Introduction

Primary production and the decomposition of detritus are fundamental processes driving ecosystem functioning (Lindeman 1942, Odum 1956). Ecological research on these two processes has largely developed independently, despite plausible mechanisms linking the activities of primary producers and microbial decomposers. The balance between detritus mineralization by decomposers and competition for inorganic nutrients in a producer–decomposer system determines the rate of carbon (C) and nutrient cycling in ecosystems (Bratbak and Thingstad 1985, Harte and Kinzig 1993, Daufresne and Loreau 2001, and Fig. 1). High C-to-nutrient ratios of plant detritus entail that decomposers must immobilize inorganic nutrients from their environment to fulfill their stoichiometric demand (Daufresne and Loreau 2001, Moore et al. 2004). Decomposers are better competitors than producers for nutrient resources (Currie and Kalff 1984), and the growth of primary producers can be strongly reduced in the presence of decomposers (Bratbak and Thingstad 1985, Gurung et al. 1999, Mindl et al. 2005, Danger et al. 2007*b*). The dependence of decomposers on the production of detritus by producers is therefore an important condition allowing the stable coexistence of both groups, and competitive exclusion of producers should be expected in the case of high allochthonous C supply (Daufresne and Loreau 2001).

Based on metabolism estimates using energy and nutrient budgets or isotopic approaches, ecologists have

long distinguished between primary producer- and detritus-based systems where primary production or decomposition, respectively, are thought to be the dominant drivers of ecosystem functioning (Moore et al. 2004). In detritus-based systems, autochthonous primary production is often limited by abiotic (e.g., light) and/or biotic (e.g., grazing) factors. Consequently, the detrital pool is mainly fueled by allochthonous organic matter inputs from adjacent producer-based systems (Fisher and Likens 1973). Numerous studies have quantified the importance of primary production and allochthonous detritus decomposition in detritus-based systems (e.g., Rosenfeld and Roff 1991, Findlay et al. 1993, Roberts et al. 2007), and primary production is now increasingly recognized as a nonnegligible process. However, little is known concerning the influence of primary production on decomposers activity and on the potential interactions between the two types of energy sources, allochthonous and autochthonous.

A minor contribution of autochthonous primary production to ecosystem metabolism and energy flows may not necessarily indicate that living primary producers are unimportant for ecosystem functioning. In particular, living primary producers may stimulate allochthonous organic matter degradation by providing high-quality resource subsidies to heterotrophic decomposers and detritivores. There is evidence that small amounts of labile C exudates released by primary producers can substantially accelerate the decomposition of slow-turnover pools of organic matter (often referred to as recalcitrant organic matter), a process called the "priming effect" in both terrestrial (Kuzyakov et al. 2000, Fontaine and Barot 2005) and aquatic (Guenet et al. 2010, Bianchi 2011) ecosystems. In a recent review, Guenet et al. (2010) proposed that algae-mediated stimulation of the detrital pathway may depend on nutrient concentrations. Under high-nutrient conditions (Fig. 1A), competition for nutrients between decomposers and primary producers is expected to be low. Nutrient-unlimited algae should also decrease the fraction of their production released as C exudates (Scott et al. 2008, Ziegler and Lyon 2010). In contrast, under low-nutrient conditions (Fig. 1B), competition for inorganic nutrients should be maximized, resulting in reduced algal growth, since decomposers are superior competitors for nutrients than plants (Currie and Kalff 1984). Nutrient-limited algae should also increase their release of labile C exudates (Scott et al. 2008, Ziegler and Lyon 2010), which could potentially stimulate the mineralization of recalcitrant organic matter through a "priming effect" (Guenet et al. 2010). In detritus-based ecosystems, oligotrophic conditions often prevail, suggesting that even low densities of living primary producers may enhance allochthonous organic matter decomposition. In addition to the priming effect, primary producers could also directly alter detritus elemental and biochemical quality, which could affect detritivore feeding and rates of organic matter processing. Plant detritus is often a poor source of nutrients (high C to nutrient ratios, Hessen et al. 2004, 2008) and essential fatty acids (Torres-Ruiz and Wehr 2010) for detritivores. Living primary producers are rich in these essential compounds, and consumption of litter-associated primary producers by detritivores may help meet their nutritional requirements and maintain high detritus-processing activity (Franken et al. 2005, Torres-Ruiz and Wehr 2010).

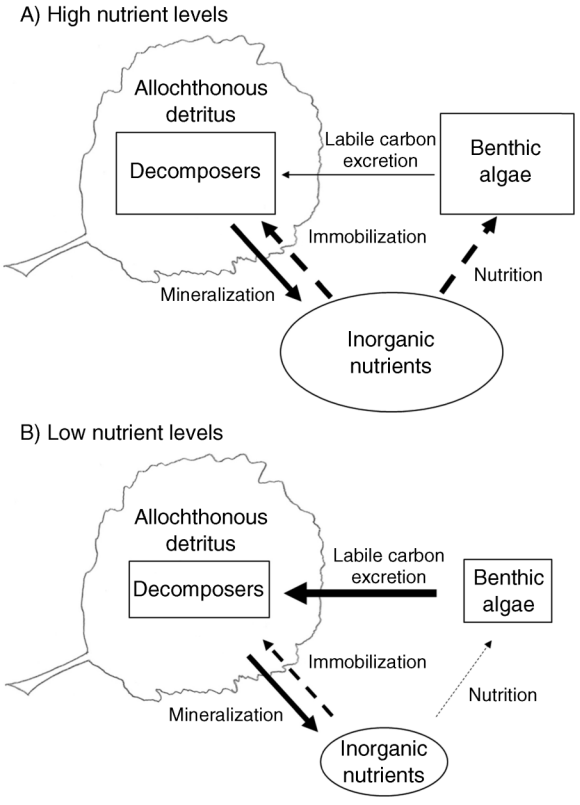

FIG. 1. A conceptual model of the interactions between benthic algae and decomposers in headwater streams (adapted from Daufresne and Loreau [2001]). Arrows represent matter transfers; arrow width is proportional to the magnitude of transfers. Dotted and continuous lines represent competitive interactions and mutualistic pathways, respectively. (A) Under high-nutrient conditions, competition is reduced, and C exudates released by nutrient-unlimited algae represent a minimal fraction of primary production (Scott et al. 2008, Ziegler and Lyon 2010). (B) Under low-nutrient conditions, competition for inorganic nutrient is high, resulting in reduced algal growth, since decomposers are superior to plants in competition for nutrients (Currie and Kalff 1984). Nutrient limitation also stimulates the release of algal C exudates (Lyon and Ziegler 2009). The use of this labile C by decomposers should, in turn, increase the mineralization of recalcitrant organic matter through a "priming effect" (Guenet et al. 2010).

Studies of forested streams, where allochthonous leaf litter is the main source of energy and nutrients (Fisher and Likens 1973, Tank et al. 2010), have contributed greatly to our knowledge about the structure and functioning of detritus-based ecosystems (Moore et al. 2004). In addition to detritivorous invertebrates, sub-

merged leaf litter is colonized and processed by bacteria and aquatic hyphomycetes (fungi), with the latter being the pioneer microbial decomposers that are dominant both in terms of biomass and litter-processing efficiency (Gessner and Chauvet 1994, Hieber and Gessner 2002). Although primary production is typically low in forested streams due to shading (Hill et al. 1995), benthic algae are often found on submerged leaf litter (Hax and Golladay 1993, Franken et al. 2005, Albariño et al. 2008). Recent studies have established links between light, aquatic hyphomycetes, invertebrate detritivores, and leaf litter decomposition, which have all been interpreted as indirect evidence of a response of litter consumers to litter-associated algae (Franken et al. 2005, Rier et al. 2007, Albariño et al. 2008, Lagrue et al. 2011). However, these studies fell short of elucidating the mechanisms underlying the apparent control of algae presence on leaf litter decomposition rates.

In this study, we used experimental microcosms to examine interactions between periphytic algae and microbial decomposers (fungi + bacteria), focusing on how algae alter decomposer activity and detritus decomposition. Because the nature and strength of the interactions between decomposers and primary producers are likely to be determined by inorganic nutrients (Fig. 1), we adopted a factorial design to assess effects of algae and nutrients on microbial decomposition of leaf litter. We also assessed the consequences of the presence of algae on detritus elemental quality. We specifically predicted that (1) decomposer activity would be controlled by nutrient availability and the presence of primary producers, such that algal production would elicit a "priming effect" on leaf litter decomposition that would be more pronounced under low-nutrient conditions; (2) primary producers would control the interactions between bacteria and fungi; and (3) primary producers would improve detritus nutrient content.

Methods

Experimental design

We conducted a $3 \times 2 \times 4$ factorial microcosm experiment, manipulating the composition of microorganism inoculum (three microbial assemblages, algae, fungi, and algae + fungi) and dissolved nutrient availability (two levels, high and low N and P contents) with measures repeated four times (10, 21, 31, and 42 d after the beginning of the experiment). On each sampling date, microcosms were destructively sampled at random to determine microbial responses. There were three (algae only) and four (fungi and algae + fungi) replicates per nutrient treatment.

Microcosms consisted of 250-mL Erlenmeyer flasks incubated at 15°C under a 12:12 hour photoperiod at 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetically active radiation intensity. Flasks were placed on orbital shakers set at 70 rpm to ensure continuous water aeration. All microcosms were supplied with 30 sterile (autoclaved, 15 min at 121°C) 15-mm-diameter disks of freshly abscised, air-dried leaves of alder (*Alnus glutinosa* Gaertn.), the dominant riparian tree species in southwestern France. The average initial leaf disk mass was determined to the nearest 0.01 mg from four independent sets of 30 autoclaved and freeze-dried leaf disks. Initial molar C:N and C:P ratios of autoclaved alder leaf litter were 20.6 and 3899, respectively. Microcosms were filled with 75 mL of either a low-nutrient (560 μg N/L and 60 μg P/L) or high-nutrient (5.6 mg N/L and 600 μg P/L) sterile medium. The N:P ratio of the culture medium (=20.7 on a molar basis) was comparable with values determined in the water of headwater streams of southwestern France. Preliminary studies enabled us to determine nutrient and C levels (1.58 g leaf C/L) in this batch experiment, in order to (1) avoid total nutrient depletion before the culture medium was renewed (i.e., 65 mL every five or six days) in high-nutrient conditions, and (2) to reach P limitation in low-nutrient conditions. Silicon (Si) was supplied in excess (250 μmol Na_2SiO_3/L), resulting in high Si:N ratios that prevented Si-limitation of diatom growth (Gilpin et al. 2004). The culture medium also consisted of all the other mineral elements making up the COMBO medium (Kilham et al. 1998), but for these elements, a fivefold dilution was applied to match the nutrient conditions of the oligotrophic softwater streams from which algae, fungi, and bacteria originated.

Biological assemblages

Microcosms were inoculated with an assemblage of six abundant, co-occuring species of aquatic hyphomycetes (*Tetrachaetum elegans* Ingold, *Tricladium chaetocladium* Ingold, *Tetracladium marchalianum* de Wildeman, *Flagellospora curvula* Ingold, *Lemmoniera terrestris* Tubaki, and *Articulospora tetracladia* Ingold), and/or a dominant diatom species (*Nitzschia palea* (Kütz.) W. Smith). We did not use more algal species for this experiment because diatoms, notably the genus *Nitzschia*, are by far the most abundant algal group occurring on decaying leaves in streams of southern France (A. Lecerf, *personal observation*). In addition, all microcosms were inoculated with an assemblage of bacteria contained in 1 mL of filtered stream water passed through sterile glass microfiber filters (GF/C, nominal cutoff: 1.2 μm; Whatman Filters, Clifton, New Jersey, USA). The purpose of this inoculation procedure was to ensure the presence of a taxonomically and functionally diverse assemblage of bacteria in the microcosms (Leflaive et al. 2008).

Aquatic hyphomycetes were isolated from single spores collected in foam from forested streams in southern France. Fungal cultures were maintained in axenic conditions on malt-agar, in petri dishes. Spores suspension of each fungal species were produced by submerging pieces of axenic colonies in agitated Erlenmeyer flasks containing a mineral salt solution (100 mg $CaCl_2$, $2H_2O$/L, 10 mg $MgSO_4$, $7H_2O$/L, 0.5 g of 3-morpholinopropanesulfonic acid/L, 100 mg KNO_3/

L, and 550 μg K_2HPO_4/L) at pH 7.0. Spores ($n = 10^3$) from each species were introduced to microcosms (treatments: fungi, fungi + algae). *Nitzschia palea* was isolated in the field and maintained in laboratory conditions. Precultures were grown in COMBO medium supplied with higher levels of Si (250 μmol Na_2SiO_3/L). Algal cells ($n = 10^4$) were introduced to microcosms (treatments: algae, fungi + algae) at the beginning of the experiment.

Response variables

On each sampling date, we determined the abundance of diatoms (free and detached from the microcosm walls) and aquatic hyphomycete spores in the culture medium of each microcosm. Using leaf disks recovered on each sampling date, we quantified the density of attached algae, biomass of leaf-associated mycelium, leaf mass remaining, and leaf C:N:P ratios. In addition, we determined bacterial density on leaf disks recovered at day 31, when algal development reached maximal values in most treatments. Diatom, fungal spore, and bacterial samples were preserved in 2% buffered formaldehyde, and stored at 4°C until processing. Leaf disks for determination of fungal biomass, leaf mass remaining, and C:N:P ratios were frozen at −18°C prior to analyses.

Diatoms that were not attached to leaf disks (i.e., free and attached to microcosm walls) were counted using a photonic microscope (Olympus BX41, Olympus, Tokyo, Japan) and a Malassez counting grid, which enables the determination of a minimum density of 10^3 cells/mL. Attached diatoms were sonicated on ice for one minute, to remove cells from leaf surfaces, and counted (>300 cells per sample) using a Malassez counting grid. Total algal abundance represents the sum of all attached and free cells counted within each microcosm.

Culture medium (1–5 mL) was filtered through a membrane filter (5 μm pore size; Millipore, Bedford, Massachusetts, USA) to trap aquatic hyphomycete spores, which were stained with 0.1% Trypan blue in 50% lactic acid. At least 200 spores were counted and identified at a magnification of 100–200×. Fungal species diversity was assessed by the Simpson's diversity index (D) calculated as follows:

$$D = 1 - \sum_{i=1}^{S} pi^2$$

where p_i represents the proportion of spores of species i and S is species richness (Magurran 2004). Fungal biomass on leaf disks was estimated using ergosterol content (Gessner and Chauvet 1993). Frozen litter samples (five leaf disks) were freeze-dried to dryness, weighed, and ergosterol extracted and partially purified by solid-phase extraction (Oasis HLB, 60 mg, 3 mL; Waters Corporation, Milford, Massachusetts, USA). Ergosterol was separated and quantified using high-performance liquid chromatography. Ergosterol concentrations were converted to fungal biomass assuming a conversion factor of 5.5 μg ergosterol/mg fungal dry mass (Gessner and Chauvet 1993). Ergosterol measurements also were used to monitor fungal contamination in algae-alone treatments.

Leaf mass remaining in each microcosm was estimated as the leaf disk mass minus the microbial biomass, i.e., attached algae and fungal mycelia. Leaf mass remaining was expressed as the percentage of final to initial mass of leaf disks. Diatom dry mass was estimated as the product of cell density per unit of leaf surface estimated through direct counts and the mean biomass of individual cells (estimated using a *Nitzschia palea* culture, 2.09×10^{-10} g/cell). Considering the low biomass of algae on leaf disks (maximum of 6.5% of leaf disk mass), potential differences in cell sizes between treatments were assumed to have a negligible effect on leaf mass loss estimations.

The density of bacteria on leaf disks was estimated to control for the development of the inoculated bacterial community in the microcosms and to assess the response of bacteria to the presence of fungi and/or algae. A 500-μL subsample of the sonicated sample used for attached algae counting, as described previously, was stained with 4',6-diamidino-2-phenylindole (DAPI) in the dark for 15 min. A small volume of the suspension was filtered on a black polycarbonate filter (Whatman, Nucleopore 0.2 μm). Bacterial densities were assessed by counting a minimum of 300 cells per treatment in stained samples (Porter and Feig 1980) using an epifluorescent light microscope (Olympus BX41).

To assess the effect of microbial inoculum treatment on leaf detritus stoichiometry, C:N:P ratios were determined on 10 freeze-dried, weighed, and ground leaf disks. C and N content were determined using a CHN elementary analyzer (NA 1500 Series 2, Fisons, Manchester, UK). Total P content was determined after persulfate digestion and ammonium molybdate reaction. All elemental ratios are expressed as molar ratios.

Statistical analyses

Treatment effects on responses were assessed using three-way ANOVA with the microbial treatment, nutrient level, and time set as fixed factors. The condition of independence was achieved thanks to the destructive sampling design adopted in our study. For parameters determined once (cumulative spore number and Simpson's diversity index, bacterial abundance), a two-way ANOVA was performed with microbial treatment and nutrient level as fixed factors. Log-transformation was performed when necessary to meet the assumptions of normality and homoscedasticity. Multiple comparisons were conducted using Tukey's HSD test. Leaf litter decomposition rates (k) were estimated using an exponential model ($m_R = m_0 \times e^{-kt}$), where m_R is the leaf mass remaining at time t (days) and m_0 is the initial leaf mass (Bärlocher 2005), and were compared among treatments using profile-likelihood 95% confidence intervals (Venables and Ripley 2002).

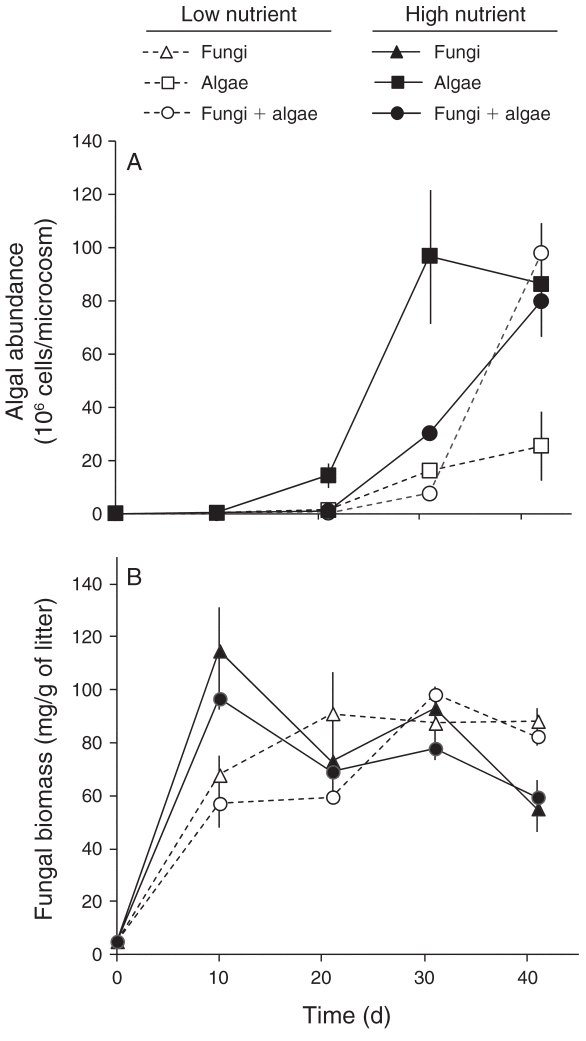

FIG. 2. Effects of nutrient level and microbial assemblage on the growth of microorganisms during the 42-day experiment. (A) Numerical response of the diatom *Nitzschia palea* to nutrient level and presence of aquatic hyphomycetes. (B) Response of mycelial biomass in leaf litter to nutrient level and presence of *N. palea*. Vertical bars represent ±SE.

All statistical analyses were performed using the program R (R Development Core Team 2010). The significance threshold was set at $P < 0.05$.

RESULTS

Diatom abundance (Fig. 2A) was on average twofold higher under high- vs. low-nutrient conditions ($F_{1,40} = 41.5$, $P < 0.0001$). A significant time × fungi × nutrient interaction ($F_{3,40} = 9.1$, $P = 0.0002$) hinted at complex responses of diatoms to treatments. The growth of diatoms under high-nutrient conditions was reduced in the presence of aquatic hyphomycetes (peak algal abundance occurred 10 days later). In contrast, under low-nutrient conditions the presence of aquatic hyphomycetes led to an increase in diatom abundance on the last date of the experiment (Fig. 2A).

TABLE 1. Effects of nutrients and algae on production and diversity of aquatic hyphomycete spores.

Nutrient conditions/ microbial assemblage	Cumulative spore number (10^3 spores/mL)	Simpson diversity index
Low nutrient/fungi alone	67 ± 11	0.53 ± 0.07
High nutrient/fungi alone	167 ± 27	0.53 ± 0.17
Low nutrient/algae + fungi	60 ± 82	0.58 ± 0.08
High nutrient/algae + fungi	198 ± 41	0.63 ± 0.05

Notes: Spore production is represented by the cumulative number of spores per milliliter throughout the 42-day experiment. All values are mean ± SD.

Fungal biomass (Fig. 2B) was not significantly influenced by nutrients ($F_{1,48} = 0.04$, $P = 0.84$) or algae ($F_{1,48} = 4.0$, $P = 0.051$). However, maximal fungal biomass was reached earlier in high- vs. low-nutrient microcosms (time × nutrient interaction, $F_{3,48} = 11.9$, $P < 0.0001$). Cumulative spore production (Table 1) was threefold greater under high- than under low-nutrient conditions ($F_{1,12} = 85.9$, $P < 0.0001$). The diversity of spores produced throughout the experiment was relatively constant under high-nutrient conditions, but sharply decreased at the last date of the experiment under low-nutrient conditions (time × nutrient interaction, $F_{3,48} = 10.9$, $P = 0.0001$, data not shown). Throughout the experiment, the presence of diatoms positively influenced fungal spore diversity as determined by the Simpson index ($F_{1,48} = 12.0$, $P = 0.001$; Table 1). In contrast, diatoms had no significant effect on cumulative spore production ($F_{1,12} = 0.9$, $P = 0.35$).

After 31 days of incubation, when spore production and diversity reached their maximal values, the density of bacteria attached to leaf disks was found to significantly differ among treatments (Fig. 3). Nutrient enrichment had a significant but moderate effect on

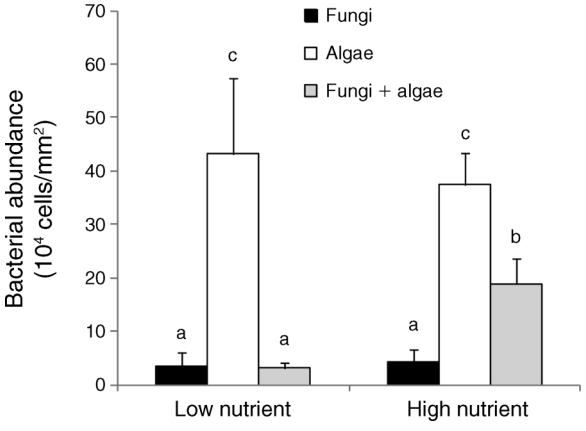

FIG. 3. Effects of nutrient level and microbial assemblage on the density of bacteria attached to leaf litter after 31 days of decomposition. Vertical bars represent +SE. The same letters above the bars indicate no significant difference ($P < 0.05$) between treatments according to Tukey's post hoc test.

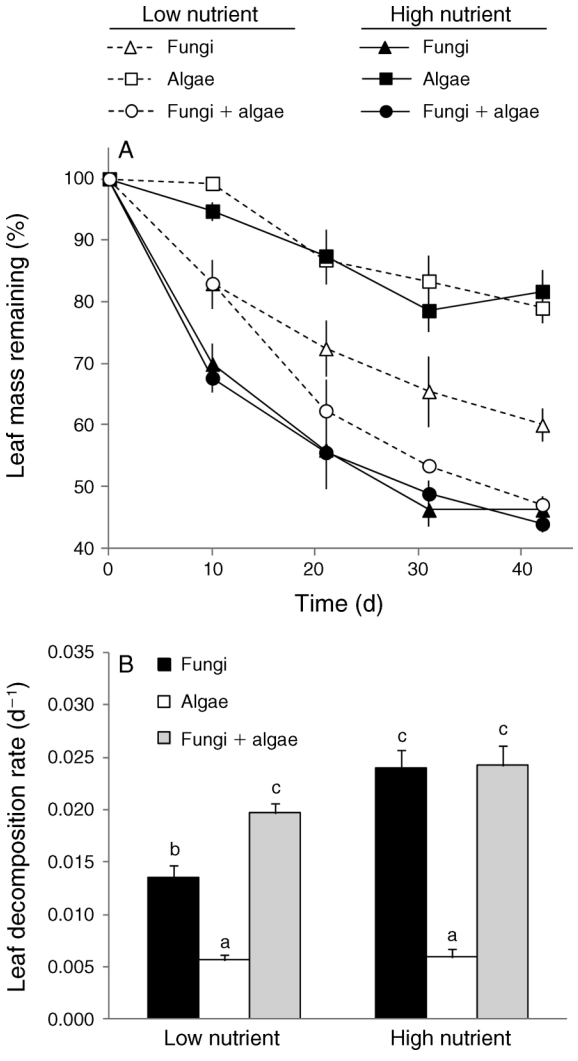

FIG. 4. Effects of nutrient level and microbial assemblage on leaf litter decomposition, represented as (A) percentage of leaf litter mass remaining through time, and (B) daily decomposition rate (k). Vertical bars represent standard errors. Same letters above the bars indicate no significant difference between treatments according to profile-likelihood 95% confidence intervals.

bacteria, with densities being 1.2-fold as great under high- vs. low-nutrient conditions ($F_{1,14} = 10.2$, $P = 0.007$). Diatom presence had a strong positive effect on bacterial abundance compared to the fungi-alone treatment ($F_{2,14} = 43.3$, $P < 0.0001$; Fig. 3). This response was absent or reduced when fungi were also added (algae + fungi) to low- or high-nutrient microcosms ($F_{2,14} = 8.1$, $P = 0.005$; Fig. 3).

Leaf litter decomposition was slowest in the absence of fungi, i.e., only in the presence of bacteria and diatoms, irrespective of the nutrient level (Fig. 4A, B). Under low-nutrient conditions, the addition of diatoms to fungi stimulated leaf litter decomposition (Fig. 4A, B). Despite delayed initial decomposition (Fig. 4A), litter decomposition rates in the presence of diatoms did not significantly differ between low- and high-nutrient microcosms (Fig. 4B). Nutrient level significantly affected litter mass remaining in microcosms ($F_{1,64} = 35.0$, $P < 0.0001$).

Nutrients, diatoms, and fungi interactively influenced litter stoichiometry (Fig. 5). Leaf litter C:P and C:N ratios were lower under high- vs. low-nutrient conditions ($F_{1,61} = 205.7$, $P < 0.0001$ and $F_{1,63} = 66.5$, $P < 0.0001$, respectively). The presence of fungi was an important factor controlling the decline in C:P and C:N ratios through time (microbial assemblage: $F_{2,61} = 12.7$, $P < 0.0001$ and $F_{2,63} = 70.6$, $P < 0.0001$, respectively). On the last date, under low-nutrient conditions, the algae + fungi treatment showed much lower leaf litter C:P ratios compared to the other microbial assemblages (microbial assemblage × nutrient × time interaction, $F_{6,61} = 2.3$, $P =$

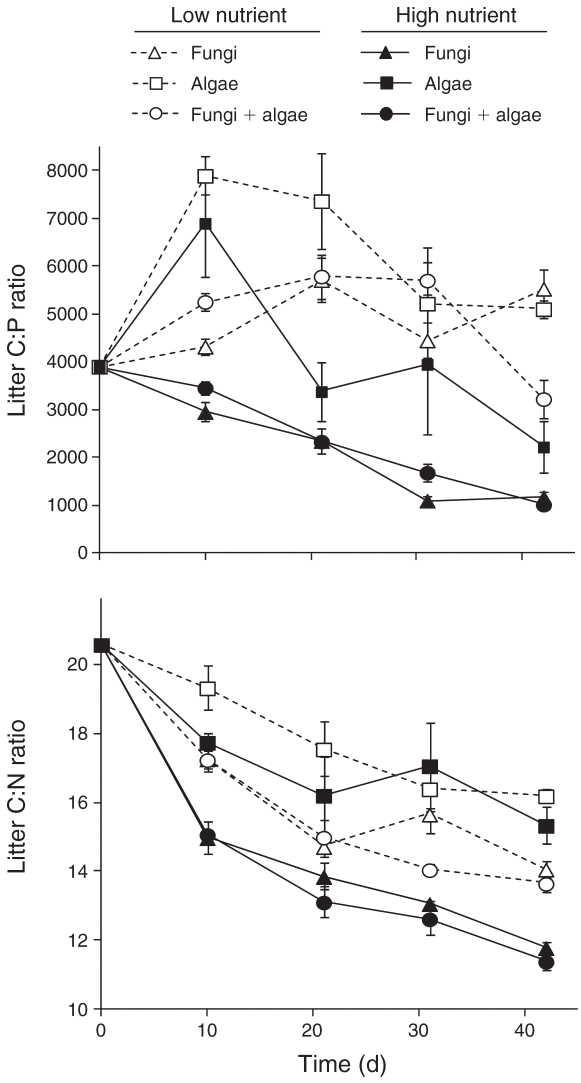

FIG. 5. Effects of nutrient level and microbial assemblage on leaf litter elemental composition (molar ratios) through time. Vertical bars represent ±SE.

0.043). In contrast, algae did not significantly alter leaf litter C:N ratios in low-nutrient treatments through time (microbial assemblage × nutrient × time interaction, $F_{2,15} = 1.2$, $P = 0.33$).

Discussion

Primary producers and heterotrophic decomposers are keystone functional groups within ecosystems, which can interact in complex ways (Bratbak and Thingstad 1985, Harte and Kinzig 1993, Daufresne and Loreau 2001). Primary producers rely on heterotrophic decomposers for the mineralization of essential nutrients, whereas decomposers are dependent on primary producers to supply energy resources. However, both groups may actively compete for the same inorganic nutrients (Bratbak and Thingstad 1985, Harte and Kinzig 1993). Considering that heterotrophic microorganisms are better competitors for nutrients than primary producers, theoretical models predict that primary producers and decomposers can only coexist if decomposers are limited by the carbon provided by coexisting producers (Bratbak and Thingstad 1985, Daufresne and Loreau 2001). In detritus-based stream ecosystems, decomposers rely almost exclusively on allochthonous organic matter, since autochthonous production is often very low (Fisher and Likens 1973). This large decoupling between plant detritus production and decomposition implies that primary producers should be competitively excluded by decomposers. This prediction was not supported by our experimental study, since diatoms were never totally excluded from fungal treatments. Our results are also in accordance with previous observations on the ubiquity of benthic algae in detritus-based streams, and repeated reports of autotrophic biofilms on submerged leaf litter (e.g., Hax and Golladay 1993). However, observations of algal presence on decaying leaf litter do not rule out the competitive dominance by fungal decomposers. Competition for inorganic nutrients may explain why diatom growth was negligible during the exponential increase in fungal biomass at the beginning of the experiment. Diatom density increased substantially following a decline in fungal biomass, when competition for nutrients was probably less important (Fig. 1). A weak competitive ability of algae has been demonstrated in bacterioplankton–phytoplankton systems (Currie and Kalff 1984, Mindl et al. 2005, Danger et al. 2007*a*). Therefore, in addition to low light levels (Hill et al. 1995), competition for nutrients between heterotrophic and autotrophic microorganisms constitutes a reasonable explanation for the generally low production of algae in detritus-based streams (Fisher and Likens 1973).

In ecological literature, interactions between bacteria and fungi have often been questioned. Total microbial activity and microbial growth can be increased when bacteria and fungi co-occur (e.g., Bengtsson 1992). Nevertheless, most studies have shown that relationships between bacteria and fungi are antagonistic, owing to antibiotic substances produced by fungi (Drews 2000) and to competition for resources (Mille-Lindblom et al. 2006). In forested headwater streams, fungi are often considered as the main decomposers of leaf litter, whereas bacteria play a secondary role during later decomposition stages (Hieber and Gessner 2002). The functional importance and strong competitive ability of aquatic hyphomycetes is supported in our study by the much faster decomposition and substantially reduced bacterial abundance in microcosms with fungi, irrespective of the nutrient level.

In the presence of algae, bacteria were greatly stimulated, and the negative effect of fungi on bacteria was reduced, which may be explained by the availability of labile, algal-based C exudates (Baines and Pace 1991, Danger et al. 2007*b*, Ziegler and Lyon 2010). Bacteria colonizing detritus are more likely to be limited by the recalcitrance of leaf C than fungi, which did not seem to grow better in the presence of algae. The latter observation is consistent with the fact that the specific enzymes and physiology of fungi enable them to break down and assimilate refractory plant polymers such as lignin and hemicellulose (Romani et al. 2006). Because fungal biomass may be only loosely related to ergosterol content, especially due to the inclusion of nonliving mycelium (Mille-Lindblom et al. 2004), fungal spore production may be more relevant to assess the influence of algal exudates on fungi. Although the presence of diatoms did not significantly stimulate fungal spore production, it did lead to an increase in spore diversity. It is plausible that algae may facilitate the coexistence of multiple fungal species through a diversification of C sources. However, this effect may be less important in streams than in our microcosms due to the high diversity of C sources available in natural ecosystems.

Despite their moderate densities in low-nutrient conditions, diatoms also strongly stimulated the decomposition of leaf litter (~20% increased mass loss). After 42 days, leaf litter mass remaining was similar under low- and high-nutrient conditions in the presence of algae. Nutrient stress is known to enhance the production of C exudates by algae (Baines and Pace 1991, Scott et al. 2008, Ziegler and Lyon 2010), and these exudates likely constitute an important C resource for decomposers in nutrient-poor streams (Lyon and Ziegler 2009). The "priming effect" mediated by algal C exudates provides a reasonable explanation of diatom-enhanced decomposition of leaf litter in our study. This process alters the mineralization rate of low-turnover pools of organic matter following inputs of high-turnover pools of C, especially in low-nutrient environments, and is mainly explained by the utilization of labile C by decomposers to process more refractory compounds (Guenet et al. 2010). The subsequent increase in inorganic nutrients released by decomposers also may explain why diatom abundance increased sharply on the last date of the experiment. This positive feedback is in

accordance with the hypothesis of mutualistic interactions between primary producers and decomposers (Harte and Kinzig 1993, Daufresne and Loreau 2001; Fig. 1). In real stream ecosystems, the intensity of the priming effect and nature of interactions between decomposers and algae may also conceivably vary with time due to changes in key abiotic factors (i.e., light and temperature). Specifically, a strong priming effect is expected to occur in spring, i.e., when primary productivity peaks (e.g., Roberts et al. 2007) and fungal biomass (and thus competition for inorganic nutrients) declines as litter becomes scarcer.

In aquatic ecosystems, labile C inputs can yield an increase of 10–500% in the mineralization rate of refractory C (Guenet et al. 2010). This wide range of variation may partially be explained by differences in labile C concentrations across the studied systems. Specifically, intensity of priming effect could be expected to be lower in streams than in standing water owing to high dilution of algal exudates in flowing water. Our closed microcosms represented an intermediate condition between lotic and lentic habitats, since culture medium was renewed periodically over the experiment, avoiding excessive exudate accumulation. In addition, an exacerbation of algal exudates importance in our microcosms can certainly be rejected based on the following calculation (see the Appendix for more details). When culture conditions are controlled (i.e., low emigration/immigration, low mortality), short-term biomass accrual rate can be used as an index of productivity (Steinman et al. 2006). Fitting exponential growth models on biomass accrual curves (Gessner and Chauvet 1997), maximal algal production in our experiment reached 11 μg C·mg $C^{-1}·h^{-1}$. Considering a C excretion of 45% of total algal primary production (the maximal value found in Ziegler and Lyon 2010), attached algal biomass (4.5 mg C per microcosm) and algal exudates accumulated at the end of the experiment (3.05 mg C per microcosm) were likely to represent a maximum of 3.8% and 2.6% of total allochthonous C (litter), respectively. These proportions are broadly comparable to those commonly found in headwater streams. For example, a headwater stream survey carried out by Rosenfeld and Roff (1991) showed that total autochthonous C produced over one year, including algal biomass accrual and C excretion, represented ~7% of total allochthonous C inputs.

Consistent with previous findings (Cross et al. 2003), leaf litter C to nutrient ratios were primarily determined by both nutrient availability and fungal growth. Changes in nutrient content often result from microbial respiration (C loss) and nutrient immobilization by fungi (Güsewell and Gessner 2009, Sinsabaugh et al. 2009). In the absence of fungi, C:P ratios strongly increased at the beginning of the experiment, probably through leaching of P-rich compounds. The decrease in C:P ratios occurring later can be explained by the growth of nutrient-rich diatoms on the surface of leaf disks. Additionally, after 42 days of decomposition, the association of diatoms and fungi significantly enhanced organic matter elemental quality through a reduction in C:P ratios in low-nutrient microcosms. Leaf litter C:N ratios were unaffected by the presence of diatoms, probably because of the high N:P ratios of culture media favoring P rather than N limitation of microbial growth. Phosphorus is a limiting element for microorganisms and invertebrates in many headwater stream ecosystems (Gessner and Chauvet 1994, Frost and Elser 2002, Cross et al. 2003). Large elemental imbalances exist between consumers and their food in detritus-based ecosystems compared with living plant-based systems, particularly with regard to P content (Cross et al. 2003, 2005). Although we still have a poor understanding of the genuine influence of detritus stoichiometry on detritivore life history traits (but see Danger et al. 2012), studies on plant–herbivore interactions have revealed that consumer growth rates are directly related to the C:P ratios of their resources (e.g., Frost and Elser 2002). Considering the generally elevated C to nutrient ratios of detritus, such elemental constraints could be far more pronounced for detritivores than for herbivores (Cross et al. 2003, 2005). Consequently, the nearly twofold decrease in leaf litter C:P ratio induced by algae in low-nutrient conditions could alleviate nutrient imbalances for detritivorous invertebrates and may indirectly promote secondary production and efficiency of energy and nutrient transfers to higher trophic levels in real-world ecosystems (Cross et al. 2003).

To conclude, our experimental study sheds new light on an interesting yet complex relationship between primary producers and decomposers in detritus-based ecosystems. Algal presence in combination with fungal decomposers promoted decomposer diversity, accelerated leaf litter decomposition, and improved the quality of detritus. Such positive feedbacks of algal presence were mainly observed under low-nutrient conditions, suggesting that environmental factors can alter the functional impact of primary producers in detritus-based ecosystems. Moreover, as invertebrates were not included in our experiment, we cannot rule out the possibility that the priming effect is less important in real-world ecosystems due to consumer control on microorganisms. If priming effect is reduced in nutrient-rich conditions, invertebrates could also reduce its intensity through local nutrient enrichment related to invertebrate excretion (Hillebrand and Kahlert 2001). Since heterotrophic streams and other detritus-based ecosystems are key sites for organic matter processing and nutrients and C retention (Moore et al. 2004, Cole et al. 2007), a better grasp of the role of autochthonous C on the fate of allochthonous material in these ecosystems is clearly needed.

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