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Influence of invasive *Acer negundo* leaf litter on benthic microbial abundance and activity in the littoral zone of a temperate river in Lithuania

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Abstract – Riparian forests are known as important source of allochthonous organic matter entering to water ecosystems *via* fallen leaves. However, leaf litter, depending on their quality, may create different conditions for benthic microorganisms functioning in littoral zone of water bodies. In order to evaluate the impact of riparian invasive *Acer negundo* on littoral water zone of the River Neris (Lithuania), we performed physicochemical and microbiological investigations in bottom sediments of three different sites of the river. One sampling site was close by riparian *A. negundo*, another close by native *Alnus glutinosa* location and a third zone was near the shore without riparian vegetation. Content of nutrients in the littoral sediments differed between invasive and native trees leaf litter accumulation sites, while not always significantly. The highest microbial densities as well as benthic community respiratory activity (expressed as the rate of organic carbon mineralization) occurred in *A. negundo* leaves accumulation site. In sediments of this site, the most intensive anaerobic terminal organic carbon mineralization process – sulfate reduction and the highest concentration of hydrogen sulfide were also observed. Differences in the intensity of mineralization processes between sites suggest that the replacement of the riparian native species such as dominant *A. glutinosa* by invasive *A. negundo* with higher biodegradability leaves may induce local changes in organic matter processing in the littoral zone of the river. The increase of littoral bioproductivity in the accumulation zone of *A. negundo* leaf litter can occur due to the inflow of available organic matter and its intensive mineralization.

Keywords: leaf litter / benthic microorganisms / river

Résumé – Influence de la litière d'*Acer negundo* invasif sur l'abondance et l'activité microbienne benthique dans la zone littorale d'une rivière en Lituanie. Les forêts riveraines sont connues comme source importante de matière organique allochtone entrant dans les écosystèmes aquatiques via les feuilles tombées. Cependant, la litière, en fonction de sa qualité, peut créer différentes conditions pour que les microorganismes benthiques fonctionnent dans la zone littorale des masses d'eau. Afin d'évaluer l'impact de l'*Acer negundo* invasif dans la zone d'eau littorale de la rivière Neris (Lituanie), nous avons procédé à des recherches physico-chimiques et microbiologiques dans les sédiments de trois sites différents de la rivière. Un site d'échantillonnage était proche de *A. negundo* riverain, un autre proche de l'emplacement d'*Alnus glutinosa* indigène et une troisième zone était près d'une rive sans végétation riveraine. Les contenus en nutriments dans les sédiments du littoral différaient entre les sites d'accumulation de déchets de feuilles d'arbres envahissants et natifs, bien qu'ils ne soient pas toujours significativement différents. Les densités microbiennes les plus élevées ainsi que l'activité respiratoire de la communauté benthique (exprimée en taux de minéralisation du carbone organique) sont observées dans le site d'accumulation de feuilles d'*A. negundo*. Dans les sédiments de ce site, on a observé le processus de minéralisation du carbone organique anaérobie la plus intensive – la réduction des sulfates et la plus forte concentration de sulfure d'hydrogène. Les différences dans l'intensité des processus de minéralisation entre les sites suggèrent que le remplacement des espèces indigènes riveraines telles que *A. glutinosa* dominante par une invasive *A. negundo* avec des feuilles de biodégradabilité plus élevées peut induire des changements locaux dans le

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traitement de la matière organique dans la zone littorale de la rivière. L'augmentation de la bioproductivité du littoral dans la zone d'accumulation de la litière d'*A. negundo* peut se produire en raison de l'afflux de matière organique disponible et de sa minéralisation intensive.

Mots clés : litière / microorganismes benthiques / rivière

1 Introduction

Riparian forest strips play an important role in regulating anthropogenic nutrient transport into water body (Weissteiner *et al.*, 2013). Although riparian vegetation acts as a filter reducing input from surroundings, it subsidizes aquatic systems with organic matter (Graça and Canhoto, 2006) and may have a negative impact due to the acceleration of littoral bioproductivity. Leaf litter is one of the most important sources of nutrients and energy supporting food webs in oligotrophic systems and small forested streams (Wallace *et al.*, 1997) and may also be important point sources of nutrients inducing siltation processes in the littoral zone of larger water bodies. Leaf litter processing has been studied extensively in forests and forested streams, particularly small ones (Fargen *et al.*, 2015), but received scant attention in littoral zones of rivers or lakes. Large rivers and streams may differ in some traits, also related to their riparian trees species, environment or biota, which potentially determine the fate of leaf litter.

Microorganisms, mainly bacteria and fungi, are key agents involved in litter breakdown and microbial decomposition of litter enhances the attractiveness of leaf detritus to detritivores that can degrade up to 50% of the annual litter input into lotic ecosystems (Hieber and Gessner, 2002). Additionally, in the bottom sediments of littoral zones, organic matter is degraded by both anaerobic and aerobic microorganisms and their composition and activity depend on the surrounding environment (Jonsson *et al.*, 2001; Dzyuban, 2003). Among physicochemical characteristics, the availability of nutrients in surrounding media is mainly determining the development of different microbial groups forming the benthic community (Artigas *et al.*, 2008).

In recent decades, native riparian vegetation has been modified by human activities, allowing the colonization by invasive tree species. Riparian ecosystems are highly vulnerable to exotic plant invasion (Hood and Naiman, 2000) due to their milder microclimatic conditions and the frequent natural and anthropogenic disturbances that create diverse niches to support invasive species (Chytrý *et al.*, 2008). Shifts from native to exotic trees may alter the quality of leaf litter inputs into water body, thus causing effects on quantity and quality of nutrients (Molinero and Pozo, 2006), biotic communities (Weijers *et al.*, 2009) and ecosystem functioning (Martinez *et al.*, 2013). Several studies have been performed to examine invasive species effects on leaf decomposition rates in aquatic ecosystems by litterbags method, but still have found mixed effects (Swan *et al.*, 2008; Marano *et al.*, 2013; Serra *et al.*, 2013). Variability in leaf litter decomposition rates in aquatic systems may be linked to the direct or indirect effect of leaf litter on the changes of benthic communities composition and activity (Bärlocher and Graça, 2002; Medina-Villar *et al.*, 2015), that highlights the importance of specific studies in order to understand the effects of invasions on ecosystem functioning (Fargen *et al.*, 2015).

Boxelder maple (*Acer negundo* L.) is an invasive plant of Lithuanian and as inspiring a potential threat to the stability of local ecosystems is controlled by the legal regulation documents of the State Plant Protection Service. *A. negundo* has become commonly distributed after its escape from cultivation during the 1930s and has been included in the list of invasive and annulled species since 2004 (Gudžinskas *et al.*, 2014). This species was deliberately introduced to Lithuania from North America and it has become wide spread, because it develops deep roots, sprout stumps, and prefers to grow in moist soils, but also tolerates drought. Due to the fact that the seeds of *A. negundo* are easily transported by water flow, it prolifically colonizes riverside communities containing black alder (*Alnus glutinosa* (L.) Gaertn.) (Gudžinskas *et al.*, 2014).

Previously, we have investigated ecotoxicological effects of *A. negundo* and *A. glutinosa* leaf litter leachates obtained in laboratory experiments during 90-day decomposition of leaves under microaerobic/anaerobic (Krevš *et al.*, 2013) and aerobic conditions (Manusadžianas *et al.*, 2014). Besides temporal and species-dependent differences in toxicity to algae and invertebrates, it has been found that *A. negundo* leaves lose biomass more rapidly and release more nutrients during decomposition, than those of *A. glutinosa*.

Because of the tight coupling between riparian and aquatic habitats, we hypothesized that intensive spread of invasive species along the shoreline of the Neris River could alter the development of benthic microorganisms and organic matter mineralization in the littoral zone of the river. Taking into account a fast decomposition of *A. negundo* leaf litter observed under laboratory experiments, we expected a higher benthic microbial densities and, consequently, higher rates of mineralization processes in bottom sediments of the *A. negundo* litter accumulation zone than those in the zone nearby native trees. To test our hypothesis, physicochemical parameters, densities of microbial heterothrophs (bacteria and fungi) and activity of benthic community (expressed as the rate of organic carbon mineralization and sulfate reduction) were investigated in the bottom sediments of three different littoral sites of the river: one site was close by riparian *A. negundo*, another close by native trees (mostly *A. glutinosa*) location and a third zone was near the shore without riparian vegetation, respectively. Leaf litter was accumulated in littoral sediments of the first two sites.

2 Study area and methods

2.1 Study area and sampling strategy

The Neris is the largest tributary of the River Neman, and it is the second longest river in Lithuania. Its watercourse is 511 km: for 276 km the river runs through Belarus and for 235 km it flows through Lithuania including the capital Vilnius, and becomes a tributary of the River Neman in Kaunas. The Neris River basin surface is 2% lakes, 14% swamps and 27% forest (Encyclopedia of Lithuania, 2008).

Due to the forested and laky basin, the water level is stable during the summer and rises only with the spring thaw. Neris is located in the temperate zone and its mean annual water temperature varies from 3 °C in January to 22 °C in August (Galvonaitė *et al.*, 2007). In native riparian areas of the River Neris, deciduous tree communities prevail, and since the eighth decade of the 20th century, *A. negundo* has rapidly distributed along shoreline of the river (Straigytė *et al.*, 2015).

The samples were collected in the River Neris segment of Vilnius vicinity (54°44′25″N, 25°17′55″E). Three sampling sites in the narrow strip of the littoral zone with slow water flow were chosen for the study in the spring–autumn period (26–28 March, 31 July to 2 August and 16–18 October) 2013–2014. One of them (the *A. negundo* leaf litter accumulation zone) was located in the littoral part of the river where the bank was invaded by *A. negundo*, whose branches were hanging low over the water. Other site (the *A. glutinosa* leaf litter accumulation zone) was close by riparian native forest composed mainly of *A. glutinosa*. Bottom sediments of these littoral sites were covered by leaf litter, especially in the autumn–spring period. A third area of the littoral zone (the zone without leaf litter) was located along riverside with no trees growing on the bank. Sampling sites spacing downstream between *A. negundo* and the zone without leaf litter was approximately 1 km, while between the zone without leaf litter and *A. glutinosa* zones about 1.5 km. Each site had a surface area of about 2 m length and 0.5–0.7 m width from the river bank. These sites did not have macrophyte and were always in contact with water. Physicochemical (T, pH, O_2, N_t, P_t, C_{org}, S/SO_4^{2-}, H_2S+HS^-) parameters, benthic heterothrophs (bacterial and fungal abundance) and the rates of sulfate reduction and organic carbon mineralization were studied in bottom sediments of these littoral sites at water depth of about 15–20 cm. Samples were collected from a surface layer of bottom sediments (0–5 cm), using a metal tube sampler. Triplicate sediment samples were taken at each site for analysis. Samples for microbiological analyses were transported to the laboratory in sterile glass containers and examined immediately. Samples for chemical analyses were placed in plastic vials and transported to a certified analytical laboratory in insulated cooler. *In situ* the water temperature, dissolved oxygen concentration and pH were also measured at each sampling site. For microbial characteristics of decaying leaf litter, *A. negundo* and *A. glutinosa* leaves were collected from bottom sediments in the research sites two times: in March and October. At the laboratory, 20–30 leaves from each site was rinsed with deionized water to remove sediments and cut into disks of 10 mm diameter for further quantification of fungal and bacterial parameters.

2.2 Physicochemical analysis

Water temperature and pH were measured using a portable universal MultiLine f/Set-3 meter (WTW). Dissolved oxygen concentration was determined with oxygen meter (Eutech Instruments). Nutrient and sulfate analyses were performed in a certified analytical laboratory (JSC Water Investigations, Vilnius, Lithuania) in accordance with standard methods (ISO 6878; ISO 11905-1; ISO 8245; ISO 10304). Hydrogen sulfide was determined according to the method described by Volkov and Zhabina (1980).

2.3 Microbial analysis

For the investigation of benthic bacteria (total number, heterotrophic and cellulose-degrading bacteria), 1 g sediments were placed in flasks with 100 mL of autoclave sterilized water and sonicated in bath (Kraintek, Slovakia) for 4 min at 38 kHz and then were extracted on a rotary shaker (Certomat® UHK-50) with shaking (200 rpm) for 15–20 min. For bacterial (total number and heterotrophic bacteria) evaluation of decaying leaf litter, 15 leaf discs were placed in tubes with 5 mL of autoclaved water and sonicated in bath for 2+2 min at 38 kHz (Artigas *et al.*, 2008). The total number of bacteria were estimated by epifluorescence microscopy after 4′,6-diamidino-2-phenylindole (DAPI) staining on 0.2 µm black filters (Millipore, Bedford, MA) (Porter and Feig, 1980). At least 200 bacterial cells in 20 fields were counted at 1000 magnification using epifluorescence microscope Nikon Eclipse (Japan). Heterotrophic bacteria were incubated on 10× diluted agar nutrient medium at 22 °C for 120 h (Kuznetsov and Dubinina, 1989). Cellulose-degrading bacteria (CDB) were incubated on solid Hetchinson medium with 1% CMC at 22 °C for two weeks. For the recognition of CDB colonies, 5 mL of 0.1% Congo red and 5 M NaCl were used in each plate (Kluepfel, 1988). To account for sulfate reducing bacteria (SRB) from surface layer of bottom sediment samples, they were inoculated into lactate-supplemented Postgate medium (Postgate, 1984).

The abundance of benthic terrestrial fungi was estimated after 7 days of cultivation on malt extract agar at constant 15 °C in darkness. For fungal analyses of decaying leaf litter, a set of 20 leaf discs were placed in Erlenmeyer flasks containing 100 mL filtrated water and incubated on rotary shaker (Certomat® UHK-50) with gentle shaking (75 rpm) for three days at 15 °C (Gulis and Suberkropp, 2006). After incubation, part of the conidial suspension was used for the evaluation of terrestrial fungi abundance and directly plated on nutrient media. To estimate aquatic fungi abundance, 50 mL of the preserved conidia suspension was filtrated through 8 µm membrane filter (Millipore), stained with 0.01% cotton blue in lactophenol and examined using a light microscope (PZO, Warszawa). One hundred microscopic fields were scanned per filter to count and identify conidia. For fungi and bacteria study, each of the three independent samples of every research site was analyzed in two sub-replicates. Microbial abundance was calculated per gram of dry weight sediments and expressed as a number of cells or colonies forming units (CFU)/g of DW sediments. The abundance of bacteria and fungi on leaf litter was evaluated in mg of dry leaf weight.

The carbon mineralization rate in bottom sediments was determined on the basis of respiratory activity of benthic aerobic and anaerobic community and measured from the amounts of consumed oxygen and released inorganic carbon in hermetically sealed stratometric tubes with a silt core and near bottom water (Kuznetsov and Dubinina, 1989). Percentage contribution of aerobic and anaerobic processes to carbon mineralization was evaluated after calculating the difference between total inorganic carbon emission and emission by aerobic respiration. For the evaluation of inorganic carbon emission by aerobic respiration, the values of consumed oxygen were converted to carbon by factor 0.44 (Kuznetsov and Dubinina, 1989). The sulfate reduction rate was ascertained using a $Na_2{}^{35}SO_4$ tracer technique (Sorokin, 1999). Bottom sediment samples (0–5 cm deep) were placed in 20 mL glass tubes and hermetically sealed with rubber stoppers. A 0.1 mL $Na_2{}^{35}SO_4$ solution (Amersham Pharmacia Biotech) of at least $2–3 \times 10^6$ imp/min radioactivity was injected into the samples by syringe with long needle. Glass tubes with bottom sediment samples were stored in dark bags placed in hermetic impact resistant thermos bottles filled with bottom water. Thermos bottles were submerged near the shoreline of the river study site and incubated for 24 h. The subsequent procedures were carried out in the laboratory. After the chemical treatment of samples, filters (0.2 µm, Millipore) were placed in vials containing 5 mL of scintillation cocktail Opti Phase Hi Safe 3 (Wallac Scintillation Products). Radioactivity was determined using a liquid scintillation counter.

2.4 Statistical analysis

Analysis of variance (ANOVA) was used to test for differences between three habitats in terms of chemical compound, microbial numbers and carbon mineralization rate. Tukey test was used to determine where the differences occurred ($p \leq 0.05$). Data were log-transformed before statistical analysis. The similarity of fungal assemblages in the bottom sediments and on leaf litter was analysed by Sorenson's index (SI). The similarity is considered to be low (<39%), moderate (40–49%), high (50–59%) and very high (>60%) (Magurran, 1988). Pearson's correlation analysis was used to examine the relationship among biotic parameters, and between biotic and abiotic parameters. The statistical analysis was carried out using the software PASW Statistics 18.0 (Predictive Analytics Software, IBM).

3 Results

3.1 Environmental conditions

Near bottom water temperature, pH values and oxidative conditions determined in different littoral zones of the river were similar and varied only seasonally. Water temperature was moderate and increased from 8 ± 1 °C in March to 22 ± 2 °C in July and decreased to 11 ± 1 °C in October. The highest dissolved oxygen concentration was detected in October and March and ranged between 9.6 and 10.7 mg/L. In midsummer its values decreased to 7.8–8.1 mg/L. The pH value of water was weakly alkaline and ranged between 7.6 and 8.2.

The shoreline area of *A. negundo* habitat was swampy, without grass cover. The upper layer of sediments in littoral part covered by silt. Near native trees, mostly *A. glutinosa* habitat, bottom sediments of littoral part of the river was composed of grey sand mixed with silt impurities. Sandy gravel without biomass residue in the bottom sediments was found in open without leaf litter littoral part of the river. The values of chemical parameters were always the lowest in the sediments of the zone without leaf litter (Tab. 1). Content of nutrients in the littoral sediments differed between invasive and native trees leaf litter accumulation sites, while not always significantly. In October, N_t and C_{org} concentration was higher in *A. negundo* and in contrast, P_t content was larger in the sediments of the native tree leaf litter accumulation zone. Also, bottom sediments showed differences in the C/N ratio among sites (Tab. 1). The amount of hydrogen sulfide was always higher in *A. negundo* leaf litter accumulation zone than in *A. glutinosa* zone and in sulfate values, with the exception of October, were significant differences between both littoral sites.

3.2 Benthic bacteria and fungi

The lowest total benthic bacterial number was detected in March and the highest values were in October (Tab. 2). In the sediments of leaf litter accumulation zone, bacterial abundance was an average 1.5–2 times higher than that in sediments without leaf litter. In March, significant increase in the number of benthic bacteria was observed in *A. negundo* leaf litter accumulation zone comparing to the site with native tree leaf litter, while in July and October the differences in their number were not significant. Sulfate reducing bacteria number varied between 10^3 and 10^6 CFU/dm^3 and was similar in the littoral sediments of *A. negundo* and native tree leaf litter accumulation zones. In the bottom sediments of zone without leaf litter their number was 100–1000 times lower than in tree leaf litter accumulation areas.

In contrast to bacteria, the highest abundance of terrestrial fungi in bottom sediments was detected in March and reached their maximum values in *A. negundo* leaf accumulation zone (Tab. 2). High similarity of fungal composition was determined in the bottom sediments of three littoral sites (71–92%). However, dominant fungi assemblages differed between tree leaf litter accumulation areas (Tab. 3). Fungi genera *Penicillium* prevailed in the sediments of *A. negundo* leaf accumulation zone. In the bottom sediments of *A. glutinosa* leaf litter accumulation zone, in March and October the assemblages of *Acremonium*, *Penicillium* prevailed, while in midsummer most abundant fungi were of the genera *Aspergillus* and *Mucor*.

3.3 Bacteria and fungi on decaying leaf litter in the bottom sediments of littoral sites

The total bacterial abundance and heterotrophic bacteria colony number for study period were higher on *A. negundo* than on *A. glutinosa* leaf litter and insignificant greater amount of terrestrial fungi was determined on *A. negundo* leaf litter as well (Fig. 1). As for aquatic fungi, in October, during the accumulation of recently fallen leaves in the littoral part of the river, their sporulation rate was 14 times higher on *A. negundo* leaf litter than on *A. glutinosa*. In March, on the contrary, the more extensive colonization occurred on *A. glutinosa* leaf litter which was poorly disintegrated from the last fall. The similarity of fungi assemblages on leaves was low (27–30%) and the composition of dominant fungi differed between both leaf species (Tab. 4).

3.4 Organic carbon mineralization processes

According to the rates of inorganic carbon emission from bottom sediments into the water, the benthic organisms were most active in October, when the total (aerobic and anaerobic) community respiratory activity (expressed as the rate of

Table 1. Chemical parameters of bottom sediments in the littoral sites of the River Neris, 2013–2014 (mean values ± SD). Different letters in a row indicate significant differences among sites for each parameter (ANOVA test with Tukey HSD, $p \leq 0.05$).

Leaf litter accumulation zones	Parameters					
	N_t, %	P_t, %	C_{org}, %	H_2S+HS^-, mg/dm^3	S/SO_4^{2-}, mg/dm^3	C/N
26–28 March						
A. negundo	–	–	7.2 ± 0.3^{a}	144 ± 11^{a}	23.0 ± 1.5^{a}	–
A. glutinosa	–	–	6.9 ± 0.1^{ab}	120 ± 8^{b}	20.5 ± 1.3^{b}	–
Zone without leaf litter	–	–	2.9 ± 0.2^{c}	44 ± 3^{c}	15.3 ± 0.9^{c}	–
31 July–2 August						
A. negundo	0.10 ± 0.01^{a}	0.025 ± 0.002^{a}	5.9 ± 1.7^{a}	265 ± 18^{a}	26.1 ± 1.4^{a}	58 ± 11^{b}
A. glutinosa	0.07 ± 0.01^{ab}	0.024 ± 0.002^{ab}	7.8 ± 0.8^{b}	218 ± 11^{b}	23.2 ± 1.3^{b}	111 ± 5^{a}
Zone without leaf litter	0.04 ± 0.02^{c}	0.016 ± 0.00^{c}	0.7 ± 0.1^{c}	150 ± 18^{c}	16.7 ± 1.0^{c}	22 ± 9^{c}
16–18 October						
A. negundo	0.24 ± 0.02^{a}	0.035 ± 0.003^{b}	9.0 ± 0.5^{a}	269 ± 11^{a}	38.4 ± 1.4^{a}	38 ± 2^{b}
A. glutinosa	0.10 ± 0.02^{b}	0.052 ± 0.003^{a}	6.9 ± 0.2^{b}	220 ± 11^{b}	37.4 ± 1.1^{ab}	72 ± 13^{a}
Zone without leaf litter	0.06 ± 0.01^{c}	0.024 ± 0.005^{c}	1.5 ± 0.4^{c}	92 ± 23^{c}	14.2 ± 2.1^{c}	25 ± 3^{c}

–, not determined.

Table 2. Microbial abundance in the bottom sediments of littoral sites of the River Neris, 2013–2014 (mean values ± SD). TNB – total number of bacteria; HB – heterotrophic bacteria; CDB – cellulose decomposing bacteria; SRB – sulfate reducing bacteria; TFung – terrestrial fungi. Different letters in a row indicate significant differences among sites for each parameter (ANOVA test with Tukey HSD, $p \leq 0.05$).

Leaf accumulation zone	Microorganisms				
	TNB, 10^6/g	HB, 10^3 CFU/g	CDB, 10^3 CFU/g	SRB, CFU/dm^3	TFung, CFU/g
26–28 March					
A. negundo	158.0 ± 2.4^{a}	20.1 ± 2.2^{a}	8.7 ± 1.8^{a}	10^5	9700 ± 818^{a}
A. glutinosa	136.0 ± 7.0^{b}	12.5 ± 0.5^{b}	7.0 ± 0.5^{ab}	10^5	5933 ± 404^{b}
Zone without leaf litter	96.5 ± 8.7^{c}	6.5 ± 1.0^{c}	2.9 ± 0.3^{c}	10^3	570 ± 61^{c}
31 July–2 August					
A. negundo	182.5 ± 30.7^{a}	218.0 ± 10.3^{a}	69.5 ± 26.0^{a}	10^6	1753 ± 129^{a}
A. glutinosa	187.2 ± 23.3^{ab}	204.2 ± 16.1^{ab}	62.2 ± 34.7^{a}	10^5–10^6	420 ± 79^{b}
Zone without leaf litter	126.3 ± 21.1^{c}	133.7 ± 21.1^{c}	36.0 ± 19.0^{a}	10^3	180 ± 27^{c}
16–17 October					
A. negundo	217.8 ± 29.0^{a}	133.0 ± 13.5^{a}	46.0 ± 28.0^{a}	10^6	1253 ± 115^{a}
A. glutinosa	191.6 ± 65.1^{ab}	114.5 ± 7.0^{b}	30.0 ± 16.0^{ab}	10^5–10^6	1587 ± 247^{ab}
Zone without leaf litter	156.1 ± 12.2^{bc}	88.0 ± 27.0^{bc}	13.2 ± 6.2^{c}	10^3	153 ± 38^{c}

organic carbon mineralization) varied from 1560 ± 54 to 2520 ± 509 mg C/m^2 d^{-1} in the zone without leaf litter and *A. negundo* leaf litter littoral areas, respectively (Fig. 2A). The parallel measurements of the oxygen uptake rate showed that aerobic organic carbon mineralization was most intensive in March (Fig. 2B), however throughout the study period anaerobic processes predominated in organic matter mineralization. Anaerobic C_{org} mineralization was more intensive in the sediments of *A. negundo* leaf litter accumulation zone and made up on average 90 ± 5% *versus* 75 ± 7% in the littoral area with *A. glutinosa* leaf litter and 64 ± 5% of the total (aerobic+anaerobic) mineralization in the zone without leaf litter. However *A. glutinosa* leaf litter accumulation zone was distinguished by the higher respiration activity of aerobic community and differences in oxygen consumption rate were observed between tree leaf litter accumulation areas during the whole study period (Fig. 2B).

In different periods of observation, the rates of sulfate reduction (SR) – the terminal pathway of organic carbon mineralization in bottom sediments were 0.26–0.87 mg S^{2-}/dm^3 d^{-1}, respectively, in *A. negundo* and *A. glutinosa* leaf litter accumulation zones and 0.09–0.2 mg S^{2-}/dm^3 d^{-1} – in the zone without leaf litter (Fig. 2C). The highest SR values were observed in *A. negundo* and native tree leaf litter accumulation

Table 3. Dominant fungi in the bottom sediments of invasive and native trees leaf litter accumulation zones and littoral zone without leaf litter, 2014 (% of the total fungi number).

Date	Leaf litter accumulation zones		Zone without leaf litter
	A. negundo	*A. glutinosa*	
March	*Penicillum* (65%) *Acremonium* (14%) *Phoma* (11%)	*Penicillum* (39%) *Acremonium* (27%) *Trichoderma* (9%) *Cladosporium* (7%)	*Penicillum* (37%) *Phoma* (24%) *Mucor* (13%) *Cladosporium* (12%) *Trichoderma* (11%)
July–August	*Penicillum* (88%)	*Aspergillus* (26%) *Mucor* (22%) *Penicillum* (19%) *Alternaria* (14%)	*Aspergillus* (39%) *Mucor* (22%) *Acremonium* (16%) *Alternaria* (10%)
October	*Penicillum* (61%) *Trichoderma* (19%)	*Acremonium* (57%) *Penicillum* (19%) *Mucor* (13%)	*Acremonium* (55%) *Penicillum* (19%) *Fusarium* (17%)

zones in July and October and ranged within 0.76 ± 0.05–0.87 ± 0.04 and 0.62 ± 0.05–0.65 ± 0.04 mg $S^{2-}/dm^3\ d^{-1}$ respectively, while in the zone without leaf litter this process was twice less. SR rates were significantly higher in sediments of *A. negundo* than of *A. glutinosa* leaf litter accumulation sites.

Direct correlation was observed between SR rate and concentration of sulfates and hydrogen sulfide in tree litter accumulation zones (Tab. 5) and no correlation was found between this process and the amount of SRB. A direct relationship was detected between total benthic bacterial numbers and rate of organic carbon mineralization (MR) for all study areas. There was no statistically significant dependence of MR and SR on the total C_{org} content in the sediments and temperature. In the sediments of leaves accumulation sites C/N ratio correlated negatively with MR and SR.

4 Discussion

The leaf fall of *A. negundo* and native *A. glutinosa* occur in different ways: *A. glutinosa* leaves fall gradually within approximately one–two months. *A. negundo* leaves fall almost at once during early autumnal frosts, forming a thick layer of leaf litter (Manusadžianas *et al.*, 2014), which creates particularly favourable conditions for microbial decomposition. During this study, we found that in spring in the littoral zone of the river *A. negundo* leaves were very soft and their tissue was high macerated in contrast to more recalcitrant species of *A. glutinosa* leaves which were quite tough and weakly disintegrated. More rapid microbial decomposition of *A. negundo* leaves compared to *A. glutinosa* has also been found in laboratory experiments under various oxygen conditions (Krevš *et al.*, 2013; Manusadžianas *et al.*, 2014). These results concur with the findings of other studies indicating that many alien trees have more rapidly decomposing leaf litter than the native species they replace (*e.g.*, Harner *et al.*, 2009; Janušauskaitė and Straigytė, 2011; Jaeger *et al.*, 2013). Despite the similar initial nutrient content between *A. negundo* and *A. glutinosa* leaves (Manusadžianas *et al.*, 2014), the higher biodegradability of *A. negundo* leaves could be due to other leaf characteristics such as, *e.g.*, toughness, content of humic substances or secondary metabolites (Moretti *et al.*, 2007) that influence the consumption rate of leaf litter by consumers. Leaf quality influences the abundance, composition and activity of microorganisms that participate in litter decomposition and changes when native species are replaced by invasive ones (Casas *et al.*, 2013). In the present study, the amount of bacteria and fungi was greater on *A. negundo* leaf litter decomposing in the littoral area indirectly indicating that leaves of this invasive species was a better nutrient source for microorganisms than of *A. glutinosa*. After leaf fall, the colonization of *A. negundo* leaves by aquatic fungi was also more extensive than that of *A. glutinosa*. Because fungi species vary in enzymatic activity (Rodrigues and Graça, 1997), low similarity of dominating species on the leaves of both tree types could induce differences in their litter decomposition rates.

Invasion of riparian forests can alter nutrient dynamics of ecosystems through increase in N inputs and decomposition of N-rich organic matter within ecosystems (MacKenzie *et al.*, 2013) with faster release of nutrients (Allison and Vitousek, 2004). This is in agreement with laboratory experiments showing that higher content of nutrients, mostly nitrogen and labile organic matter, was found in the medium with decomposing *A. negundo* leaves than with *A. glutinosa* (Krevš *et al.*, 2013; Manusadžianas *et al.*, 2014). These differences can suggest a stronger impact of *A. negundo* leaves on the chemical parameters of natural habitats. To some extent, the findings in the littoral zone of the River Neris endorse these general assumptions, since the nutrient content in the sediments increased in autumn after leaf fall, and that a little higher N_t and C_{org} concentration was recorded in the *A. negundo* leaf litter accumulation zone. Higher proportion of N in organic matter reflects the better nutrient availability of substrates for microbial mineralization

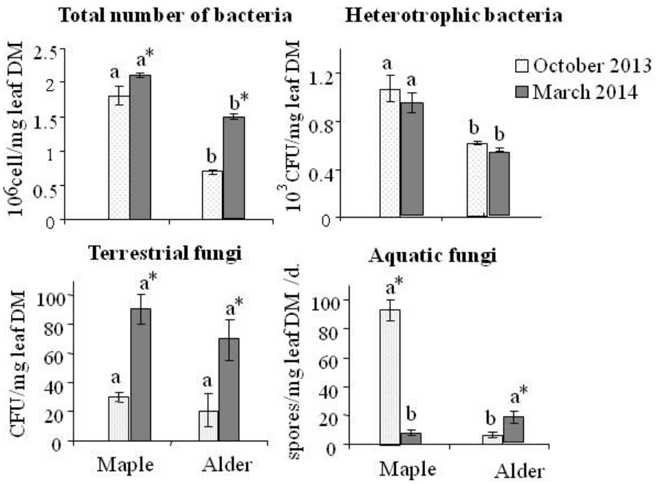

Fig. 1. Microbial densities on *A. negundo* (maple) and *A. glutinosa* (alder) leaf litter decomposing in the littoral zone of the River Neris. Different letters (a > b) indicate significant differences among leaf species obtained with Tukey test at $p \leq 0.05$. *Differences in the microbial number (significant higher number) on the same leaf species between sampling time.

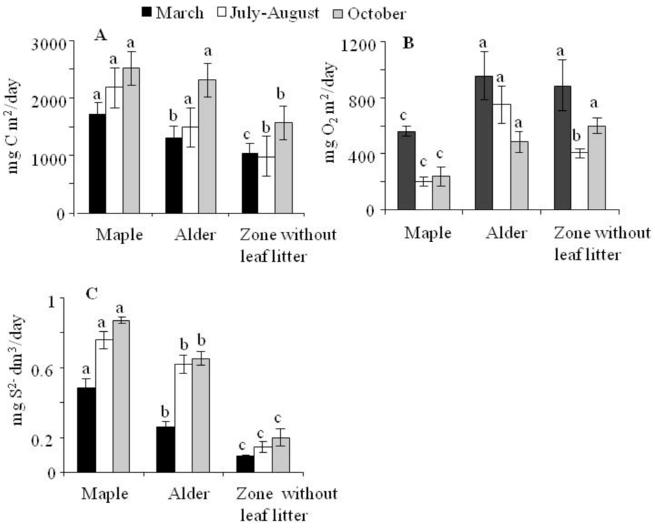

Fig. 2. The rate of inorganic carbon emission (A), oxygen consumption (B) and sulfate reduction (C) in the bottom sediments of *A. negundo* (maple), *A. glutinosa* (alder) leaf litter accumulation sites and littoral zone without leaf litter of the River Neris. Different letters (a > b > c) indicate significant differences between parameters among sites (Tukey test at $p \leq 0.05$).

Table 4. Dominant aquatic fungi species on *A. negundo* and *A. glutinosa* leaf litter decomposing in the littoral zone of the River Neris (% of the total production of conidia).

Date	*Acer negundo*	*Alnus glutinosa*
October 2013	*Tetracladium marchalianum* (53%) *Flagellospora curvula* (36%)	*Tricladium angulatum* (56%) *Xylomyces* sp. (9%) *Alatospora acuminata* (6%) *F. curvula* (6%)
March 2014	*Anguillospora* spp. (37%) *F. curvula* (19%) *Anguillomyces acadiensis* (15%) *Mirandium* sp. (11%) *Titaea complexa* (11%)	*A. acuminata* (22%) *Trinacrium* sp. (16%) *Tetracladium* sp. (13%) *Trifurcospora irregularis* (13%) *Camposporium* spp. (10%)

Table 5. Pearson correlation test between the rates of mineralization processes in the bottom sediments of littoral sites and environmental conditions (TR, SR, TNB stand for mineralization rate, sulfate reduction and total bacterial number, respectively).

Parameters	Leaf litter accumulation sites		Zone without leaf litter	
	TR, mg C/m^2 d^{-1}	SR, mg S^{2-}/dm^3 d^{-1}	TR, mg C/m^2 d^{-1}	SR, mg S^{2-}/dm^3 d^{-1}
T, °C	0.10	0.45	0.29	0.09
C_{org}, %	0.36	0.11	0.11	0.41
C/N	−0.86**	−0.81**	−0.11	−0.08
S/SO$_4^{2-}$, mg/dm^3	0.71**	0.84**	−0.22	0.18
H$_2$S+HS$^-$, mg/dm^3	0.61**	0.91**	0.30	0.44
TNB, 10^6/g	0.75**	0.40	0.54*	0.20

*$p \leq 0.05$.
**$p \leq 0.01$.

(Mansson and Falkengren-Grerup, 2003). According to C/N ratio, sediments with leaf litter of *A. negundo* had a higher content of available organic matter than sediments of *A. glutinosa* leaf accumulation site. As a result of mineralization and resuspension in water, in midsummer the amount of nutrients was approximately the same for both *A. negundo* and native tree leaf litter accumulation areas, but their content was always higher than in the sediments of littoral area without leaf litter. So, the features of *A. negundo* leaves fall with forming of a thick layer of leaf litter, the accumulation of available organic matter and its transformation products in sediments might be the reason of extension of swampy area that was observed along the shoreline of *A. negundo* mass growth.

In the bottom sediments of littoral zone, microorganism composition and activity primarily depend on the structure of organic matter and also on the surrounding environmental variables such as temperature, redox potential, and physical disturbance (Jonsson *et al.*, 2001). In our study, the environmental conditions that affected the microbial densities and activity varied. As a result, heterotrophic and cellulose-decomposing bacterial colony numbers reached maximum in midsummer at the highest water temperature. In contrast to bacteria, the greatest abundance of benthic fungi was detected at the lowest water temperature. However, despite the seasonal variations, higher numbers of fungi and bacteria were observed in littoral sediments with *A. negundo* leaf litter than in native tree leaf litter accumulation zone that could be related to differences in organic matter availability. Based on microbial structure data we may expect that microbiological situation in littoral area will change if *A. negundo* continues to displace native species from the ecotones of the River Neris.

After leaf fall, enrichment of the bottom sediments with fresh organic matter favoured the activity of benthic communities. Additionally, microbial activity depended on the qualitative composition of organic matter rather than on the total OM content. This was supported by the absence of a statistically significant relationship between community respiration rate and total concentration of C_{org} and by the presence of negative correlation between mineralization rates and C/N ratio in the sediments of leaf litter accumulation sites. The highest rates of inorganic carbon emission from bottom sediments into the water were found in *A. negundo* leaf accumulation zone in October and were comparable to those for shallow low-running eutrophic lakes (Krevs and Kucinskiene, 2012). Despite the shallow depth and oxidative conditions in the near-bottom water ($O_2 > 8$ mg/L) due to accumulation of organic detritus, the anaerobic processes prevailed in organic carbon mineralization in leaf litter accumulation zones. Similar trends in organic carbon mineralization have been also observed in the sediments of shallow lakes and in the shallow areas of the lakes with a high content of organic matter (Kučinskienė and Krevš, 2006; Krevs and Kucinskiene, 2012). More active anaerobic bacteria and, in turn, intensive anaerobic organic carbon mineralization occurred in *A. negundo* leaf litter accumulation zone; however, *A. glutinosa* leaf litter site was distinguished by the higher activity of aerobic community.

Anaerobic conditions, sulfates and available OM are known to be the major factors that determine the activity of sulfate-reducing bacteria (SRB), which play a crucial role in the terminal anaerobic organic carbon mineralization, while temperature is only partially responsible for the seasonal SRB activity in aquatic ecosystems (Li *et al.*, 1996; Holmer and Storkholm, 2001). During the summer–autumn period in bottom sediments of leaf litter accumulation zones under sufficient sulfate concentration, the activity of sulfate reducing bacteria was promoted due to accumulation of labile organic matter and partly because of temperature. A higher abundance of heterotrophic bacteria determined in bottom sediments of leaf litter accumulation zone in its turn could produce a greater variety of substrates for sulfate reducing bacteria (Parkes *et al.*, 1989) and intensify SR process. In litter accumulation zone, in spite of the oxidative conditions in the near-bottom water, the abundance and activity of SRB were similar to those in profundal zone of stratified lakes with anaerobic hypolimnion (Krevs and Kucinskiene, 2012). Changes in the structural composition of organic matter might have a stronger influence on the succession of SRB physiological groups and their activity than on their amount (Karnachuk *et al.*, 2006). Similarly, in the present study, a direct relationship between the amount of SRB and SR intensity was not observed. The higher rates of SR in *A. negundo* than in *A. glutinosa* leaf litter accumulation sites indicated that organic substrate there was more available for the development of SRB. The end product of SR is hydrogen sulfide, a substance which is highly toxic for benthic fauna (Cook, 1992). Also, the highest concentration of hydrogen sulfide was recorded during midsummer–autumn in the bottom sediments of littoral site with *A. negundo* leaf litter.

Thus, our results have shown that on average during the study period the higher number of microorganisms and their community activity, with prevailing anaerobic processes, occurred in the littoral sediments of *A. negundo* leaf litter accumulation zone than in sediments of the river close by riparian native tree location. In shallow zones, anaerobic processes have negative consequences, because they promote the accumulation of fermentation products and other intermediate mineralization compounds (Kuznetsov *et al.*, 1985) as well as benthic phosphorus release (Woszczyk *et al.*, 2011), which, in its turn, may stimulate secondary eutrophication and littoral silting. On the other hand, increasing anaerobic sulfate reduction accelerates the growth of hydrogen sulfide concentration what in the future may have a negative impact on the quantitative and qualitative structure of benthic organisms. We think that more studies that focus on the effects of this alien riparian tree species on the littoral zone of freshwater systems are needed. These studies may be useful for predicting and minimizing the impact of invasive riparian vegetation on aquatic ecosystems.

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