The aquatic processing of sclerophyllous and malacophyllous leaves on a Mediterranean island (Corsica) : spatial and temporal pattern

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Keywords : decomposition, leaves, *Alnus glutinosa, Quercus ilex*, macroinvertebrates, Mediterranean ecosystem, temperature.

Leaves of two species, alder (*Alnus glutinosa*) and holm-oak (*Quercus ilex*), were exposed in bags of two mesh sizes in two climatically contrasting sites of a Corsican softwater stream. Leaves were incubated both in winter and in summer for about 6 months. The field experiment was designed to determine the influence of both spatial (climate) and temporal (season) variations of temperature, as well as differences in the chemical and physical properties of sclerophyllous and malacophyllous leaves, on leaf decomposition rates. Comparisons were made between leaves colonized by macroinvertebrates and leaves protected by fine-mesh. In winter and summer, holm-oak leaves were colonized much less by macroinvertebrates than alder leaves. Spatial and temporal differences in leaf litter processing were mainly dependent on three factors (i) the chemical and physical properties of the leaves, (ii) the abundance of macroinvertebrates in the sediment and (iii) the temperature. The climatical pattern of temperature had a greater influence than its seasonal pattern. In contrast with many other studies, abiotic factors dominated over biotic factors in this study.

La dégradation aquatique des feuilles sclérophylles et malacophylles sur une île méditerranéenne (Corse) : dynamique spatio-temporelle

Mots clés : dégradation, feuilles, *Alnus glutinosa, Quercus ilex*, macroinvertébrés, écosystème méditerranéen, température.

Des feuilles d'aulne (*Alnus glutinosa*) et de chêne vert (*Quercus ilex*) ont été exposées dans une rivière de Corse, dans deux stations différentes d'un point de vue climatique, l'une méditerranéenne et l'autre montagnarde. La dégradation a été suivie et comparée dans deux types de sachets à fine (0.3 mm) et grosse (5 mm) maille. L'expérimentation avait pour but de déterminer l'influence des variations de la température à la fois dans l'espace (climat) et dans le temps (saison), sur le taux de dégradation des feuilles. Des différences dans les propriétés chimiques et physiques des feuilles sclérophylles et malacophylles, ainsi qu'entre des feuilles colonisées ou non par des macroinvertébrés ont été observées. Les feuilles de *Quercus ilex* ont été toujours beaucoup moins colonisées que celles d' *Alnus glutinosa*. Les différences spatio-temporelles de la dégradation des feuilles dépendaient surtout de trois facteurs (i) les qualités physiques et chimiques des feuilles, (ii) l'abondance des macroinvertébrés dans le sédiment et (iii) la température. L'influence de la température est apparue plus importante au niveau climatique qu'au niveau saisonnier. La dégradation dans la rivière est davantage influencée par les facteurs abiotiques que par les facteurs biotiques, ce qui contraste avec beaucoup d'autres études.

1. Introduction

In the past three decades, many authors have emphasized that the energy input to small temperate lotic ecosystems is largely supplied by the woody riparian vegetation (Minshall 1967, Benfield et al. 1979, Chauvet et al. 1984). The processing dynamics of this allochthonous organic matter, once in the stream, depends on both physico-chemical and biotic factors (Wallace et al. 1982, Webster 1983). Their relative importance is determined mainly by the geographical location and consequently by climate. A prominent factor of climatic and seasonal variability is temperature. On the one hand, it directly controls the processing of coarse particulate organic matter by determining the rate of leaching and the speed of metabolic processes (Nykvist 1962). On the other hand, temperature influences the life history patterns of the micro- and macrofauna and

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the aquatic and the riparian flora as well. In this paper, the former phenomena will be called direct, the latter indirect influences. All of the following reflections focuse on a comparative analysis of climatic and seasonal characteristics of the study sites, which are considered as spatial and temporal pattern.

To date most research on the decomposition of organic matter in streams has been performed in temperate regions of the Northern Hemisphere, and it has focused primarily on the transformation of autumn-abscised leaves. The impact of climatic differences and seasonal variations of leaf characteristics (Stout et al. 1985) on processing rates has attracted less attention, and the published results are contradictory. Some authors found temperature to be the major controlling factor (Reice 1974, Benfield et al. 1979, McArthur et al. 1988), while others reported a predominance of factors such as the structure and chemical composition of the leaves (Chergui & Pattée 1990). As for climate, the influence of temperature appears to be obvious: the warmer the region, the faster the decomposition. However, a comparison between temperate and warmer climates reveals that it is difficult to discriminate between a direct or indirect influence of temperature (Chergui & Pattée 1991), because there are many interfering factors:

1) Under the conditions of a Mediterranean climate, leaf abscission of several species (e.g. holm-oak) occurs not only in autumn but also in early summer;

2) Hydrological regimes of streams in Mediterranean regions are different from those in temperate regions, resulting in different disturbance regimes;

3) The riparian vegetation is interspersed with sclerophyllous species, whose leaves have a morphology and contain substances, which are likely to reduce their palatability for macroinvertebrates and hamper microbial decomposition. This influence of leaf characteristics on community structure has become widely recognized (Cameron & Lapoint 1978, Bengtsson 1992);

4) The macroinvertebrate communities are composed of different species;

5) Furthermore, each stream ecosystem has its own variability of properties, be it on the microclimatical or the biotope level. This results in a considerable within-stream variability of leaf breakdown dynamics, as has been demonstrated for temperate regions (Reice 1974, Rosset et al. 1982, Mutch et al. 1983).

In order to ascertain the role of temperature in leaf processing it is necessary to find a study area where at most some of the above mentioned variabilities can be isolated or excluded. The Porto River in Corsica meets these requirements. It allows a simultaneous experimental study on the influence of temperature on leaf processing dynamics in both spatial (climatic zone) and temporal (season) respect. The leaves studied were of the species alder and holm-oak, both common along the Porto River. They form a stream corridor typical of many Mediterranean freshwaters (Dierschke 1974, Chauvet et al. 1984).

This investigation on the influence of temperature as a seasonal and climatical variable is one aspect of this study. In order to study the influence of macroinvertebrates on leaf decomposition rates under these conditions, we used two mesh-sizes, one of them excluding macroinvertebrates. Another aspect is understanding the characteristics of sclerophyllous leaves (here: evergreen, e.g. holm-oak) as opposed to those of malacophyllous leaves (here: leafless in winter, e.g. alder). Additionally, the differences in the aquatic decomposition of naturally fallen yellow-brown summer leaves and green winter leaves of holm-oak were studied. Under natural conditions green holm-oak leaves will rarely enter streams; hence, they are to be considered as an uncommon substrate.

2. Study area

The study was performed at two sites in the Porto River, a softwater, mountain stream located in western Corsica (France). The headwaters spring at 1580 m, and after 22 km the stream flows directly into the Mediterranean Sea (Fig. 1). The mean channel gradient is about 6 %. Owing to the steep slope and the altitude of the mountains on the west coast, even this small stream crosses several climatic regions from its source to its mouth. The stream is second order (Strahler system) at the mountain site (P1) at 1130m a.S. and fourth order at the Mediterranean site (P2) located at 213m a.S.. The climate of P1 is comparable to that of temperate zones of Central Europe; the climate is Mediterranean at P2. Water temperatures ranged seasonally between 0.3 °C (January) and 12.5 °C (July) at P1 and between 2.5 °C and 16.5 °C at P2 (Fig. 2). The streambed of both sites is mainly composed of cobble (P1 14%, P2 22 %) and boulders (P1 67 %, P2 69 %). Many stream parameters are similar, such as chemical composition of the water (Table 1), current velocity (Table 1), sediment complexity and species composition of macroinvertebrate «leaf-decomposers» (Table 2). Adjacent to the study area the predominant trees are *Alnus glutinosa* (L.) Gaertn., *Fagus sylvatica* (L.) and *Pinus nigra* Arnold subsp. *laricio* (Poiret) Maire at P1. At P2 the woody riparian vegetation is dominated by *Alnus glutinosa* (L.) Gaertn. interspersed with specimens of *Quercus ilex* (L.).
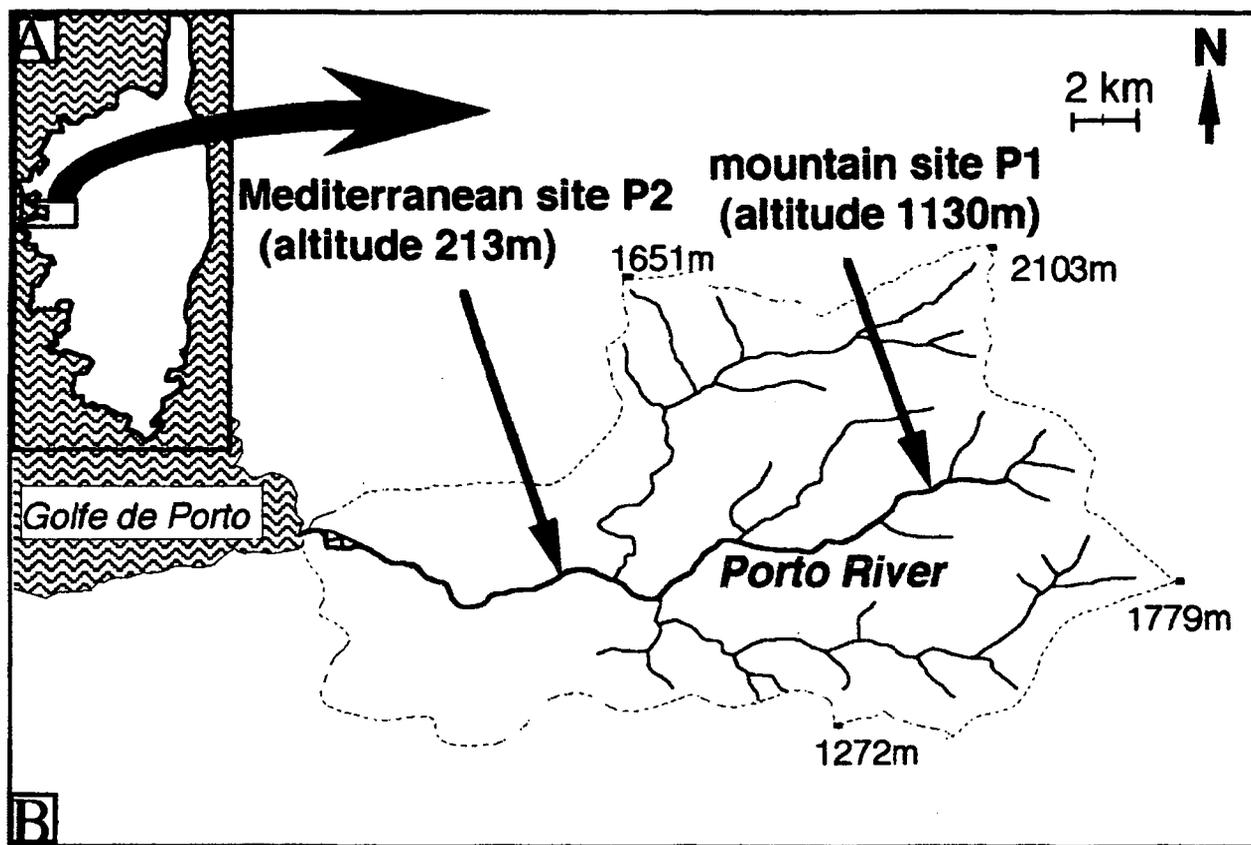
Fig. 1. Geographic location of the study sites. **A**. Position of the catchment area. **B**. Hydrographic system of the Porto River with the study sites.

Fig. 1. Localisation géographique des stations d'étude. **A**. Situation du réseau hydrographique. **B**. Système hydrographique de la rivière Porto avec les stations d'étude.
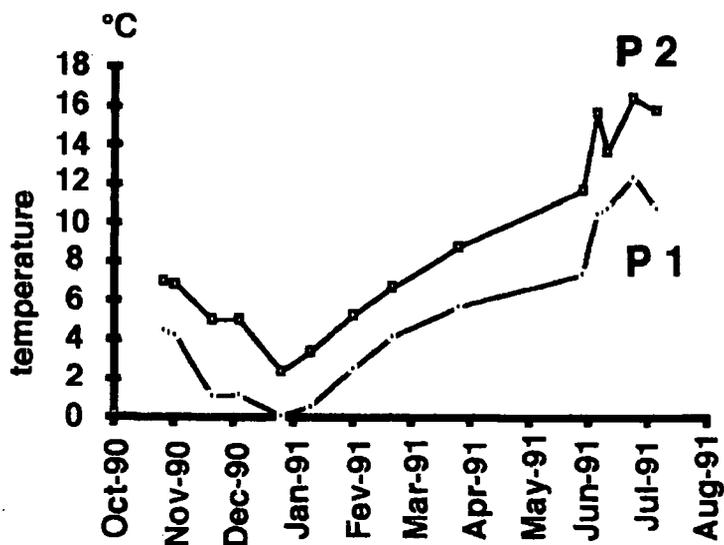

Fig. 2. Water temperature at the mountain and the Mediterranean site during the study period.

Fig. 2. La température de l'eau aux stations montagnarde (P1) et méditerranéenne (P2) pendant la période d'étude.

3. Materials and methods

The experiments for comparing processing rates of sclerophyllous and malacophyllous leaves were car-

ried out at the mountain site starting on 20.11.1990 (winter incubation). The influence of temperature as a climatic variable was studied comparing the mountain and the Mediterranean sites during summer, starting on 20.06.1991 and using holm-oak (summer incubation). The influence of temperature as one seasonal variable was studied at the mountain site by exposing two series of holm-oak leaf bags in winter and in summer.

3.1. Winter incubation

Fresh leaves of two species, alder and holm-oak were collected on 19.11.1990. The green, malacophyllous, naturally abscised alder leaves were collected on the ground. Only undamaged leaves were taken. The green, sclerophyllous holm-oak leaves were picked from the trees. Alder and holm-oak leaves were stored in plastic bags and taken off only for the short time of manipulations. The leaves were weighed fresh in batches of 15.0 ± 0.05 g for alder and 13.00 ± 0.05 g for holm-oak and enclosed in 30 x 10 cm mesh bags of two different mesh sizes of $\emptyset$ 0.3 and 5 mm. Most macroinvertebrates were excluded by 0.3 mm meshes, whereas according to Rosset et al. (1982) even the large fungal spores have free access to the leaves. The co-

Table 1. Chemical and hydrological characteristics of study sites. The data are mean values over the study period from November 1990 to July 1991. NO^3-N, NH^4-N, P-PO^4 were measured following the French standard procedure (NF), Ca^{2+} the German standard procedure (DIN) respectively.

Tableau 1. Caractères physiques et chimiques des stations d'étude. Les données représentent des valeurs moyennes, calculées sur toute la période d'échantillonnage de novembre 1990 à juillet 1991. NO^3-N, NH^4-N, P-PO^4 ont été mesurées selon la norme française (NF), Ca^{2+} selon la norme allemande (DIN).

	mountain site	Mediterranean site
conductivity (μS . cm^{-1})	78	96
pH	6.6	7.0
NO_3-N (μg . l^{-1})	800	1000
NH_4-N (μg . l^{-1})	300	100
P-PO_4 (μg . l^{-1})	<10	<10
Ca^{2+} (mg . l^{-1})	6.6	7.0
mean current velocity (m · s^{-1})	0.3	0.3
mean water depth (m)	0.35	0.55
mean bankful width (m)	5.3	15.8

arse-mesh size of 5 mm provided a free access to most stream invertebrates, while minimizing the loss of large particles (Rosset et al. 1982, Mutch et al. 1983). Every single mesh bag was supported by a fence-wire frame (diameter 7 cm), thus preventing collapse and ensuring water circulation inside the bag. For both species, a total of 120 bags were submerged, 60 at each site, including 30 coarse- and 30 fine-mesh bags. The bags were separately tied to a cable that was pressed down with cobbles on the stream bottom and exposed in slow-flowing zones of the Porto stream. From collection to submersion passed at most 18 hours. In addition, 9 batches of holm-oak and 7 batches of alder leaves were not submerged, but dried (105 °C, 42 h) immediately after collection and weighed in order to convert fresh-mass to dry-mass. The calculated values of initial dry-mass per leaf-batch were 5.68 ± 0.18 g for alder and 7.51 ± 0.9 g for holm-oak. After 6, 22, 95 and 212 days, from November 1990 till June 1991, 3 replicates of each leaf species and mesh size were removed at random from the stream and stored in an icebox until arrival at the laboratory (2.5 h drive), where they were frozen at -18 °C. This experimental procedure could be carried out only at the mountain site. At the Mediterranean site, most mesh bags were lost due to a rain spate, four days after exposure.

The abundance of macroinvertebrates in the sediment was also determined. The sampling was effected all 2-3 weeks between December 1990 and March 1991, of which the data from 14.12.1990 and 23.02.1991 are presented in the figure 7. Three replicates were taken by surber-sampling (respectively $0.33m^2$), the macroinvertebrates picked out immediately and later counted and determined to the lowest possible taxon according to various literature references (Giudicelli 1968, Tachet et al. 1987 i.a.).

3.2. Summer incubation

As one of the abscission periods of holm-oak is in early summer (the second in early autumn), naturally abscised leaves were collected in June, 1991. The leaves had a yellow-brown colour and were dry and crisp. After being dried at 105 °C (48 h), their mass loss was 38.2 %, compared to 42.2 % for the green leaves in November. For exposure, the non-dried leaves were also weighed into portions of 13.00 ± 0.05 g and enclosed in mesh bags of the same type as those used in the winter incubation. The calculated value of initial dry-mass per leaf-batch was 8.03 ± 0.08 g.

A total of 60 bags was submerged, 30 (15 coarse- and 15 fine-mesh bags) at each site. 3 replicates of each mesh size at each site were retrieved after 7, 12, 25, 37 and 199 days over a period of 6 months of incubation (June 1991 - January 1992). In the following, the samples were treated in the same way as those of the winter incubation. However, uninvited human curiosi-

Table 2. Listing of the taxa of macroinvertebrates found in the leaf-batches. F stands for very frequent and f for less frequent. Differences in sites (mountain and Mediterranean site) are shown (+ present, - absent).

Tableau 2. Liste des taxons de macroinvertébrés trouvés dans les feuilles exposées. F signifie très fréquent et f moins fréquent. Les différences par stations (mountain and Mediterranean site) sont montrées (+ présent, - absent).

Taxa	SEASON		SITE	
	Winter	Summer	moun.	Med.
Ephemeroptera				
Habrophlebia fusca (Curtis)	F	F	+	+
Baetis sp.	F	F	+	+
B. ingridae (gr. rhodani) (Thomas&Soldan)	f		+	+
Ephemerella ignita (Poda)	F	F	+	+
Caenis gr. luctuosa (Burmeister)	f	F	+	+
Plecoptera				
Isoperla sp.	f		+	+
Leuctra budtzi (Petersen)		F	+	+
Euleuctra geniculata (Stephens)		f	+	+
Trichoptera				
Philopotamus sp.	f	f	+	+
Wormaldia mediana (Mac Lachlan)		F	-	+
Polycentropus sp.		f	+	+
Plectrocnemia sp.		f·	+	+
Micrasema togatum (Hagen)		f	-	+
Allogamus corsicanus (Ris)	F		+	-
Silonella aurata (Hagen)		F	-	+
Setodes argentipunctellus (Mac Lachlan)		F	+	+
Sericostoma clypeatum (Hagen)	f		+	+
Diptera				
Chironomidae	F	F	+	+
Tipula sp.	f		+	+
Ibisia marginata (Fabricius)	F	F	+	+

ty caused the removal of mesh bags and therefore gaps in the data (samples after 199 days in the Mediterranean site and after 37 days in the mountain site).

3.3. Preparation and chemical composition of the leaves

Recovered leaves were removed from the mesh bags and cleaned with a soft paint brush under a gentle stream of water during defrosting. Invertebrates, sediment and detritus were removed. Leaves were dried at 105 °C for at least 42 h and weighed on a Mettler balance to the nearest mg. Then, they were ground to fine powder and dried again before subsamples were weighed for the chemical analyses. Replicate samples were analysed separately for the determination of phosphorus content and ash-free dry-mass and then pooled for the C- and N-analyses. Ash-free dry-mass was determined by burning samples of leaf material in a muffle furnace (4 h at 550 °C). Analyses of carbon and nitrogen were performed on a Heraeus CHN-O-Rapide elemental analyzer for the samples of the summer period and those of the first sampling date in winter. The other samples were analysed for N using the Kjeldahl technique. Phosphorus content was determined after acid digestion ($H_2 SO_4$, $H_2 O_2$, 180°C).

The macroinvertebrates retained on a 300 μm sieve were picked under a binocular microscope with 12x magnification, counted and determined to the lowest possible taxon. Chironomids were not determined to the subfamily level.

The daily exponential processing coefficient k was calculated from the equation wt = wo . e^{-kt} (model 1), in which wt = residual mass at time t and wo = initial mass (Olson 1963). Log e - transformed values were linearly regressed (including time=0 days) to calculate the decay coefficients k. Differences in breakdown rates were tested by analysis of covariance (ANCOVA).

4. Results

4.1. Comparison of alder (malacophyllous) and holm-oak (sclerophyllous) leaves

Within species, the processing of alder leaves was significantly slower in mesh bags excluding macroinvertebrates than in mesh bags with macroinvertebrates (Fig. 3 A). In holm-oak leaves only the last amount, after 212 days (30 weeks), showed a significant difference (Fig. 3 B). Between species the curves of the coarse-mesh bags exhibited higher decomposition rates for alder than for holm-oak leaves from the beginning of the exposure period (p < 0.05 after 6 days).

The simple exponential model did not give a perfect fit for the mass loss data. The theoretical T_{50} (time to decompose 50% of the initial mass) calculated for alder with that model is 51 days for the coarse-mesh size and 546 days for the fine-mesh size (Table 3), whereas

the actual T_{50} measured for alder in coarse-mesh bags was 112 days (Fig. 3 A).

Nitrogen was present in higher concentrations in alder than in holm-oak (Fig. 4 A). There was an initial increase in relative N content which was more pronounced in alder than in holm-oak leaves. The dynamics of the phosphorus concentrations were also characterized by a marked increase from day 0 to day 6 in all cases. The initial concentration in holm-oak leaves (0.149 % of dry-mass) was twice as high as in alder leaves (0.076 % of dry-mass) (Fig. 4 B).

After 6 days a mean number of 25 macroinvertebrates (5,18 individuals per gram leaf dry-mass) was found on alder leaves but not a single macroinvertebrate on holm-oak leaves; after 22 days there were 36 (7,8 see above) and 5 (0,7 see above) individuals, respectively, on the two leaf types (Fig. 5 A). Macroinvertebrates were always more abundant in alder than in holm-oak (Fig. 5 A). The highest number of taxa (mainly species level) found in the leaves was 10 for both species and was reached in June, at the end of the exposure period.

4.2. Influence of temperature (only holm-oak)

4.2.1. Temporal pattern (season)

The initial daily loss of mass was higher during the summer incubation than during the winter incubation (1.0 % per day and 0.8 % per day respectively) in both mesh sizes (p < 0.01). No significant seasonal difference in residual dry-mass of holm-oak was observed

Table 3. Values of Wo (mg) and k (d⁻¹) for winter and summer incubations in coarse- (5 mm) and fine- (0.3 mm) mesh bags. The data sets were fitted to a simple negative exponential model. Time (days) to 50 % weight loss (T_{50}) was also calculated with the exponential model (see in the text explanation of terms).

Tableau 3. Valeurs de Wo (%) et k (d⁻¹) des incubations hivernale et estivale dans des sachets de grosse (5mm) et fine (0.3 mm) maille. Les données ont été adaptées à un simple modèle exponentiel négatif. Le temps (jours) de 50 % de perte de masse (T_{50}) a été calculé avec le modèle exponentiel (voir dans le texte l'explication des termes).

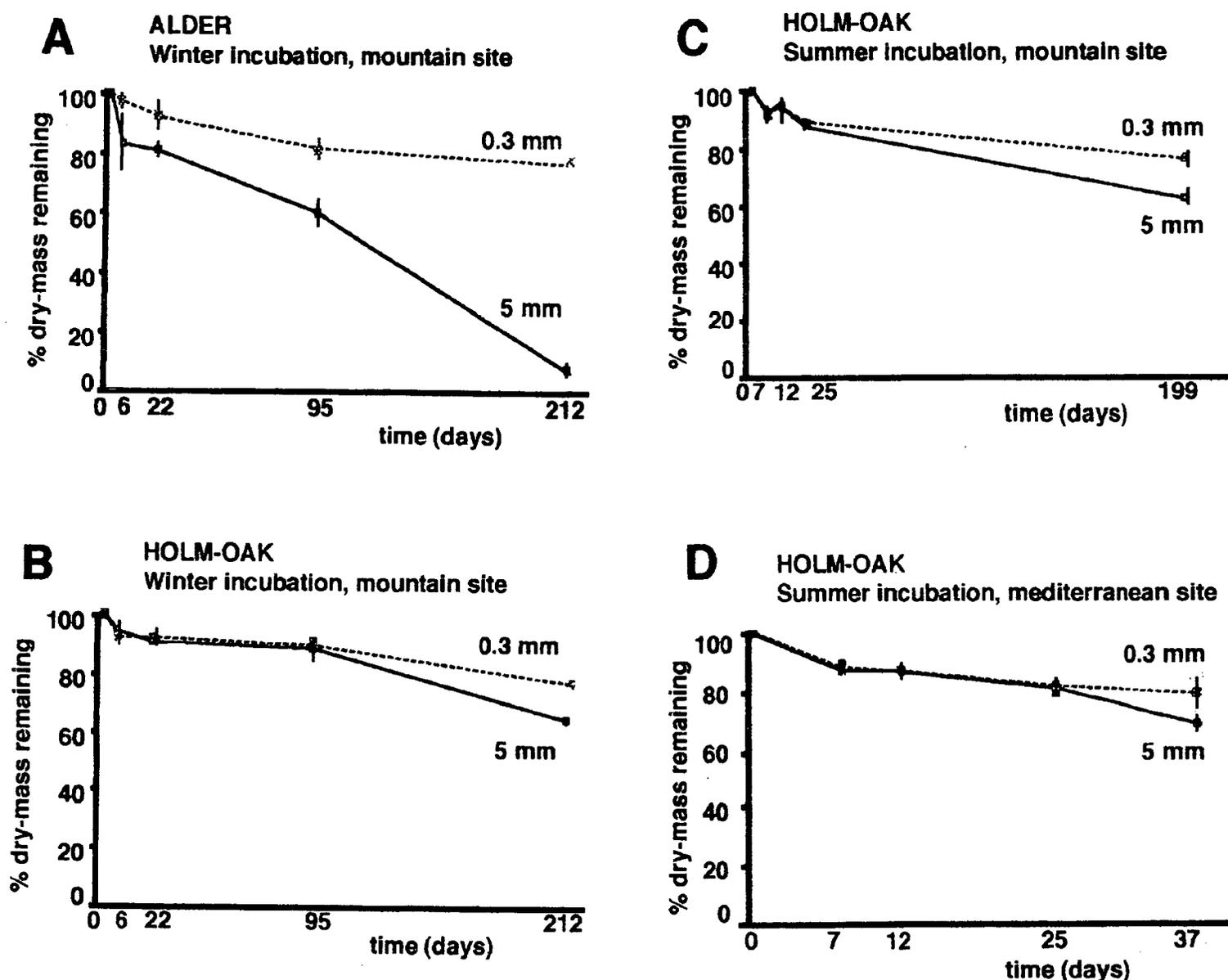|			Wo	r	k	T_{50}
Winter incubation						
P 1	alder	0.3 mm	98.24	0,94	-0.0011	546
	alder	5 mm	108.27	0.96	-0.0117	51
P 1	holm-oak	0.3 mm	97.07	0.96	-0.0010	656
	holm-oak	5 mm	98.67	0.96	-0.0018	365
Summer incubation						
P 1	holm-oak	0.3 mm	94.52	0.93	-0.0011	606
	holm-oak	5 mm	96.39	0.99	-0.0022	303
P 2	holm-oak	0.3 mm	94.65	0.91	-0.0055	121
	holm-oak	5 mm	97.55	0.97	-0.0091	73

Fig. 3. Breakdown of alder (**A**) and holm-oak (**B, C, D**) leaves in bags with fine- (0.3 mm) and coarse- (5 mm) meshes at the mountain site (**A, B, C**) and at the Mediterranean site (**D**). Error bars indicate 95 % confidence intervals.

Fig. 3. Dégradation des feuilles d'aulne (**A**) et de chêne vert (**B, C, D**) dans des sachets à fine (0.3 mm) et à grosse maille (5 mm) à la station montagnarde (**A, B, C**) et à la station méditerranéenne (**D**).

(Fig. 3 B, C).The concentrations of phosphorus and nitrogen were both higher in green winter leaves (0.149 and 1.29 % of dry-mass respectively; Fig. 4 A, B) than in yellow-brown summer leaves (0.087 and 0.85 % of dry-mass respectively; Fig. C, D). The C/N ratio was 39:1 for winter leaves and 60:1 for summer leaves before exposition, even though the summer leaves were colonized faster and with higher initial abundances by macroinvertebrates (Fig. 5 A, B). 101 individuals colonized the leaves after 7 days during summer incubation, whereas no macroinvertebrates could be found after 6 days during winter incubation (Fig. 5 A, B).

4.2.2. *Spatial pattern (climate)*

During the entire study period, from November 1990 until July 1991, the temperature of the two study sites differed by at least 2.5 °C (Fig. 2). The mass loss (Fig.

3 D) and the processing coefficients (Table 3) also differed clearly between the two study sites. Nitrogen concentrations reached higher values from the beginning at the Mediterranean site and continued to increase (Fig. 4 C). The number of taxa was higher at the Mediterranean (18) than at the mountain (10) site, but the main taxa appearing on the leaves were the same. At the Mediterranean site Ephemeroptera were always dominant (Fig. 6 B), while at the mountain site chironomids and Ephemeroptera alternated in dominance (Fig. 6 A). This was observed over about the same period at the mountain (27.06.91 - 15.07.91) and at the Mediterranean site (27.06.91 - 27.07.91). The composition of the macroinvertebrate community colonizing the leaves was not representative of the community found in the sediment (Fig. 7).
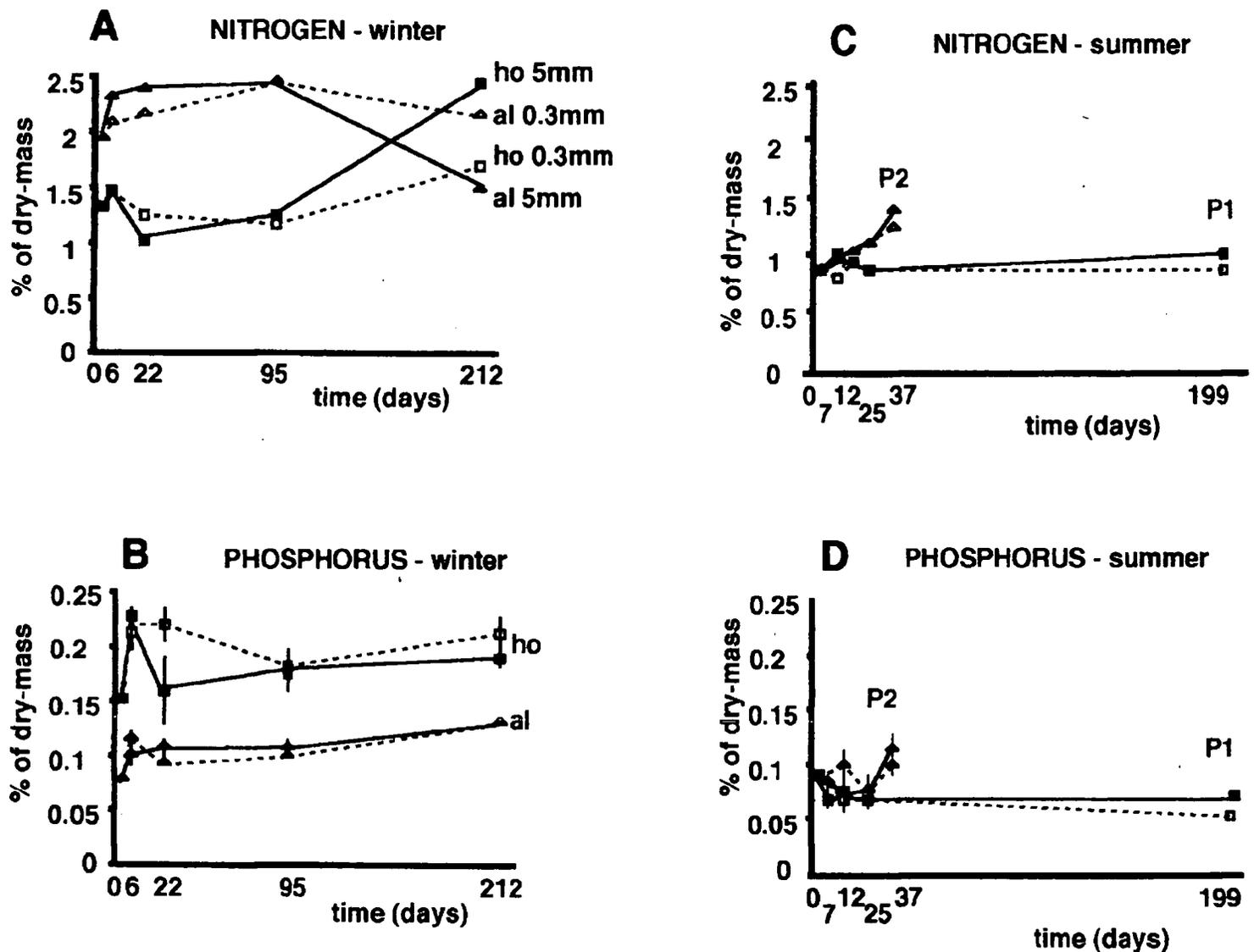
Fig. 4. Nitrogen (A, C) and phosophorus (B, D) concentrations in alder (al) and holm-oak (ho) leaf litter during decomposition in fine- (0.3 mm) and coarse- (5 mm) mesh bags at the mountain site in winter. Error bars indicate 95 % confidence intervals.

Fig. 4. Concentrations d'azote (A, C) et de phosphore (B, D) dans des feuilles d'aulne (al) et de chêne vert (ho) pendant la décomposition hivernale à la station de montagne dans les deux types de sachets - fine (0.3 mm) et grosse (5 mm) maille.

5. Discussion

5.1. Comparison: alder leaves in the Porto and in other studies

It is difficult to compare the leaf processing coefficients calculated in this study with those published by other authors on the basis of the negative exponential model (Olson 1963), because of major differences in experimental designs (Winterbourn 1978, Benfield et al. 1979, Dance 1981, Rogers 1983, Robarts 1986, Chergui & Pattée 1990). Thus, we only compared the coefficients determined for the same leaf species and obtained with the same method, e.g. exposure of leaves, enclosed but loosely stocked in mesh bags and

not tied together as leaf packs. Even then, methodological differences remain due to the different mesh sizes used, the sizes of the leaf-batches and the positions of mesh bags in the current and the stream-bed during exposure (Reice 1974, Benfield et al. 1979, Mutch et al. 1983).

With the former assumptions in mind, we found that in the Porto River, with $k = 0.0117 . d^{-1}$, the alder broke down slower than in the Steina River, a softwater stream in the Southern Black Forest (Germany), where the decay coefficient was $k = 0.0229 . d^{-1}$ (10 mm mesh size) (Gessner et al. 1991). The study sites of both streams are similar in sediment and chemical compositions, as well as in climatic conditions. The difference

A WINTER INCUBATION

B SUMMER INCUBATION

A MOUNTAIN SITE

B MEDITERRANEAN SITE

Legend:
- **Diptera**
- **Ephemeroptera**
- **Trichoptera**
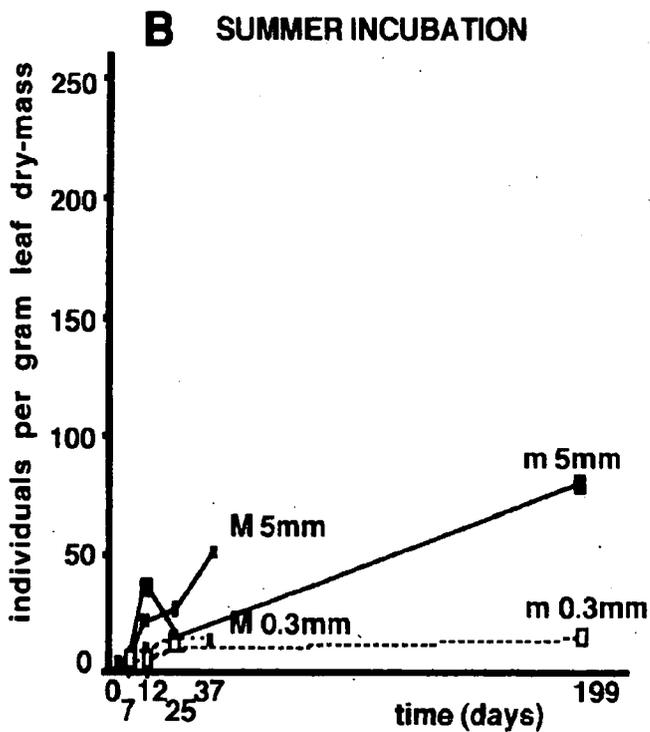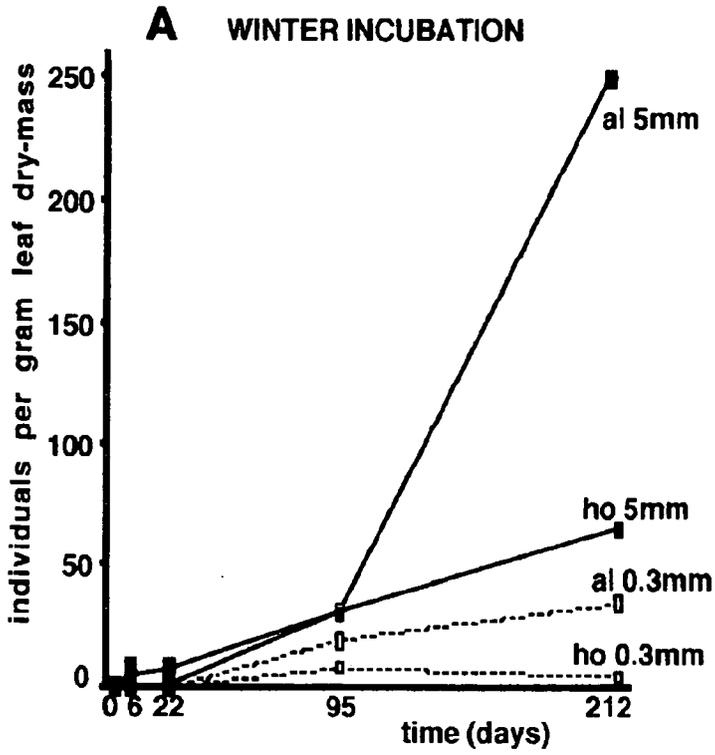- **Plecoptera**
- **other taxa**

Fig. 5. Density of macroinvertebrates on alder (al) and holm-oak (ho) leaves in fine- (0.3 mm) and coarse- (5 mm) mesh bags. Data shown as numbers per gram remaining leaf dry-mass. A represents alder and holm-oak at the mountain site, B only holm-oak but at two sites, the mountain (m) and the Mediterranean (M) site.

Fig. 5. Densité des macroinvertébrés sur feuilles d'aulne (al) et de chêne vert (ho) dans les sachets de fine (0.3 mm) et de grosse (5mm) maille en hiver. Les données sont présentées en nombre d'individus par gramme de poids sec résiduel. A représente l'aulne et le chêne vert à la station montagnarde, B seulement le chêne vert mais dans les deux stations montagnarde (m) et méditérranéenne (M).
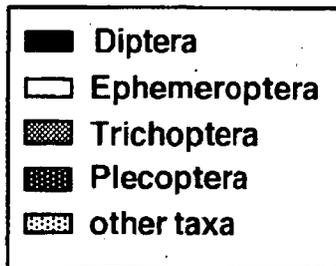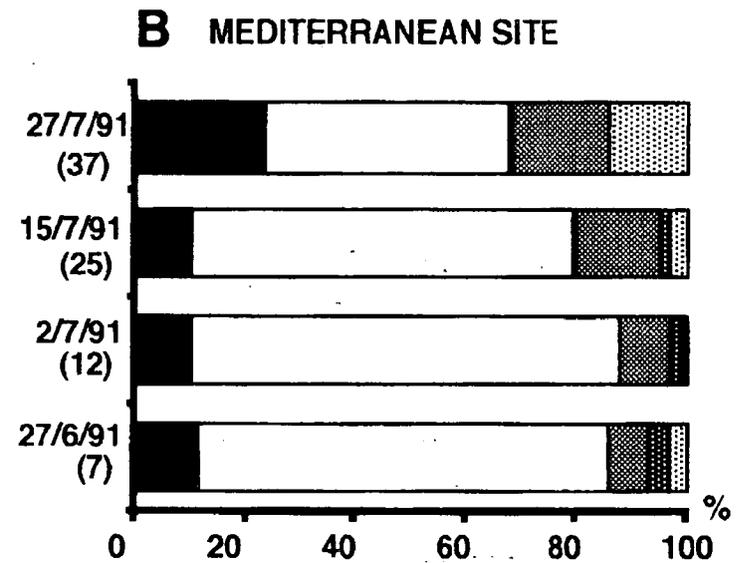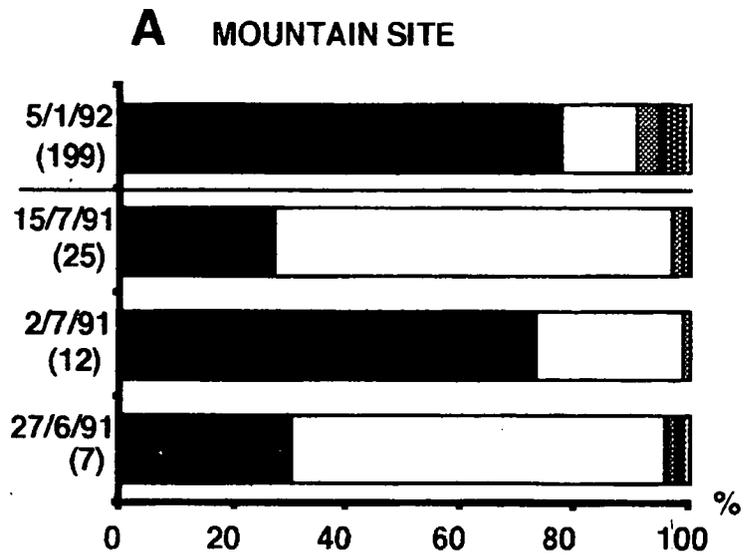
Fig. 6. Percentages of taxonomic groups on holm-oak leaves in coarse-mesh bags during summer incubation at the mountain (A) and the Mediterranean (B) site. Days of exposure are given in brackets under each date.

Fig. 6. Pourcentage des groupes taxonomiques sur feuilles d'aulne et de chêne vert dans des sachets à grosse maille pendant l'été à la station de montagne (A) et à la station méditerranénne (B). Les jours d'exposition sont marqués entre paranthèses sous chaque date.
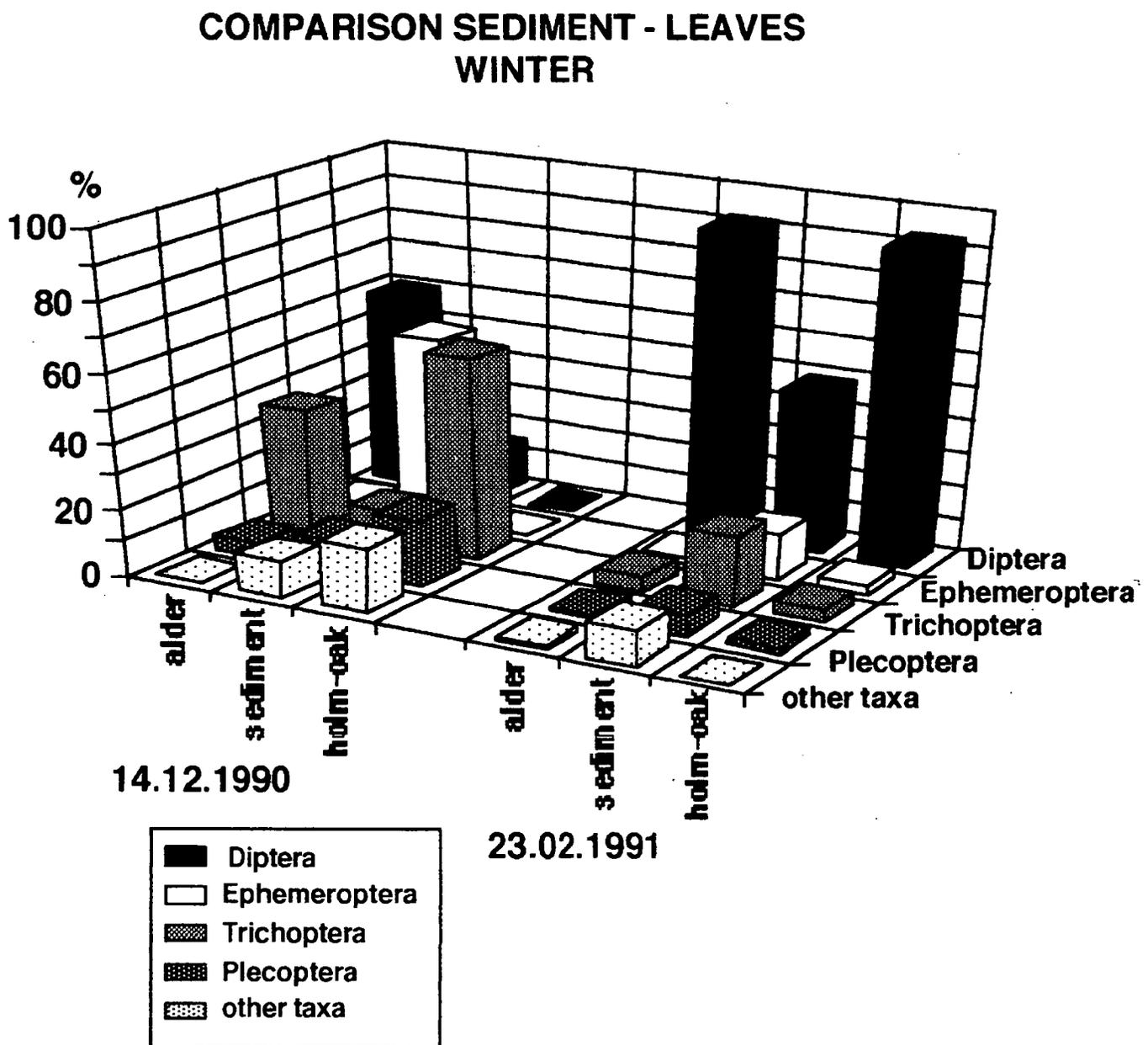
COMPARISON SEDIMENT - LEAVES
WINTER

Fig. 7. Comparison between the fauna found on leaves of alder and holm-oak in coarse-mesh bags and in the sediment.
All data only shown for the mountain site.

Fig. 7. Comparaison entre la faune trouvée sur les feuilles d'aulne et de chêne vert dans des sachets à grosse maille et
dans le sédiment. Les données sont celles de la station montagnarde.

between the decay coefficients becomes even more evident when one takes into consideration that the exponential model overestimated the breakdown rate of the Corsican alder. Chergui & Pattée (1990), who also used a mesh size of 10 mm, calculated a breakdown coefficient of $k = 0.010 \cdot d^{-1}$, using predried leaves and exposing the mesh bags in a lentic system. In spite of using the same mesh size here as Gessner et al. (1991), the decay coefficients of these two studies clearly differ. Even taking into account that the quantity of particles lost by hydraulic stress (Ward 1984) increases with the mesh size and the current velocity, it is not clear why studies using the same mesh size (Gessner et al. 1991, Chergui & Pattée 1990) and exposing leaves

in comparable morphodynamic units (Gessner et al. 1991, this study) produce such different decay coefficients.

We expect, that one explanation for the difference between slow and rapid decomposition of alder leaves could be the characteristics of the invertebrate communities on the sediment. The general influence of invertebrates on the breakdown of organic debris has been demonstrated experimentally by the treatment of a small stream with insecticides, which caused reduced aquatic insect densities and consequently a reduction in the breakdown rates of leaf detritus (Wallace et al. 1982). In our study, the same effect can be observed by comparing the breakdown rates of alder leaves in fine-

and coarse-mesh bags. Without macroinvertebrates, the percentage of remaining dry-mass after 6 months remains the same, independent of leaf species and season, while the influence of macroinvertebrates, especially for alder, causes higher decay coefficients.

Regarding the extent of influence, there is a close connection between the abundances of invertebrates on the sediment and the invertebrate densities in the leaf-batches. For the Porto and the Steina rivers such an effect can be clearly demonstrated. High abundances in the exposed leaves (176 ind./mesh bag, after 3 days) correspond to high densities on the sediment (15000 ind./m^2) (Meyer 1992), whereas in the insular Porto River low abundances in the leaves (25 ind./mesh bag after 6 days) correspond to low densities on the sediment (500 ind./m^2). Hart & Howmiller (1975) also noted a higher «biomass density» (mg wet-mass of invertebrates per g dry-mass of leaves) on leaves of *Quercus macdonaldii* that had been exposed in a continental Southern Californian stream (Refugio Creek) than of those exposed in an unnamed stream on Santa Cruz Island. Unfortunately, no data are given on slope or discharge, so we can only note that in both studies the insular running waters had a lower density of invertebrates on exposed leaves than the continental running waters. It would be interesting, above all for theoretical development, to stick to the insular effect and perhaps to combine it with the hypothesis from Irons et al. (1994) about the latitudinal gradient in the relative importance of invertebrate v microbial processing changes, with invertebrates being more important at high latitudes.

However, when we consider that the density of macroinvertebrates in Meyer's study (1992) described above was about 30 times as high as in our study, we may assume that the influence of macroinvertebrates in the Porto River is smaller. Since the influence of microorganisms also is not important, as shown by the results of the 0.3mm mesh-bags, we conclude that this lotic-system is controlled mainly by physical factors such as the steep slope and the high discharge amplitudes, implying an increased instability and a decreasing amount of breakdown of leaf litter (Reice 1974). We suggest, that most leaves, once in the Porto, are not processed but transported unprocessed downstream.

5.2. Comparison : malacophyllous and sclerophyllous leaves

The holm-oak leaves had the typical morphological and chemical characteristics of sclerophyllous leaves, namely a thick cuticle on the top side and a transpiration protection in the form of stellate hairs on the lower

side (Guttenberg 1907), as well as a high content of polyphenols (Gessner 1991). The content of nitrogen and phosphorus of the summer leaves were much lower than those of the winter leaves, and the surfaces were obviously aged (Guttenberg 1907, Juniper 1991). The holm-oak leaves were processed much more slowly than the alder leaves, the decay coefficients for both coarse- and fine-mesh sizes being more than ten times lower. After 3 weeks of leaf exposure, no macroinvertebrates at all had appeared on the holm-oak leaves, and at the end of the exposure time, after 30 weeks, alder was still more 'attractive' than holm-oak in all cases, although the alder leaves were almost completely decomposed. In contrast, holm-oak leaves had scarcely been processed at the end of the experimentation period. We hold the hypothesis that there are mainly two factors explaining these results: the concentration of phenolics and the physical toughness of the leaves. Phenolics are known to slow down the rate at which decomposers utilize allochthonous debris and to inhibit decomposer population size, either directly by toxicity or indirectly by causing poor resource availability. Hence, high concentrations of phenolics serve as a deterrent for invertebrates as well as for hyphomycetes and bacteria. This affects not only the initial stage of decomposition, which lasts from 1 (Cameron & Lapoint 1978) to 2 weeks (Suberkropp et al. 1976) after incubation, but also later on the palatability of leaves, when the phenolics have not been extracted completely by stream water and form complexes with proteins (Rosset et al. 1982). In green, fresh holm-oak leaves measured phenolic concentrations of 13 % of dry-mass, while alder attained only 4.7 % of dry-mass (Gessner 1991). In addition, the physical thoughness of the holm-oak leaves may protect against forces of the current, invertebrate jaws and attacks of microbes as well (Allen et al. 1991).

We conclude that the lower processing of the holm-oak leaves is indeed mainly an expression of their lower food-value, in comparison to alder leaves.

5.3. Influence of temperature (only holm-oak)

5.3.1. *Temporal pattern (season)*

We found a significantly faster processing of the summer holm-oak leaves than of the winter leaves in mesh bags of both sizes during the first week. Winter leaves immersed for 212 days and summer leaves immersed for just 7 days, both exposure periods ending in summer, had been colonized with similar abundances of macroinvertebrates (101 and 103 ind./ mesh bag respectively). It seems that over a longer exposure period the recalcitrant effect of winter leaves can be compen-

sated, but is still important in comparison with alder leaves. Beyond that, the yellow-brown summer leaves are presumably from the beginning less recalcitrant, because they are in a way leached. However, no one has measured the concentrations of phenolics in holm-oak summer leaves. Beside these leaf internal factors, again the abundance of invertebrates on the sediment must be considered. The number of individuals per mesh bag colonizing holm-oak summer leaves after 7 days was four times as high as that found on alder leaves in winter, although the latter are a far better food source in terms of C/N ratio. This phenomenon can be explained by the abundances found on the sediment in summer (738 ind./m^2), which were much higher than in winter (446 ind./m^2). The indirect influence of temperature intervened, causing the seasonal variations in invertebrate communities (Garden & Davies 1989). Here, as elsewhere, we found a close connection between the abundances of invertebrates on the sediment and their densities in the leaf-batches. This close connection is therefore one of the most important reasons for the differences in breakdown rates regarding the seasonal ranges within one and the same, as well as between several freshwater systems. The latter has been shown by Rowe et al. (1996), who compared three different streams of the Cheat River drainage in north-central West Virginia. Beyond this comparison that showed significant differences for all variables considered, including breakdown rates, invertebrate densities, invertebrate biomass, the authors also compared two study periods of one and the same stream respectively and found no significant differences. From this they conclude that changes in temperature may be relatively less important to stream processes than physical and chemical differences among streams. But, if one looks to the periods compared that last from October to January and from November to February one may ask if this socalled periods really stay the hypothesis about the less importance of temperature over time.

Our results are also in contrast to those of McArthur et al. (1988), who found highest total oxygen consumption and the highest activity of shredders/leaf-pack in autumn, drawing the conclusion that the life histories of invertebrates are keyed to the main import of allochthonous detritus to freshwaters in autumn. We cannot support this hypothesis, because in our study the abundances of invertebrates in the leaves and on the sediment were always higher in summer (July) than in late autumn (December). We also could not find a difference between the colonization dynamics of leaf-batches at the mountain site, where no significant input of organic matter in summer occurs, and at the

Mediterranean site, where a natural organic input occurs in June. The benthic community of the Porto River does not seem to depend directly on the input of organic matter in terms of freshly fallen leaf litter. The results of a study conducted by Mackay & Kalff (1969) on seasonal variation and species diversity of the insect community confirms this hypothesis. They found that the number of insects in the leaves ranged from low in October, associated with dispersal into the freshly fallen leaves, to high in September when entire leaves were at a minimum.

5.3.2. Spatial pattern (climate)

Significantly faster processing occurred at the Mediterranean site than at the mountain one. The decay coefficient of the former site was four times higher than the latter, for the both mesh sizes. Phosphorus and nitrogen both reached higher concentrations at the lower site. The initial increase in nitrogen concentration is commonly ascribed to colonization by microorganisms, thus microbial activity at the Mediterranean site appears to have been much higher than at the mountain site. Presumably, the direct influence of higher temperatures intervenes here. This influence certainly also affected the leaching phase, which could not be characterized by measurements but was indicated by the increased mass loss after one week of incubation, independent of mesh size and study site. In the literature, this influence of temperature on leaching and microbial metabolic activity is well known (Nykvist 1962) and has been discussed extensively (review Chergui & Pattée 1990).

As for the colonization by macroinvertebrates, there were similar abundances at both sites, but the invertebrate communities in the leaf-batches were structured differently. However, it seems that the holm-oak leaves exposed at the Mediterranean site were somehow more attractive for the macroinvertebrates:

1) the concentration of nitrogen continued to increase (Table 4), indicating an increasing or at least a constant microbial activity (Suberkropp et al. 1976);

2) the curves with and without invertebrates diverged at least from 6 weeks onward (Fig. 3 D). Losses of particles, due to higher hydraulic stress, can be excluded (Rosset et al. 1982);

3) the similar dominance of the invertebrate community in the leaf-batches indicate their stability.

We assume that the direct influence of temperature on the metabolism of the microorganisms at the Mediterranean site resulted in a higher microbial production and thus a higher biomass available for the macroinvertebrates. This means that the climatic (spatial) in-

fluence of temperature was more important than the seasonal (temporal) influence.

Further studies must be performed to test the influence of other important factors controlling the processing of leaf litter, e.g. the abundance of macroinvertebrates in the sediment and the composition of the microbial community colonizing recalcitrant leaves.

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