed decomposition processes in the Lake Alimini complex may be attributable to limitation of the shredding fauna colonizing the leaf packs. This hypothesis is supported by two principal points:

(1) Shredders are less likely to be limited in lakes, where detritus decomposition processes are slower, shredder density is generally lower, and microbial activity has a major role.

(2) In streams, however, where the speed of decomposition processes is generally regulated by benthic invertebrate activity, there seems to be a limitation of the shredding fauna; this is supported by the higher reed processing rates found in sampling stations with an artificial stream bed and small amounts of detritus than in stations with a natural stream bed and plant detritus retention during autumn–winter.

5 CONCLUSIONS

The results of the present study are consistent with the following conclusions:

(1) *P. australis* reed leaves in the Lake Alimini complex decompose at medium-fast decay rates.
(2) The decomposition rates of *P. australis* leaf litter differ significantly along an ecological gradient of ecosystem types from freshwater stream to freshwater lake and brackish lake.
(3) Comparisons of intra- and inter-habitat variability of *P. australis* leaf processing provide information on the major ecological abiotic forces driving decomposition processes in the studied ecosystems.

The present investigation emphasizes the differences in reed decomposition processes among ecosystems of different types and suggests that a complex ecosystem made up of a plurality of ecosystem types, such as the Lake Alimini basin, constitutes an interesting field laboratory in which to test directly hypotheses on factors limiting detritus processing in aquatic ecosystems.

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