Microbial dynamics on decaying leaves in a temporary Moroccan river. I - Fungi

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With 7 figures and 3 tables in the text

Abstract: Monthly variations of fungal biomass and assemblages on leaves exposed to the air and submerged, of sporulation and specific richness in the water, and of cellulolytic activity in the leaves were investigated in a warm temporary river. The biomass of terrestrial fungi was relatively low in the dry air and cellulolytic activity also was low. During submersion, biomass and activity of the aquatic hyphomycetes were greater. The fungi were most active in spring when the water was flowing and when breakdown was fast. Complete exclusion of one fungal species on one leaf species, presumably by competition, was observed twice. From June onwards, though fungal biomass remained high, fungal diversity and activity decreased, and further decay was presumably due to other microorganisms. No major difference to the same processes in temperate permanent streams appeared except that initiation of the sequence was the onset of the aquatic phase and not deciduous leaf fall.

Introduction

The capacity of certain microorganisms to use dead leaves as a source of nutrients and energy on land (KILBERTUS & REISINGER 1975) as well as in water (BÄRLOCHER & KENDRICK 1974), has been known for a long time. These mi-

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croorganisms are mainly fungi and bacteria. They invade and decompose plant litter (FINDLAY & ARSUFFI 1989), thus increasing its quality as food for invertebrates (HARRISON 1989). The contribution of bacteria and fungi to the breakdown of submerged litter is difficult to measure, but it seems that in temporary as well as in permanent lotic ecosystems, bacteria become predominant on smaller particles (SAUNDERS 1976). The application of selective antibiotics (SUBERKROPP & KLUG 1980, PATTEE et al. 1986) has shown that fungi are usually active during the initial phases of litter breakdown. Among these fungi, aquatic hyphomycetes are known to be major agents of leaf decay in well oxygenated freshwaters (WILLOUGHBY 1974, PATTEE & CHERGUI 1995). However, few of these seem fully capable of metabolizing lignin in the field (FISHER et al. 1983, HASIJA & SINGHAL 1991) as shown by the persistence of submerged wood. In terrestrial environments, the impact of fungi seems greater as several species, mainly basidiomycetes, have extra-cellular enzymes that attack the large polymers of wood while their hyphae invade the tissues (JONES 1982, SWIFT 1982, GRIFFIN 1985). The occurrence of terrestrial fungi on decomposing leaves has been consistently recorded (BÄRLOCHER 1992). A part of them are indeed higher fungi that begin colonizing senescent leaves on the trees and persist after leaf fall, even in streams where they are finally supplanted by aquatic hyphomycetes (BÄRLOCHER & KENDRICK 1974, CHERGUI & PATTEE 1988). These terrestrial fungi seem less well adapted to low winter temperatures (BÄRLOCHER & KENDRICK 1974) and they also need some water. Both temperature and moisture may not be sufficient during dry winter periods under the Moroccan climate described by MAAMRI et al. (1997).

After the assessment of litter breakdown (MAAMRI et al. 1997) in temporary Oued Cherraa, the aim of the present paper was to evaluate fungal biomass and activity in the same samples, and the possible role of both categories of fungi in litter decomposition during the aquatic and terrestrial phases of the river.

Material and methods

Investigations extended from November 1994 to September 1995. During this period, little rainfall occurred except on the very last days of February and during the month of March 1995. Oued Cherraa flowed from March to July or September 1995 depending on the site. After the initial flood, discharge remained high (300 to >700 L/s) at the end of March and in April, and the water became stagnant in May until the river dried out. These changes are recorded under the abscissae of Fig. 1.

Oued Cherraa is the lower temporary part of a Northeastern Moroccan watercourse, the upstream reaches of which, called Oued Zegzel, are permanent and which were the subject of numerous papers (e.g. MAAMRI et al. 1994). A detailed description of Oued Cherraa and the three study sites was given in MAAMRI et al. (1997). Here we shall only recall their main characteristics.

Site n° 1 is a permanent pool approximately 1 km from the end of permanent Oued Zegzel. Its mean area is 4×6 m. lt was flooded and flowed with the river in March and April 1995. It is bordered by oleander (*Nerium oleander*) bushes and overgrown by *Potamogeton.*

The other two sites were in the temporary reach of the river. Both of them were some 100 m long.

Site n° 2, called Upstream Cherraa, was located 500 m further down, along the steep left bank of the river. The riparian vegetation (poplar, oleander and willow) is scanty and the rest of the bed is bare cobble and boulders. This site was submerged for 7 months (March–September) in 1995.

Site n° 3, called Downstream Cherraa, was 2 km from the Upstream site, as the valley opens into the plains. The bed is broader and its gradient is low, and the sediment is cobble, sand, and silt. Terrestrial vegetation (oleander, poplar, willow, *Ricinus, Juncus,* grass) has developed in the bed itself. This site was submerged for 5 months (March–July) in 1995.

When present, 250 ml of water were sampled at the end of each month from November 1994 to September 1995 at each site. Note that we could not avoid including a small amount of foam in some of the samples when the water was flowing (none was present in standing water). Foam is known to concentrate hyphomycete spores (MERCE 1987) and this shall be examined in the discussion. From each 250 ml sample of water, the spores in 100 ml were fixed by adding 15 ml of form-acetic alcohol (INGOLD 1975), i.e. 40 % formalin (5 ml), 70 % ethanol (80 ml) and concentrated acetic acid (15 ml) (BÄRLOCHER & PETERSEN 1988). The spores were stained with lactic cotton blue and identified under an inverted microscope according to INGOLD (1975), CARMICHAEL et al. (1980) and CHAUVET (1990) in decanted volumes of 40 µl in which spores were concentrated (or 200 µl in some cases when spores were scarce in late summer).

As explained in MAAMRI et al. (1997), 5 ± 0.5 g of fresh deciduous willow (*Salix pedicellata*) or evergreen oleander (*Nerium oleander*) leaves were enclosed in plastic bags with 2-mm mesh size and deposited in the field in the last days of October 1994. The bags were in water in the Pool and in the deeper parts of the dry bed at the other two sites. Bags were sampled after 3, 7, 15 days, and at the end of each month until June 1995 (Pool, in which, owing to faster breakdown, insufficient leaf fragments were available for microbial investigation after this date) or September (both river sets). However, two samples for fungal biomass and cellulolytic activity were collected at two weeks' interval in March, when the river began flowing (hence the double columns at the end of March in Fig. 1). Most bags were used for the breakdown investigations recorded by MAAMRI et al. (1997) but one bag of each leaf species was used each time for the microbial (fungal and bacterial) investigations and carried to the laboratory in ice. There, four to six 10-mm discs were cut from each leaf for fungal investigation.

One or two leaf discs from each sample (date and site) were wrapped in aluminium foil and frozen at −20 °C. Then they were packed in dry ice and sent to the CESAC CNRS Laboratory in Toulouse (France) for evaluation of fungal biomass. Ergosterol, a membrane component mostly restricted to eumycotic fungi, was used as the index of fungal biomass (GESSNER et al. 1991). Ergosterol was extracted from the lyophilized leaf discs by 30 min refluxing in alcoholic base, purified by solid-phase extraction

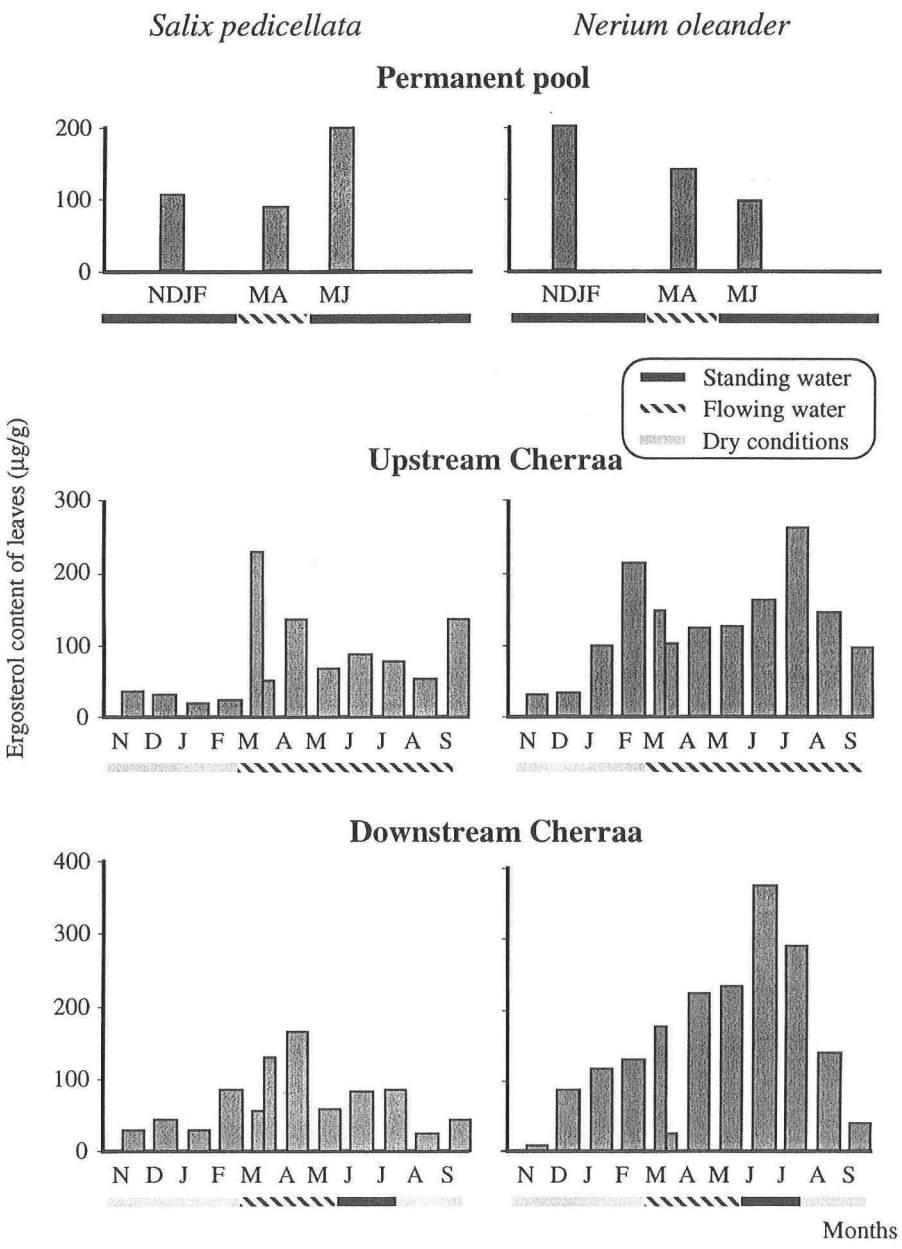

Fig. 1. Ergosterol content per g dry mass of willow, *Salix pedicellata,* and oleander, *Nerium oleander,* leaves during the investigation period at the three sites of Oued Cherraa. The data for the permanent pool represent the means for several months.

(GESSNER & SCHMITT 1996), and quantified by measuring UV-absorbance after purification by HPLC (GESSNER et al. 1991). Owing to the amount of leaf material available and to uncertainty as to the quantity of ergosterol that would be found after stocking and transport, the samples from the permanent site were pooled into three groups: first stagnant period, flowing period, and second stagnant period. As the amount of ergosterol turned out to be sufficient, distinct analyses were performed on each sample from the temporary sites.

For the investigation of terrestrial fungi, the discs were cut from the leaf packs collected from the dry bed. Twelve discs for each leaf species and each sampling date were individually wrapped in aluminium foil and carried to Lyon (France). A first survey was performed under a binocular microscope. The conidiophores thus detected were collected with a Pasteur pipette and mounted in distilled water for identification.

Then the discs were deposited on filter paper soaked with sterilized distilled water in sterilized Petri dishes. The dishes were sealed with Parafilm sheets and incubated for three weeks at room temperature. During this time, they were examined each week under the binocular microscope so as to detect and identify possible new conidiophores.

Overall generic frequency (number of times a genus was identified/total number of comdiophores identified) and generic occurrence on the leaves (number of discs inhabited by a genus/number of discs examined) were calculated.

For the investigation of aquatic fungi, three leaves were taken from each sample and 4 discs were cut from each leaf, placed separately in 50 ml vials and incubated with 20 ml of sterilized distilled water for 24 hours at 10 °C. Then the discs were removed from the water and both surfaces of each disc were thoroughly scraped in the air. The detrital matter released by scraping was carefully collected and mounted in lactic cotton blue. Spores were observed under an inverted microscope and identified according to INGOLD (1975), CARMICHAEL et al. (1980) and CHAUVET (1990). Occurrence of the main aquatic hyphomycete species was evaluated as percent presence on the 12 discs of each sample.

For the investigation of cellulolytic activity, five leaves were sampled from each bag collected for the microbial study. After having been drained of external water and weighed fresh, they were ground in 8 ml of pH 5 acetate buffer at 4 °C. Two ml of the supernatant were incubated for 48 h at 37 °C in 2 ml acetate buffer with 20 mg CMC (Carboxymethylcellulose) and a drop of toluene (toluene destroys microbial membranes, SINSABAUGH & LINKINS 1990). After 48 h the reaction was stopped by lowering the temperature to 0 °C. Reducing sugar content was measured with a SIGMA (n° 16-UV method) glucose kit. Cellulolytic activity was expressed as mg glucose $h^{-1} g^{-1}$ leaf fresh weight.

This method is commonly used to evaluate fungal cellulase (SUBERKROPP & KLUG 1976, CHAMIER et al. 1984), but of course it also takes into account the cellulase of other microorganisms.

Results

No clear changes in fungal biomass (Fig. 1) seem to have been caused in the Permanent Pool by water flow.

Fungi developed on the leaves during the dry period in the temporary sites. After the water began flowing, there was an abrupt change between the first and second samplings in March. At the Downstream site, aquatic biomass was significantly smaller ($p = 0.040$) on willow than on oleander, on which it peaked in early summer and declined again as the river dried out. Based on an average ergosterol-to-biomass conversion factor established for aquatic hyphomycetes (GESSNER & CHAUVET 1993), peak fungal biomass was estimated to range from 31 mg/g detrital dry mass (willow at Downstream site) to 66 mg/g (oleander at Downstream site).

Only 6 taxa of terrestrial fungi were detected during the first dry period (November–February) in the temporary river. The most frequent ones were *Cladosporium herbarum* and *Aspergillus* sp. (Table 1). Sterile mycelia and several unidentified taxa were also recorded.

C. herbarum was present on most leaves, *Aspergillus* sp. came next. *Penicillium* sp. occurred on more leaves upstream than downstream (Table 2).

Conidiophores were conspicuously more numerous on willow than on oleander leaves.

Altogether, 13 hyphomycete species were identified on the leaves (Fig. 2) as well as in the water. *Anguillospora longissima* was most common on both leaf species and at all three sites. In contrast, *Tetracladium marchalianum* and *Clavatospora longibrachiata* only occurred on willow and at the Downstream site. Most species were found in the Pool and Upstream site and least at the Downstream site.

Table 1. Percent frequency of terrestrial fungi on the decaying leaves during the first period of emersion at the two temporary sites of Oued Cherraa.

	Upstream station	Downstream station
Cladosporium herbarum	51	44
Aspergillus sp.	12	14
Penicillium sp.	9	10
Fusarium sp.	6	6
Trichoderma sp.	4	5
Verticillium sp.	3	2
Other	15	19

Table 2. Mean occurrence of fungal genera on 12 discs of willow and oleander leaves during the first dry period at the two temporary sites of Oued Cherraa.

% occurrence	Upstream Cherraa	Downstream Cherraa
65–90	*Cladosporium*	*Cladosporium*
30–65	*Penicillium, Aspergillus*	*Aspergillus*
10–30	–	*Penicillium, Fusarium*
1–10	*Fusarium, Trichoderma, Verticillium*	*Trichoderma, Verticillium*

Figs. 3, 4, and 5 show the monthly occurrence of three common hyphomycete species on the leaves. In the Pool, spores of *A. acuminata* and *L. aquatica* were only found on one of the two leaf species and never on any disc of the other throughout the study period. When present, their maximum occurrence was in March, during the first month of water flow. *A. longissima* was less common in winter and its maximum occurred later than that of the other two species. The last data were reported from June because the leaves were skeletonized by July.

The three hyphomycete species were present in the temporary bed as early as March, immediately after submersion (except for *A. longissima* whose presence on oleander in March at the Upstream site was insignificant). Maximum occurrence in June was frequent. The three species persisted at the Upstream site until the end of the study in September but they disappeared from the Downstream site in August.

Spores were most abundant in the water (results not shown) in March and April, but this may, at least partly, have been due to the presence of a little foam in the samples. However spores were also numerous in November and May in the Pool and in June and July in the Upstream site, where no foam oc-

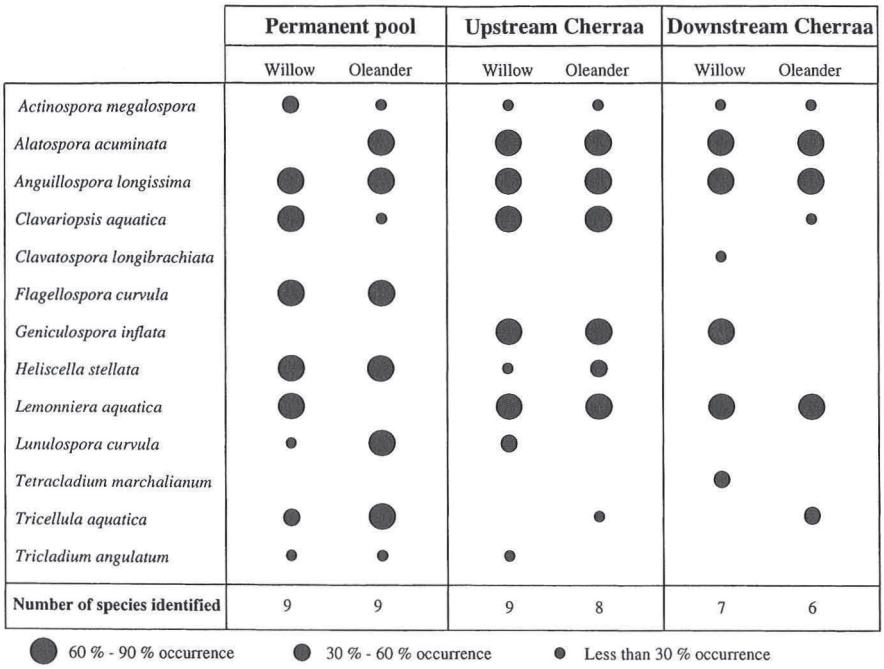

Fig. 2. Mean occurrence of aquatic hyphomycetes on the submerged leaves of willow and oleander at the three sites of Oued Cherraa. Occurrence was evaluated from 12 leaf discs in each sample.

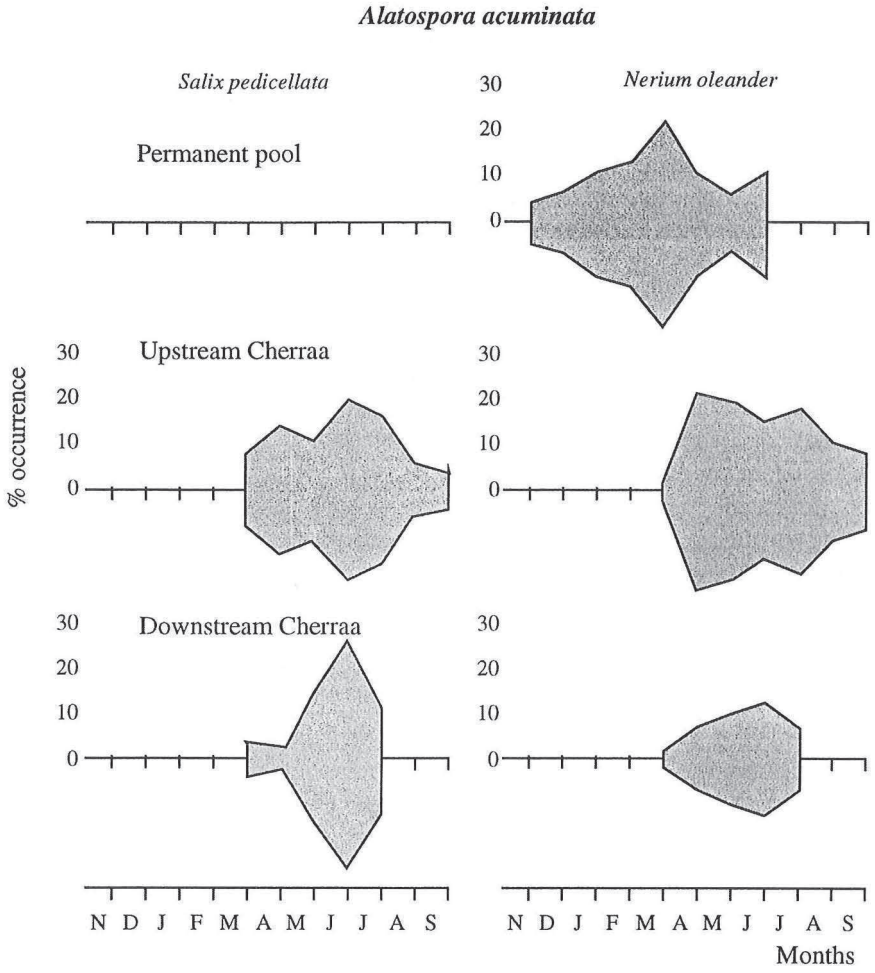

Fig. 3. Monthly occurrence of *Alatospora acuminata* on 12 discs of willow and oleander leaves at the three sites of Oued Cherraa. At both temporary Cherraa sites the water began flowing in March. The figures on the ordinates represent half the occurrence.

curred. They were rare in the pools of the Downstream site while these were drying out in June and July.

The numbers of hyphomycete species found in the water (Fig. 6) were congruent with the numbers of spores: peaks are visible from March to May, and numbers decreased before (in the Pool) and after (at all sites) high water. The same species were found in the water as on the leaves, but Fig. 6 shows temporal changes that did not appear in Fig. 2. During the last period, only one, two, or three of the following species persisted: *T. marchalianum* (at the

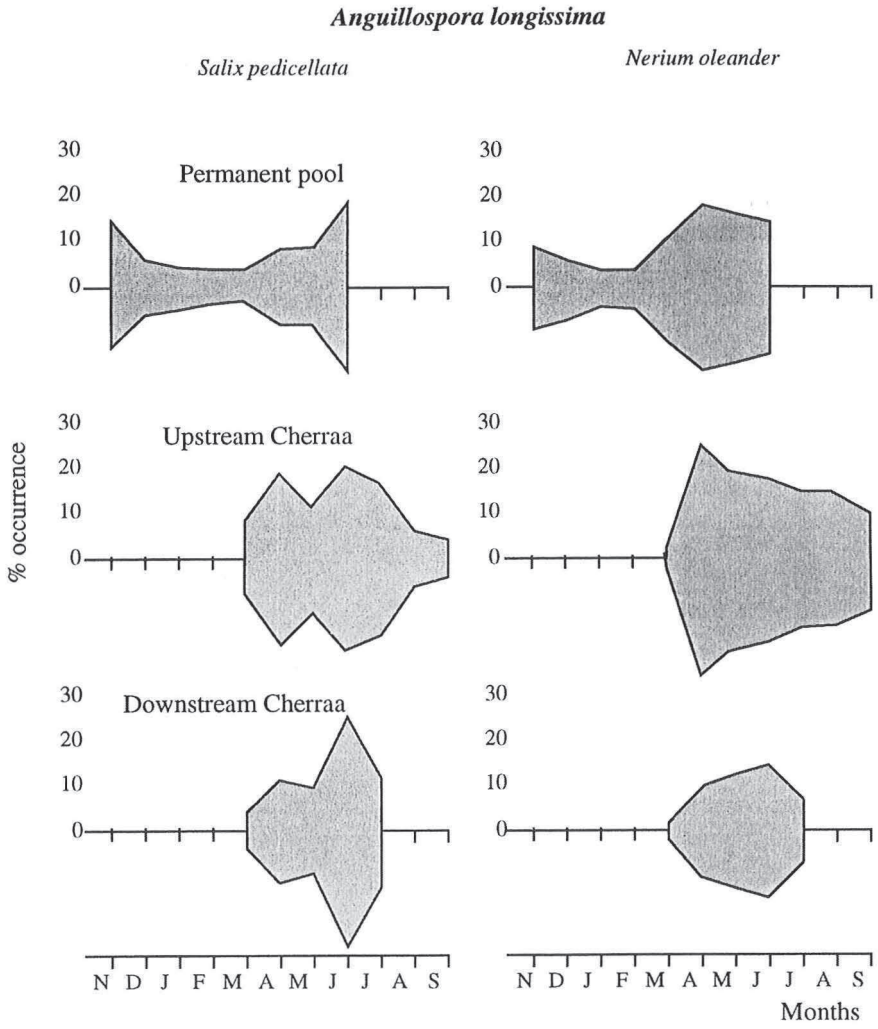

Fig. 4. Monthly occurrence of *Anguillospora longissima* on 12 discs of willow and oleander leaves at the three sites of Oued Cherraa. At both temporary Cherraa sites the water began flowing in March. The figures on the ordinates represent half the occurrence.

Downstream site), *Lunulospora curvula, L. aquatica* and/or *C. longibrachiata* at the other sites.

Thus, species richness in the water was greatest during waterflow.

A major peak of cellulolytic activity (Fig. 7) also appeared during water flow at all three sites. It clearly began during the first fortnight of March in the Pool, but only during the second fortnight (except perhaps at the Downstream site on oleander) in the temporary river. It extended over March and April in

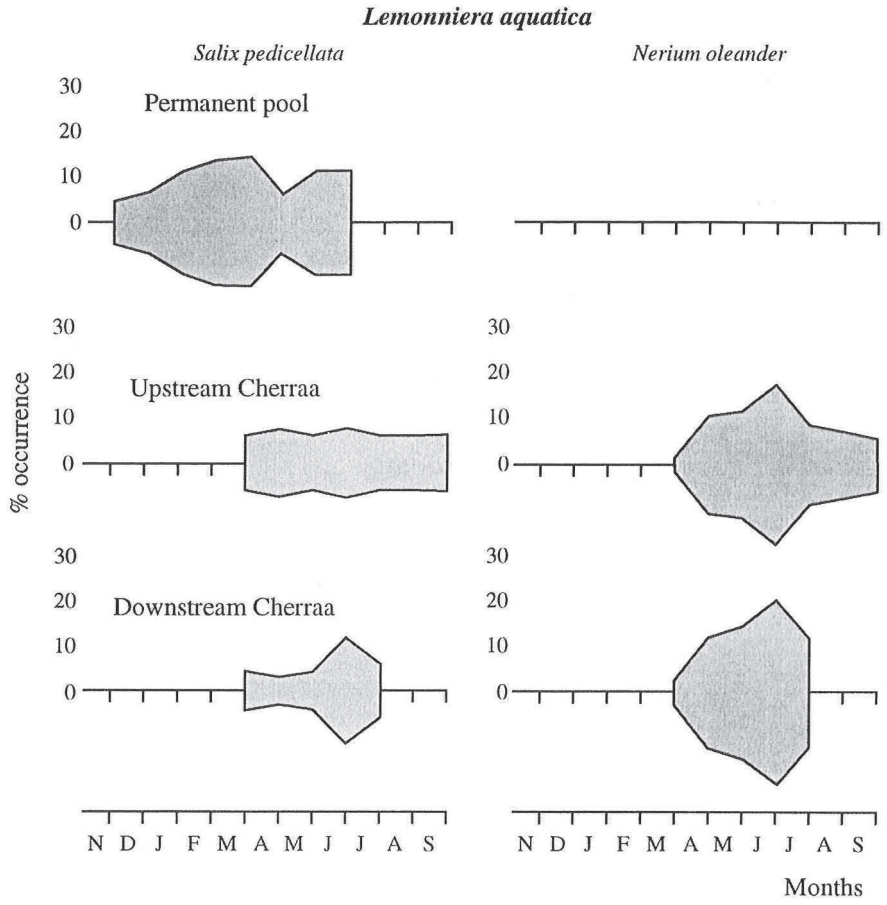

Fig. 5. Monthly occurrence of *Lemonniera aquatica* on 12 discs of willow and oleander leaves at the three sites of Oued Cherraa. At both temporary Cherraa sites the water began flowing in March. The figures on the ordinates represent half the occurrence.

the Pool, over March, April, and May in the river. Cellulolytic activity became negligible after May at both temporary sites but persisted at a low level in the Pool.

A minor peak occurred at the end of November (under water) in the Pool, and one month later (in air) in the dry river bed.

Mean activity was greater ($p < 0.05$) in the Pool than at the temporary sites, and the peaks during submersion were also higher (1 and 0.7 mg Glc h^{-1} g^{-1} fresh weight of willow and oleander leaves in the Pool, versus 0.8 and 0.6, and 0.6 and 0.4 mg Glc h^{-1} g^{-1} at the temporary sites).

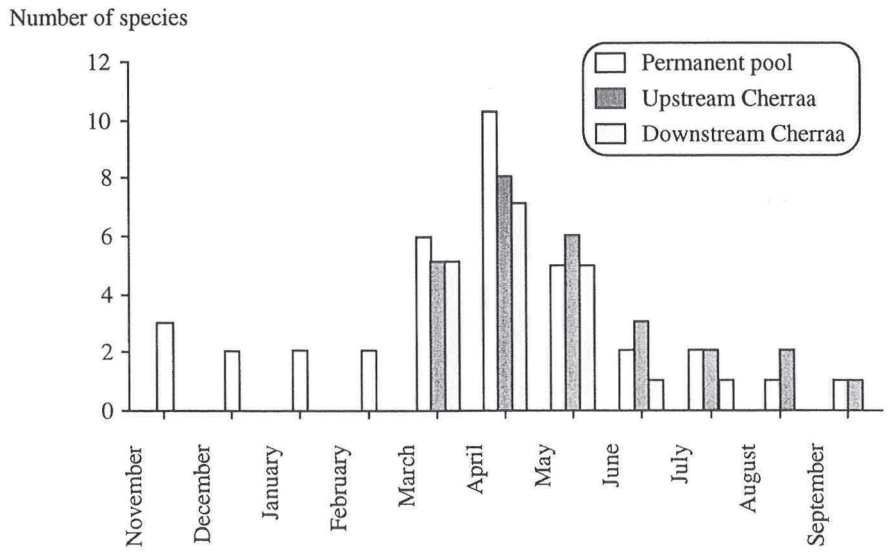

Fig. 6. Numbers of hyphomycete species identified in the samples of water from the three Cherraa stations.

Discussion

With peaks of biomass ranging from 3 to almost 7 % of the detrital mass, the fungi appear to be major colonizers of the leaf litter decomposing in the temporary river. Such values are in the lower- to mid-range of those measured with the same method in other streams (GESSNER & CHAUVET 1994, SUBERKROPP 1995). These somewhat low values may be partly due to the unfavourable quality of willow and oleander leaves that had dried on the stream bed for four months before being submerged. In accordance with the substantial development of microfungi, a high cellulolytic activity associated with leaf litter was detected. Peak values from the temporary river (0.4–1.0 mg glucose $h^{-1} g^{-1}$ leaf fresh weight, i.e. 1.0–5.0 mg glucose $h^{-1} g^{-1}$ leaf dry weight assuming a dry-to-fresh leaf mass ratio of 1 : 2.5 for oleander and 1 : 5 for willow) are in the same range as, or somewhat higher than, values previously reported from permanent streams (0.5–1.1 mg glucose $h^{-1} g^{-1}$, calculated from JENKINS & SUBERKROPP 1995).

We clearly identified two groups of fungi: 6 terrestrial and 13 aquatic taxa.

The terrestrial fungi were investigated only during the first period of exposure to the air and we have no information on their residence time in the leaves. They do not sporulate when submerged and hence could not have been detected even if present in the water. According to isolates on plates, they are

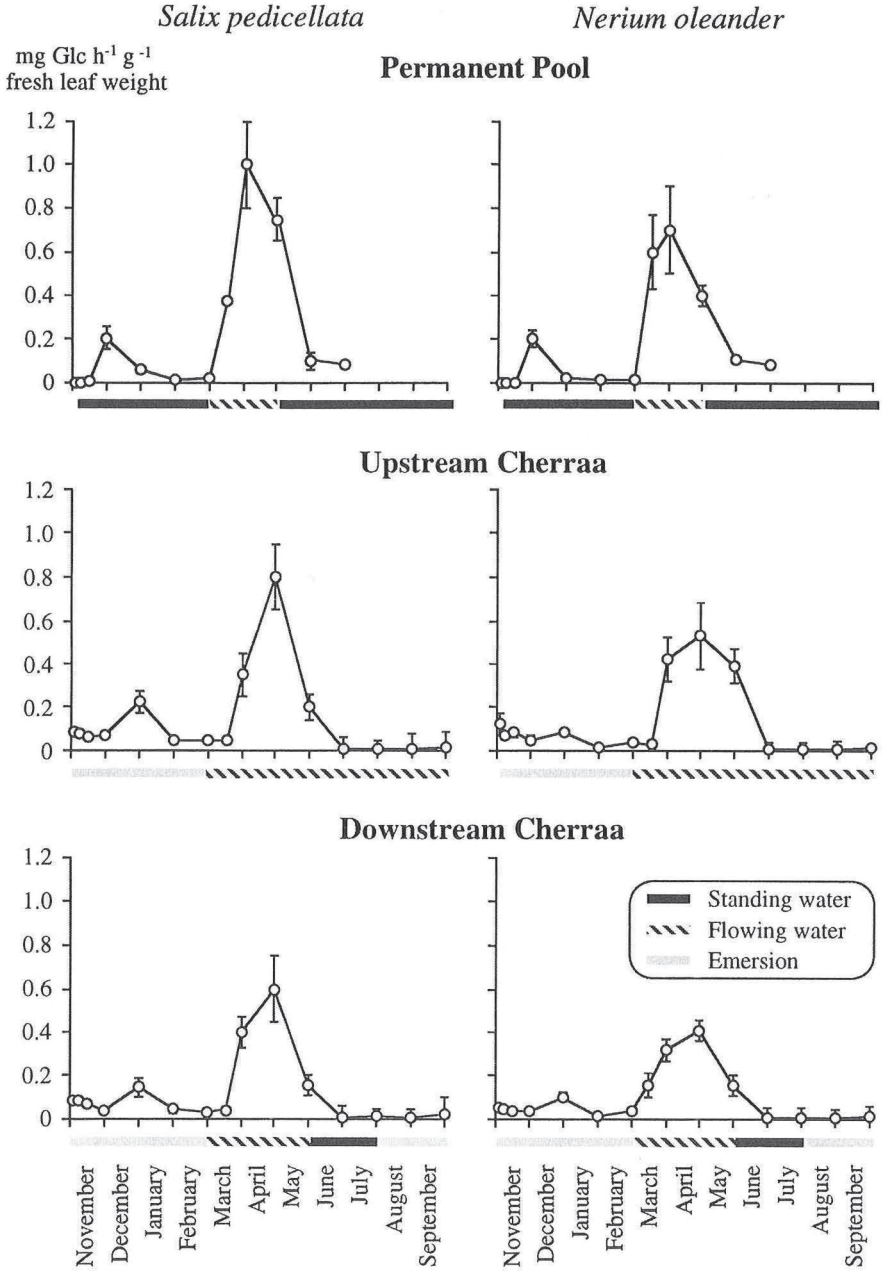

Fig. 7. Cellulolytic activity on initially fresh leaves of willow and oleander exposed from November 1994 to September 1995 in Oued Cherraa (the leaves were fresh when they were exposed in November but they had dried by the time they were flooded in March). Error bars represent standard deviation on 3 replicates.

Table 3. Daily breakdown coefficients (−k) of fresh willow, *Salix pedicellata* (first value), and loeander, *Nerium oleander* (second value), leaves at the three stations of Oued Cherraa (after MAAMRI et al. 1997). Overall breakdown was faster ($p < 0.01$) in the pool than in both river stations; no significant difference ($p > 0.05$) appeared between leaf species. Breakdown in the water was also faster ($p < 0.05$) in the pool than in both river stations and here there was a difference ($p < 0.05$) between leaf species.

	Permanent pool		Upstream Cherraa		Downstream Cherraa	
First dry period	–		0.0015	0.0013	0.0007	0.0007
Aquatic period	–		0.0069	0.0048	0.0056	0.0047
Overall	0.009	0.007	0.005	0.004	0.004	0.003

said to become less active at the temperatures that prevail in streams in winter under temperate climates (BÄRLOCHER & KENDRICK 1974).

Late autumn 1994 was very dry in Eastern Morocco, with only 15 mm rainfall in November and 10 mm in October and in December. Nevertheless some fungal biomass was detected in the leaves and the amounts were substantial in oleander though they were always lower than in the Permanent Pool at the same period, and fungal development was delayed at both temporary sites until water began flowing.

These terrestrial fungi were dominated by *Cladosporium herbarum,* a species already present on live plants and which develops in leaf litter (ARPIN et al. 1975). However its participation in litter decay seems moderate, as recorded by HENNEBERT (1977): during 6 weeks' cultivation it caused only 5–20 % weight loss from cellulose substrates, whereas *Trichoderma* and *Verticillium* caused 20–55 % weight loss. These latter taxa were not frequent in Oued Cherraa.

These fungal assemblages are in agreement with the slow but consistent leaf breakdown in Oued Cherraa during the dry period (Table 3). Indeed, there was a small peak of cellulolytic activity in December, two months after deciduous leaf fall. Considering the almost complete absence of bacteria at the Downstream site (MAAMRI, in press), this peak may be attributed to the fungi.

Most of the aquatic hyphomycetes recorded from Oued Cherraa are cosmopolitan (WEBSTER & DESCALS 1981, BHAT & CHIEN 1990). *Flagellospora curvula, Lemonniera aquatica, Alatospora acuminata* are some of the most common species worldwide.

Some differences in aquatic hyphomycete assemblages appeared between Oued Cherraa and its upper course Oued Zegzel (CHERGUI 1990). Two species present in Oued Cherraa, *Clavatospora longibrachiata* and *Geniculospora inflata,* were absent from Oued Zegzel, but seven species reported from Oued Zegzel were not found in Oued Cherraa. However, of these seven species only two, *Triscelophorus monosporus* and an unidentified *Tetracladium* species

were reported from the Lower Zegzel, and these two species were never abundant.

In the Permanent Pool, sporulation and cellulolytic activity seem to have been stimulated by deciduous leaf fall in November, when the occurrence of *A. longissima* and overall specific richness were also rather high. These variables subsequently decreased until the water began flowing in March, when spore and species numbers in the water sharply increased. Sporulation of *A. acuminata* on oleander leaves and of *L. aquatica* on willow leaves peaked in March though no clear difference appeared in fungal biomass on the leaves.

Whether the water was standing or flowing, no *A. acuminata* spores were found on the willow leaves and no *L. aquatica* spores were found on oleander leaves. The hypothesis of antagonism by the first colonizers preventing the development of newcomers (CHAMIER et al. 1984, ROSSET & BÄRLOCHER 1985, SUBERKROPP 1992) can explain this remarkable absence but it implies that the gradual increase in occurrence of other fungal species on the opposite leaf species was due to the late sporulation of individuals that had existed from the start and not to late colonization. As the fungi were only detected by their spores, another possible process might have been be complete inhibition of sporulation despite mycelial growth, but this would also be difficult to explain. The result is a strong selection of the fungi for one of the leaf species in the pool. Although some substrate preferences of aquatic hyphomycete species cannot be ruled out (e.g. CHAUVET et al. 1997), such a specific selection has never been reported.

Moreover, *A. acuminata* and *L. aquatica* coexisted on both leaf species in the temporary sites. Hence, exclusion only occurred when colonization began in November and in water that was standing from November to February. Mean air temperatures were 17 °C in November, 12.8 °C in January, 13.5 °C in February, 15.3 in March and 20.8 °C in May (MAAMRI et al. 1997): the period of colonization was somewhat colder in the pool than in the river. Temperature modified fungal growth and sporulation of two species grown in pure and mixed cultures (WEBSTER et al. 1976); it may have influenced competition in Oued Cherraa. Standing water obviously causes less spore mobility and provides less opportunities for colonization than flowing water. Both explanations remain highly speculative and deserve further investigation.

At the temporary sites, the abrupt changes in fungal biomass that occurred in March may be interpreted as the replacement of terrestrial by aquatic colonies.

During the period of submersion at these sites, there was no clear correspondence between fungal biomass in the leaves and the possible indices of fungal activity (spore and species numbers in the water and cellulolytic activity in the leaves). Indeed, these indices peaked in March–April while fungal biomass per gramme oleander leaf peaked in July–August. However max-

imum absolute amount of fungal biomass in the leaf batches generally occurred earlier (data not shown). Maximum occurrence of the spores of the three common hyphomycete species was most often in June but that of *A. acuminata* and *A. longissima* on oleander was in April. The spores of all three species disappeared from the leaves at the Downstream site in August when the puddles dried out, although some fungal biomass did persist in August and September.

There are several records of sporulation stimulation by water flow in the literature, e.g. WEBSTER & TOWFIK (1972), WEBSTER (1975), SANDERS & WEBSTER (1980) and the spring peak noted by BÄRLOCHER (1991). Other papers mention stimulation by leaf fall, as in New Zealand (AIMER & SEGEDIN 1985). Both relationships were noted in Oued Cherraa.

Moreover fungal activity after litter submersion may also be explained by the leaching of anti-microbial substances from the leaves that had dried in the bed of the river since November, as stressed by BUNN (1988), BÄRLOCHER (1991), GESSNER & SCHWOERBEL (1989), and CHERGUI & PATTEE (1993). In streams, WILLOUGHBY & ARCHER (1973) and BÄRLOCHER (1982) observed peak fungal activity four or five weeks after leaf submersion. COOKE & RAYNER (1984) postulated that vegetative growth precedes reproductive output in saprophytic fungi. SUBERKROPP (1991) showed that biomass and reproduction in aquatic hyphomycetes are largely synchronized, but that reproduction may occasionally lag behind growth. However, other studies (e.g. GESSNER & CHAUVET 1994) showed that sporulation may actually peak before maximum biomass is reached.

At all sites leaf breakdown was fast in April–May (MAAMRI et al. 1997) during the period of hyphomycete activity. ZEMEK et al. (1985) demonstrated that most of the 35 aquatic hyphomycete species that they screened were able to degrade polysaccharides as well as other major constituents of leaf litter. The dominant species in Oued Cherraa, namely *Alatospora acuminata, Anguillospora longissima* and *Lemonniera aquatica,* belong to this group of species active in leaf breakdown. Moreover CHERGUI & PATTEE (1991) examined the weight loss of dry leaves of *Salix pedicellata* and *Nerium oleander* caused separately by these three fungal species and *Tetracladium marchalianum* from Oued Zegzel. Weight loss was greatest under the influence of *L. aquatica* and least under that of *T. marchalianum.*

In Oued Cherraa, the decrease in specific richness and cellulolytic activity began in May. It may be explained by the following processes:

- much lower water velocity at the temporary Upstream site and water stagnation in the Pool and Downstream site,
- changes in residual leaf substrate (approximately 40 % of leaf weight were left in June at the temporary sites and 10–15 % in the Pool). Though fungal biomass per unit leaf mass distinctly peaked in July–August on oleander,

breakdown almost stopped at the Downstream site (MAAMRI et al. 1997). At the other sites, the leaves were skeletonized.

- competition with bacteria, as witnessed by ARPIN et al. (1975). Most bacterias' thermal optimum is higher than that of hyphomycetes (summer water temperature was approximately 30 °C in the Pool and 25 °C in the temporary bed).

Table 3 shows that overall leaf breakdown proceeded faster in the Pool than at the temporary sites. This difference was partly due to the very slow breakdown in the air during the dry periods of the river. Nevertheless, breakdown was also faster in the Pool than during submersion at the temporary sites. Though no clear differences in fungal biomass appeared, hyphomycete specific richness and cellulolytic activity were also greater in the Pool than during submersion at the temporary sites. The same relationship between hyphomycete activity and breakdown rate had been noted in Oued Zegzel by CHERGUI & LEGSSYER (1995).

Conclusion

In Oued Cherraa, terrestrial and aquatic fungi developed on leaf litter. Despite non-negligible biomass, the former seemed less diverse and showed little activity in leaf decay, either because of lack of efficient enzymes, or because of the dry atmosphere, or because of insufficient time for growth. The aquatic hyphomycetes developed on submerged litter and leaf breakdown proceeded rapidly during water flow in spring while they were most active. They were presumably responsible for the cellulolytic activity recorded during this period. Fungal biomass persisted in summer as water velocity decreased and as leaf cuticle and leaf tissues were gradually eroded. Fungal development and activity in the temporary sites differed from that of permanent streams by the fact that the triggering event was the end of the dry period and not leaf fall.

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