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# Influence of the environment on willow leaf litter decomposition in the alluvial corridor of the Garonne River

By E. CHAUVET

With 4 figures in the text

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## Abstract

A net bag method has been used to study the decomposition of *Salix alba* leaves in five Garonne corridor sites (fast running water, slow flowing water, standing water, floodable willow stand, non floodable willow stand). Changes in the contents and the amounts of some leaf litter constituents were assessed over a 40 week period. Willow leaves decomposed rapidly and, in some cases, this could be described by an exponential model ( $k = 0.0040$  to  $0.0121 \text{ d}^{-1}$  depending on site). Carbon content was rather stable. An absolute increase in nitrogen was observed at all sites for the first weeks. Cellulose loss was less rapid in slow flowing or standing waters and on floodable soils. The lignin fraction accumulated rapidly and was generally 50% after 40 weeks. Decomposition rates were not significantly different at aquatic and terrestrial sites. Both in waters and on soils, oxygen levels and temperature control the decomposition kinetics, especially of cellulose and lignin.

## Introduction

The banks of large rivers, as in other types of wetlands, are usually characterized by being very productive (LIETH, 1975). The transition zones between terrestrial and aquatic ecosystems are influenced by flooding and are subject to considerable spatial and temporal variations in such parameters as water content and oxygen level. The riparian forests play a part in the Nutrient Spiralling Flux (WEBSTER, 1975; NEWBOLD et al., 1982 a, b; ELWOOD et al., 1983) along the "river continuum" (VANNOTE et al., 1980; MINSHALL et al., 1985). A portion of the matter and energy originating upstream are ultimately immobilized in the form of riverside plant production and as sediment deposited following flooding. The biomass thus produced can return to the rivers in the form of leaf litter, either by falling directly into the water or indirectly via the soil. The significance of the leaf litter in the functioning of lotic ecosystems is acknowledged both upstream (BIRD & KAUSHIK, 1981) and downstream (SWANSON et al., 1982; SEDELL & FROGGATT, 1984). After a variable period in different receiving environments the riparian forest leaf litter thus influences the nutrient cycle in rivers. All this has been investigated in streams, however little is known about the extent it also applies to rivers. PATTEE et al. (1986) recently

demonstrated that the type of aquatic environment (stream, main river channel, oxbow) did have an influence on the disappearance rate of dead leaves.

The aim of the present study is to compare the kinetics of decomposition of willow leaves at five sites rising from the river up to higher non floodable levels. In addition the change in carbon, nitrogen, cellulose and lignin leaf litter contents is studied as these parameters are generally considered as good indicators of decomposition processes (TRISKA et al., 1975; BRINSON, 1977; MELILLO et al., 1983).

### Localities

The wooded river banks (*Salix alba* L.) studied are located on the Garonne River, south of Toulouse and downstream of the Ariège inflow (Fig. 1 A). Fig. 1 B represents a schematic section of the Garonne River bed and six sites, three aquatic (fast running water, slow flowing water, standing water) and three terrestrial (floodable willow stand, non floodable willow stand, island). However, these six sites are not adjacent, with the sites of the slow flowing water and island being located several kilometers downstream of the four other sites. At the fast running water site the mean depth was 60 cm and the substratum composed of pebbles and gravel while at the slow flowing water site the depth was

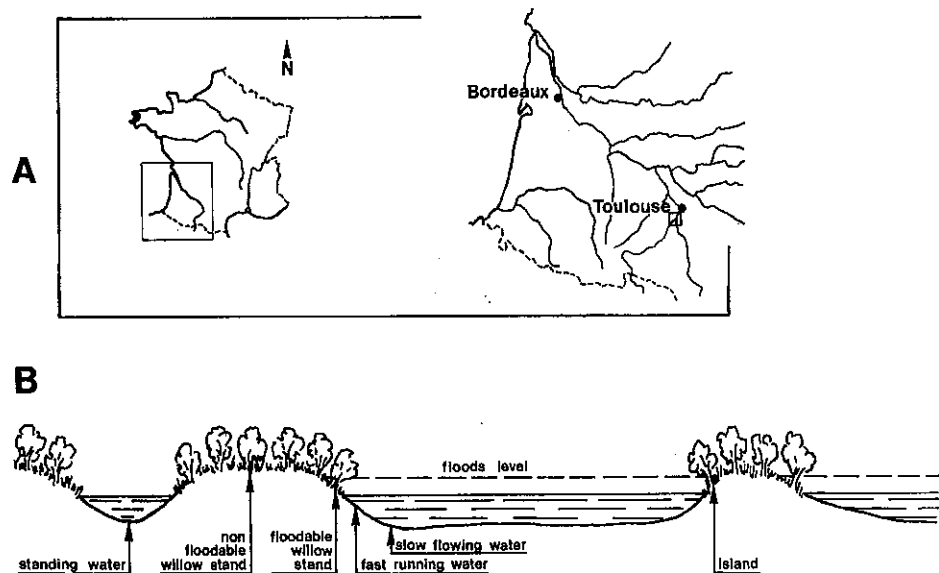


Fig. 1. Location map (A) and section of the Garonne River with the sites (B).

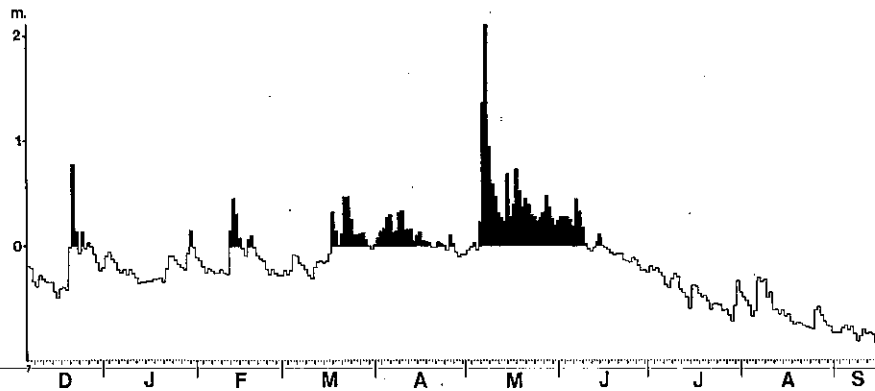


Fig. 2. Daily water level change in the Garonne River during the study period (in metres). Black parts indicate flooding at site 4.

about 2 meters and the bottom consisted of silt and sand. At the oxbow site (standing water) located 400 meters from the Garonne River itself, the depth was approximately 1.5 meters and the substratum composed of silt and decomposing plant matter. The water temperature varied from 4 to 20 °C during the year with the mean pH lower in standing water (7.6) than in the Garonne River (8.2). The non floodable willow stand was located 60 meters from the Garonne River whereas the floodable willow stand was found where trees overhang the river. This latter site was subject to alternate periods of flooding and desiccation. In spring the site can be flooded for several days (Fig. 2) and after the drawdown the leaves were usually covered with sediment. The one hectare island was an almost pure willow stand that remained largely unflooded; however, the chosen site here did flood to the same extent as the floodable willow stand site. As decomposition rate and chemical changes were quite the same in the floodable soil and the island sites, the latter has been omitted for the discussion of the results. In addition to the willow trees these sites consisted of a high and usually very thick herbaceous layer (approximately 2.7 tons of dry matter/hectare/year) almost exclusively made up of *Urtica dioica* L. and *Impatiens Roylei* Walpers or *I. parviflora* DC (CHAUVET et al., in preparation). The soil temperature varied annually between -5 and +20 °C.

### Material and methods

The nylon net bag method used has been described (CHAUVET, 1987). Although it must be used cautiously (PARK, 1974; BENFIELD et al., 1979) the method is common to both terrestrial (ANDERSON, 1973 a; ABER et al., 1984) and aquatic (HODKINSON, 1975; IVERSEN, 1975) environment studies. Samples of whole newly-fallen leaves (5 g.), air dried for a week, were placed in 2 mm-mesh net bags. In the aquatic environments the bags

were tied to weights which kept them close to the river bed while on land the bags were staked to the forest floor. The bags were put into place 7th December 1984 and three samples were removed after 4, 8, 16, 24, 32 and 40 weeks, respectively, at each site. The leaves were carefully washed with tap-water and dried at 50 °C for three days. After weighing, the samples were ground. For each determination, a 250-mg sample was used. The organic matter content was measured after being placed in an oven at 550 °C for two hours. The carbon content was measured by conductometrical determination of CO<sub>2</sub> liberated after combustion (Carmograph Wösthoff apparatus). The Kjeldahl nitrogen determination was made following mineralisation (H<sub>2</sub>O<sub>2</sub> 50% + H<sub>2</sub>SO<sub>4</sub> conc) with the Nessler's colorimetric reaction. The cellulose and lignin were determined according to GOERING & VAN SOEST's (1972).

## Results

The quantities of leaf constituents measured at each date and at each site are expressed as the percentage of the initial amounts (Fig. 3) and as the content of each component related to the ash free dry weight (Fig. 4).

### a) Organic matter

In the three aquatic environments the amounts of organic matter fell to less than 7% of the initial amount after 40 weeks (Fig. 3). Decomposition was the most rapid in fast running water and the least rapid in standing water followed closely by the slow flowing water. The disappearance of organic matter in the Garonne currents was very rapid: within the first 8 weeks almost 50% of the leaf had disappeared and at the end of 40 weeks the leaves were almost completely decomposed. The decline fitted quite well to an exponential model of the  $W_t = W_0 \cdot e^{-kt}$  type (OLSON, 1963) where  $W_t$  represents the weight remaining at time  $t$ ,  $W_0$  the initial weight and  $k$  the decomposition rate constant. The correlation coefficient ( $r$ ) calculated from the semi-logarithmic linear regression was 0.986 whilst, according to the linear hypothesis, the coefficient would have been 0.921. However, the comparison of the two coefficients is only indicative because the semi-logarithmic transformation distorts the computed coefficient of an exponential curve (CHAUVET, 1987). The conclusion was reached then that an exponential model applied quite well to the data. However, it would now appear that, over a longer period, neither an exponential model ( $r = 0.902$ ) nor a linear model ( $r = 0.958$ ) is suitable. In fact, after a 24 weeks period when the decomposition rate decreased and tended towards a limit of approximately 50% of the initial mass, decomposition set in again and within 16 weeks the second 50% of the leaf decomposed (3% remained). The same phenomenon was found in standing water with the first phase of decline (67% of the initial mass) after a shorter period (16 weeks) and a second one during which 60% of the leaf decomposed (7% remained).

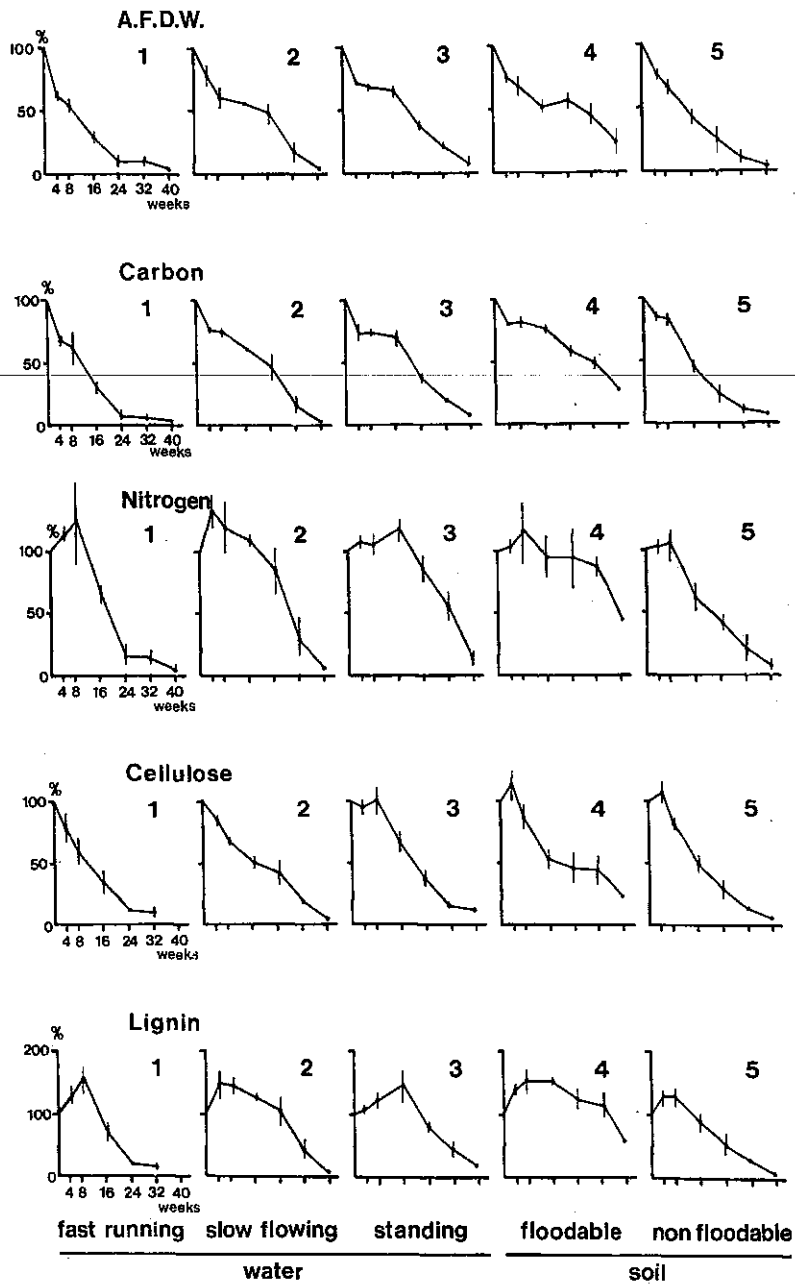


Fig. 3. Change in the ash free dry weight (organic matter), carbon, nitrogen, cellulose and lignin quantities of willow leaf litter, expressed as a percentage of the initial amounts (mean  $\pm$  S.D).  $n = 3$  except for the 40th week where only 1 to 2 samples were recovered. The cellulose and lignin values of site 1 are missing for the 40th week (the sample mass was insufficient for analysis).

In the case of the terrestrial environments the decomposition pattern in the non floodable willow stand differed very sharply from that in the floodable site. Out of reach of flooding, half of the leaf litter decomposed in approximately 3 months and disappearance was almost complete in 40 weeks. In this case both an exponential model ( $r = 0.976$ ) and a linear model ( $r = 0.979$ ) could be satisfactorily applied to the decomposition kinetics. A rather rapid decomposition occurred on the floodable soil during the first 16 weeks (50% of the initial mass) followed by an increase in the organic matter amount (2 to 5%), followed by a second decrease with a 25% residue after 40 weeks. The slight increase in the organic matter coincided with the spring flooding which deposited on the leaf litter a layer of sediment of up to 10 cm. Thus this exogenous organic matter was probably of sedimentary origin, because the sediments contain about 7% of organic matter and washing couldn't be so efficient on such samples. In the case of the floodable site a decomposition in three stages was observed with firstly a relatively rapid decline as in the case of the higher levels, followed by a slowing-down if not a halt due to the sediment deposit, and finally a starting-up again of decomposition in summer. Moreover, the same pattern applied to the kinetics observed in slow flowing water because the leaves there acted as sediment traps.

#### b) Carbon

The carbon fraction in the leaves remained relatively constant during decomposition (Fig. 4). Changes in carbon contents showed increases and decreases depending on the site, but were generally not significant. Because of the relative stability of carbon content during decomposition, the change in carbon amount followed quite closely that in organic matter amount (Fig. 3).

#### c) Nitrogen

In both the aquatic and terrestrial sites the nitrogen content increased considerably and usually reached a maximum after 8 to 16 weeks (except in site 3), then decreased (sites 1–2) or remain high and constant at a mean content of 2 to 2.5% at the end of the experiment (Fig. 4). The shape of the curve was the same in fast running water and in slow flowing water, but the phenomenon was more prominent in site 1, with a maximum of 3.9%; than in site 2 with a maximum of 3.3%. A very sharp increase in nitrogen concentration in standing water was also observed, but later and with a maximum of 4.6% after 32 weeks. The phenomenon appeared to be less pronounced in the terrestrial than in the aquatic sites.

Whatever the site, there was an absolute gain in nitrogen during the first 12–16 weeks of decomposition (Fig. 3). This could only come from a contribution of nitrogen of exogenous origin. In the aquatic sites the gain, with a

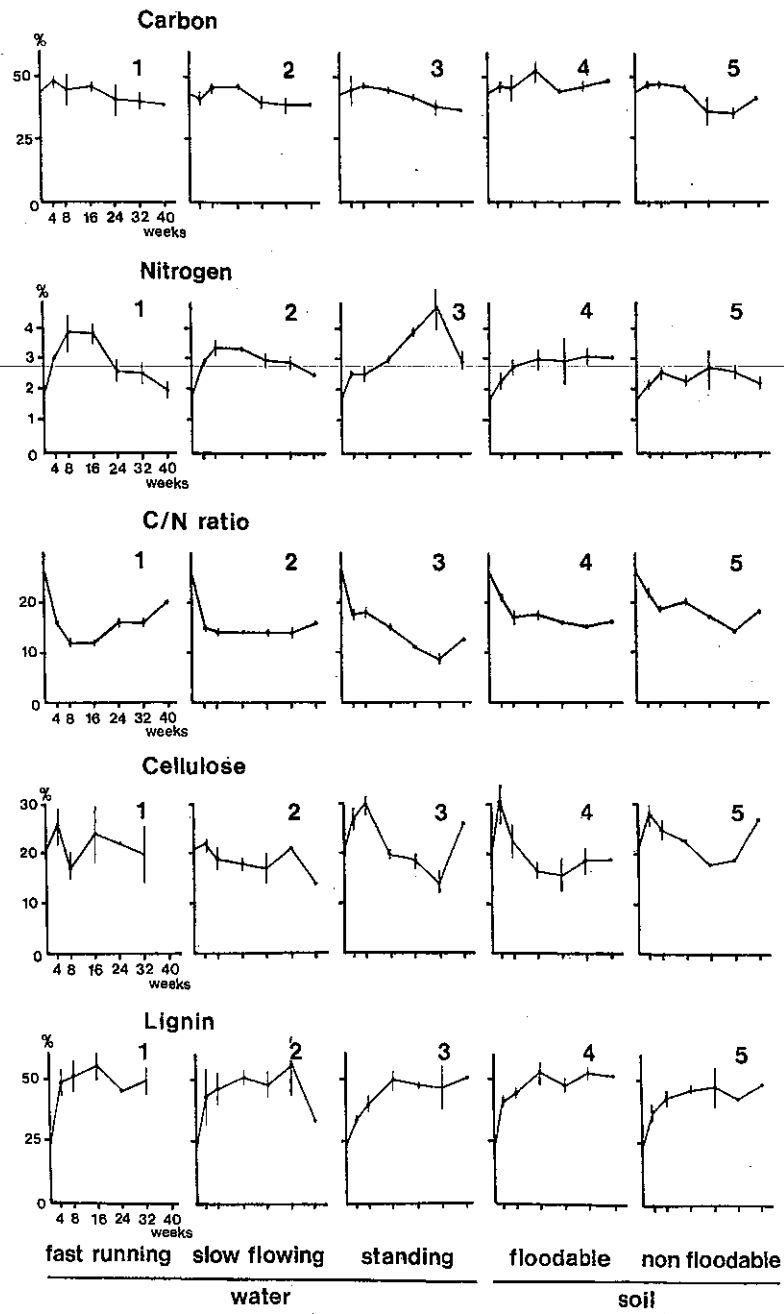


Fig. 4. Change in the carbon and nitrogen contents, in the C/N ratio and in the cellulose and lignin contents of willow leaf litter, expressed as a percentage of the ash free dry weight.



maximum of 18 to 34 % depending on the site, was slightly higher than in the terrestrial ones with a maximum of 16 % in the floodable site and only 5 % in the non floodable willow stand.

During the first months of decomposition there was a sharp and systematic decline in the C/N ratio of leaves, to 12 in fast running water and 8.4 in standing water (Fig. 4). The fall was slightly less pronounced in the terrestrial sites where the minimum ratio was from 14 to 15 after 32 weeks on floodable or non floodable soils. At the end of decomposition (40th week) the C/N ratio increased noticeably because of the fall in nitrogen amounts, except in slow water, where the C/N was almost stable after the 1st month.

#### d) Cellulose

The change in the cellulose contents was rather irregular and varied depending on the site (Fig. 4). However, a significant increase was observed during the first 4 weeks, with a concentration which went from 20.6 to 22–31 % of the organic matter amount, depending on the site. In fast running water the amount decreased to 17 % after 8 weeks, increased again after 16 weeks then decreased. In slow flowing water, the concentration declined up to the 24th week. It then increased up to the 32th week and finally decreased to a minimum of 17 %. In standing water the change was similar to that in the terrestrial sites, with an initial pronounced increase, then a decline up to approximately the 32th week, followed by an increase towards the end of the experiment.

The cellulose curve (Fig. 3) allowed a differentiation between the river waters sites and the others. In the Garonne River the change in the amount of cellulose was on the whole comparable to that of organic matter or carbon, but was slightly more rapid in site 1. In the standing water the cellulolysis appeared to be stopped during the first two months since 100 % of the initial amount of cellulose was recovered after 8 weeks but the following change was quite rapid. At the terrestrial sites a systematic increase of 6 to 14 % of the initial amount of cellulose during the first 4 weeks was observed, followed by a decomposition phase whose kinetics were comparable to those of organic matter or carbon.

#### e) Lignin

During decomposition, the lignin content changes were approximately the same in the different types of sites (Fig. 4). A sharp increase was observed during the 16 first weeks, followed by a relative stability at about 50 % of the organic matter amount until the end of decomposition (except in site 2). In the fast running water the lignin content went from 22.3 to 47 % within 4 weeks and reached 54 % within 16 weeks. In the slow flowing water the concentration increased to 55 % during the first months of decomposition but then de-

creased to 33% after 40 weeks. On land the contents were also subjected to a sharp increase during the first months. This increase can be compared with that of the cellulose content which developed in a similar but more pronounced way.

The lignin amounts increased considerably beyond 100%, whatever the environment (Fig. 3). The maxima were reached within 8 weeks in sites 1 to 5, with 159% of the initial amount. This corresponded to a minimal exogenous contribution of 59% of lignin type compounds. The period during which the lignin amount was greater than the initial amount changed with site and might indicate that the mineralisation processes were temporarily halted. Thus, in fast running water or on non-floodable soil the initial lignin amount began to diminish after approximately 3 months, whilst in slow or standing water the phenomenon began at the 5th–6th month. On the floodable soil a period of more than eight months was necessary before the lignin declined below 100%.

### Discussion

By analysing the decomposition rates in the different terrestrial and aquatic sites, it was hoped to discover the physical parameters, that controlled decomposition. A previous study had been carried out on the comparison of the kinetics of leaf litter decomposition of three species native to the Garonne riparian forest, the common alder *Alnus glutinosa* GAERTN., the black poplar *Populus gr. nigra* and the white willow *Salix alba* L. in the Garonne River (CHAUVET, 1987). Although they are soft-wood species the leaves proved to be quite slow in decomposing and could be classified in Group III (the "slowest" species Group on a scale of 3 Groups) with an exponential coefficient  $k$  inferior to  $0.005 \text{ day}^{-1}$  (PETERSEN & CUMMINS, 1974). It is appropriate to adjust these values, obtained over 6 months, and replace them with coefficients calculated as in the present study over a period of 40 weeks. Then the willow decomposition follows an exponential slow flowing water kinetic with a coefficient  $k$  of  $0.0065 \text{ day}^{-1}$  whilst the previous coefficient was  $0.0050 \text{ d}^{-1}$ \*.

In fact, these slow flowing water kinetics can be interpreted as a twostage succession in the decomposition process. In winter and at the beginning of spring there is both a leaching of hydrosoluble products and the decomposition of certain constituents of the softest parts of the leaf, with the decomposition limited to approximately 50% of the initial leaf mass. At the end of spring and in summer, with an increase in the water temperature, the biological activity intensified and the most resistant constituents could be reduced so that at the end of summer only the leaf stalk and the main leaf veins remained. A succession with two exponential phases was also observed in the case of *Nyssa aquatica* leaves whose decomposition in an American swamp was slowed

\* Values obtained directly by the non-linear model  $y = e^{-kt}$ .

down, towards the 12th week, to a level of approximately 70 % of the initial organic matter (BRINSON, 1977). TIWARI & MISHRA (1983) also pointed out this phenomenon in the case of pine needles and dead teak leaves.

In the present study, the site had much more influence on the decomposition rates than the plant species. Willow leaves decomposed more rapidly in fast running water ( $k = 0.0121 \text{ day}^{-1}$ ) than in slow flowing water ( $k = 0.0065 \text{ day}^{-1}$ ) or than in standing water ( $k = 0.0062 \text{ day}^{-1}$ )\*, while no significant difference was noticed among the common alder, black poplar and white willow whose C/N and lignin/N ratios were in fact different (CHAUVET, 1987). Decomposition was more rapid in the non floodable willow stand ( $k = 0.0080 \text{ day}^{-1}$ ) than in the floodable site ( $k = 0.0040 \text{ day}^{-1}$ )\*.

The oxygen levels appear to be determinant since in both the aquatic and terrestrial environments the most rapid decomposition (fast running water, non floodable site) coincided with the highest oxygen levels. Conversely leaves were less rapidly processed in standing water or on soil liable to flooding and covered with sediment. Similarly, GODSHALK & WETZEL (1978) showed experimentally that decomposition of aquatic macrophytes was slightly slower in anaerobic than in aerobic conditions while in a swamp forest DUEVER et al. (1975) observed a less rapid decomposition on soils flooded 50 % to 16 % of the time than on non floodable soils. NESSEL (1978) too noticed a more rapid disappearance of leaf litter for two species on a wet site and for one species on a dry site. However, BRINSON et al. (1981) could find no evidence for or against the influence of the frequency and the duration of submersions on decomposition rates.

The disappearance rate of organic compounds during the first days was high in both the terrestrial and aquatic sites, since within 4 weeks the loss of organic matter was 16 to 37 %. Leaching was known to be predominant during the first days following immersion but these rates were very varied and depended on the plant species as noted by PATTEE et al. (1986). SUBERKROPP et al. (1976) observed losses of 22 % for hickory and 7 % for white oak after 2 weeks in a river. According to ANDERSON (1973 a) the major part of chestnut and beach leaf decomposition on the forest soil was due to leaching. Whatever the case, the initial decomposition phase of willow leaves (4 weeks) was not significantly different in the terrestrial and aquatic environments. However, measurements carried out over a shorter period (1 day) would probably reveal a more rapid leaching in water than on soil.

Carbon content was relatively constant during decomposition, a fact which had been noted by ANDERSON (1973 b) in a terrestrial environment and by TRISKA et al. (1975), RICHARD et al. (1982) and CHAUVET (1987) in the case of different species in an aquatic environment. RICHARD et al. (1982) observed a relative carbon enrichment in the case of poplar leaves. This increase for willow leaves in the Garonne corridor could be noted but was generally not sig-

nificant. As the carbon was largely in the form of a resistant lignocellulose compound, carbon decomposition occurred later.

An increase in the content as well as an absolute gain of nitrogen in decomposing leaves have been observed frequently both on soils (e.g. GILBERT & BOCOCK, 1960; BERG & SÖDERSTROM, 1979) and in waters (e.g. MATHEWS & KOWALCZEWSKY, 1969; HODKINSON, 1975). This overall increase has often been attributed to exogenous nitrogen contributed by the appearance of bacteria and fungi on the leaves after a few weeks (e.g. KAUSHIK & HYNES, 1971; ANDERSON, 1973 b). However, according to IVERSEN (1973) only 1 to 4% of the nitrogen enrichment of beech leaves in a stream was due to the microbial biomass. This suggests that a part of the nitrogen corresponds to microbial exoenzymes, themselves more or less linked to phenolic compounds of foliar origin (SUBERKROPP et al., 1976). Moreover, in a forest environment JANEL (1978) observed a loss of protein foliar substances during the first stages of decomposition and an increase in humic nitrogen. Because of its blending with products resistant to decomposition, part of the nitrogen may turn out to be more or less stabilized and thus relatively unavailable.

The C/N ratio has frequently been used as an indication of the nutritive quality of plant matter for decomposers. However, WARD & CUMMINS (1979) have pointed out that the C/N ratio does not take into account the nitrogen availability limited by its blending with phenolic products. The initial nitrogen concentration in the willow leaves (1.68% of the organic matter) was rather high compared to that of other deciduous or coniferous species. The willow, with a C/N of 26, like the alder or the poplar (CHAUVEY, 1987) could be considered easily decomposable species, as compared with "hard-wood" species (beech, oak) or conifers. The C/N change in willow leaves during decomposition in the Garonne currents (a decrease during the first 8 weeks, followed by an increase) was comparable to that obtained by RICHARD et al. (1982) for alder and poplar leaves in an oligotrophic river. The rise of C/N at the end of decomposition coincided with the gradual disappearance of the leaf blade. Moreover, the stability of the C/N ratio, after an initial drop, appeared to be characteristic of slow, less oxygenated waters since the same results have been found in ponds (HODKINSON, 1975).

Cellulose decomposition in the Garonne sites was not as continuous as found elsewhere by SUBERKROPP et al. (1976) and TIWARI & MISHRA (1983). In the waters or on the soils along the Garonne the cellulolyse increased only after several weeks and the cellulose disappeared more rapidly in oxygenated environment than in standing water or on floodable soils. BRINSON (1977), using pure cellulose sheets, showed the influence of the season and of the alluvial forest site on cellulose decomposition kinetics. His monthly cellulose losses were linearly and positively related to soil and water temperatures. The most rapid decomposition took place in the river, it was less rapid on the

swamp forest floor and slowest on the natural rarely submersed levee. However, the contradiction with the present results is only superficial, with the lower oxygen levels acting as an efficient barrier to the cellulolysis process in standing water. Moreover, the water content appeared to be the limiting factor for the cellulolysis on the levee, between the swamp and the river, since flooding induced cellulose decomposition because of ensuring a better contact between the cellulose and moist soil particles (BRINSON, 1977). This was not the case for the Garonne riparian forests soils where the forest canopy and the thick herbaceous layer ensured a sufficient moisture level. On the other hand the sediment deposits, and particularly the burying of leaf litter under several centimeters, slowed down both cellulolysis and the whole decomposition process.

Lignin was the most resistant leaf constituent to decomposition, both on the soil and in the water, since after several months more than half the leaf was made up of lignin. The increase in the lignin amount observed in the present study on both soils and in waters has been noted by numerous authors (e.g. KING & HEATH, 1967; TRISKA et al., 1975; SUBERKROPP et al., 1976; ABER et al., 1984). The parallel increase in the lignin and nitrogen and the fact that the lignin extracted during decomposition contained a consistent percentage of nitrogen led SUBERKROPP et al. (1976) and MELILLO et al. (1984) to suggest that microbial exoenzymes are chelated by polyphenols and lignin fragments during decomposition, forming a nitrogen compound similar to "lignin". Ligninolysis, even more than cellulolysis, appeared to be limited by oxygenated conditions as previously also shown by MELILLO et al. (1984). On the flooded Garonne soils the refractory products, covered by water or sediment, only began to decrease after the 32th week of decomposition. Laboratory experiments have shown that ligninolysis was less intense in standing waters than in rivers and, furthermore that the submersion of riverside soils also slowed down lignin degradation (FUSTEC et al., 1988).

### Conclusion

The decomposition of dried willow leaves was rapid in the alluvial corridor of the Garonne River and the kinetics did not appear to differ significantly between the waters and the riparian forest soils. MERRITT & LAWSON (1978) have shown that the overall ecological processes occurring in a floodplain were similar to those occurring in a stream, although the timing of leaf litter processing activity differed and decomposition rates were higher in the stream. In contrast, in a large river like the Garonne, the rates of decomposition can be as high on the land as in the water, quite possibly the result of an apparent paucity of aquatic macro-invertebrates on the sediments (about this a work is in progress). Moreover, oxygenation and temperature factors can,

within limits, be more important than the quality of the decomposing plant matter. As also noted by PATTEB et al. (1986) on the Rhône, we suggest that the lower the oxygenation the lower will be the decomposition rate. Leaf litter decomposition (especially of cellulose and lignin) on the Garonne River banks that are submerged during flooding and then covered with sediment was greatly reduced. Floodable soils acted as traps for organic matter rich in refractory nitrogen products whose turn-over was slowed down. The temperature increase at the end of spring and in summer was linked to a renewal of decomposition.

In studies about the ecological functioning of large rivers, in contrast to those dealing with streams, it is impossible to dissociate the processes within the river from those taking place on the banks (floodable zones) and in the adjacent aquatic environments (oxbows). To understand matter and energy fluxes in rivers it is essential to consider a corridor wider than the river itself plus the contribution from upstream.

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