

Leaf litter decomposition from native and non-native species in a freshwater forested wetland of Chile

Descomposición de hojarasca de especies nativas y exóticas en un humedal boscoso de agua dulce de Chile

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ABSTRACT

Decomposition of leaf litter is a fundamental process for the functioning of forested wetlands. The rapid increment of forest plantations has involved a greater contribution of leaf litter of exotic origin to these ecosystems. The decomposition rate between leaf litter of native and exotic origin in a forested wetland of the Mediterranean zone of Chile was compared, as well as the contribution of bacteria and macroinvertebrate to this process. It was determined that the decomposition rate of the leaf litter presented significant differences ($p < 0.05$) between species, being faster in those of non-native origin. This could be due to differences in ecophysiological aspects of the leaves like the presence of chemical compounds such as waxes or oils. Both analyzed communities were relevant in the studied process. However, bacteria contributed mostly to the decomposition of both types of leaves. The implications of the physical and chemical characteristics of the leaves and the water on the processing of the foliar material are discussed.

KEYWORDS: Allochthonous detritus, bacteria, lentic ecosystem, macroinvertebrates.

RESUMEN

En los humedales boscosos, la descomposición de la hojarasca es un proceso fundamental para su funcionamiento. El rápido incremento de las plantaciones forestales ha implicado un mayor aporte de hojarasca de origen exótico a estos ecosistemas. Se comparó la tasa de descomposición entre hojarasca de origen nativo y exótico en un humedal boscoso de la zona Mediterránea de Chile, así como la contribución de las bacterias y macroinvertebrados a este proceso. Se determinó que la tasa de descomposición de la hojarasca presentó diferencias significativas entre las diferentes especies ($p < 0,05$), siendo más rápido en especies de origen exótico. Esto podría ser dado por diferencias en algunos aspectos ecofisiológicos de las hojas como la presencia de compuestos químicos tales como ceras o aceites. Ambas comunidades analizadas fueron relevantes en el proceso estudiado. Sin embargo, las bacterias contribuyeron mayormente a la descomposición de ambos tipos de hojas. Se discuten las implicaciones de las características físicas y químicas de las hojas y el agua en el procesamiento del material foliar.

PALABRAS CLAVE: Detritus alóctono, bacterias, ecosistema léntico, macroinvertebrados.

INTRODUCTION

In Chile, forested wetlands show a wide distribution (29° S – 42° S), though they mostly dominate in the Mediterranean zone (MZ) (33° S – 39° S). In that zone, most wetlands

show some degree of human intervention (e.g. urbanization, wood extraction and introduction of exotic species) (Correa-Araneda *et al.* 2011), which has led to their fragmentation, eutrophication and reduced ecosystem services. Arboreal vegetation of these ecosystems is fundamental for their

functioning, because it causes a low penetration of light, limiting the primary activity of phytoplankton (Benfield 1996) and it implies that their main source of organic matter is the material coming from the woody component (e.g. leaves, twigs, flowers and fruits) (Correa-Araneda *et al.* 2011). This material has been mainly supplied by hydrophilic native species from the Myrtaceae family, such as *Blepharocalyx cruckshanksii* (Hook. & Arn.) Nied and *Myrceugenia exsucca* (DC) Berg (Correa-Araneda *et al.* 2012). However, in the last four decades they have been replaced by exotic species, mainly *Pinus radiata* (D. Don) and *Eucalyptus globulus* (Labill), which have been steadily increased in the Chilean Mediterranean Zone (ChMZ) (Shulz *et al.* 2010, 2011; CONAF 2011). For these species, an increase of up to 53% in the period 1975 – 2000 has been registered, with an annual growth that reached 10.5% (Pizarro *et al.* 2006; Little *et al.* 2009) and currently representing more than 17% of the forest area of the country (CONAF 2011).

The replacement of native vegetation of the ChMZ by monocultures of exotic species could be influencing the processes that regulate flows of matter and energy to and within the system, as reported in lotic systems (Canhoto & Graça 1995; Canhoto *et al.* 2013). One of the processes involved in the energy flows in the wetlands corresponds to the degradation of the leaf litter and includes several trophic levels (Solada *et al.* 1996). This process starts with the release of soluble compounds (Solada *et al.* 1996), followed by a colonization of bacteria and fungi (BF) that facilitates the subsequent fragmentation and consumption by benthic macroinvertebrates (BMI) (Abelho 2001; Weyers & Suberkropp 1996; Gessner *et al.* 1998). This indicates that both communities (BF and BMI) play a critical role in maintaining the flows of matter and energy (Sylvestre & Bailey 2005; Boyero *et al.* 2011).

Recent studies have determined that the decomposition of the leaf litter in freshwater ecosystems is influenced for both environmental variables (e.g. pH, temperature, water regime) and structural components of the leaf itself, such as lignin, cellulose, cutin and tannins (Richardson *et al.* 2004; Swan & Palmer 2004; Graça & Cressa 2010). That is why any change in the type of vegetation that is incorporated into the water component of the forested wetlands would impact significantly on the functioning of the system, affecting the capacity of processing this material (Graça & Canhoto 2006). However, the mechanisms are not entirely clear, since wetlands have been very poorly studied (Correa-Araneda *et al.* 2011). Because of the abovementioned backgrounds, the present study is aimed to evaluate the degradation process of the leaf litter carried out by the communities of BF and BMI on the foliar component of native and non-native plants from the forested wetlands.

MATERIAL AND METHODS

STUDY AREA

The study area was located at the Petrenco forested wetland (39°02'35" S - 72°38'54" W) (Fig. 1). This wetland belongs to the *Blepharocalyo-Myrceugenieta exsuccae* (temu-pitra) vegetation association (Ramírez *et al.* 1995) which presents a permanent water regime, with depths that vary between 31 and 70 cm. The climate in the area corresponds to Mediterranean with oceanic influence and presents an annual temperature and rainfall of 12°C and 1,553 mm, respectively (Di Castri & Hajek 1976).

EXPERIMENTAL DESIGN

In order to evaluate the degradation process of foliar material, we used: leaves coming from the species *Blepharocalyx cruckshanksii* (Temu), *Myrceugenia exsucca* (Pitra), dominant native species in the wetland (Ramírez *et al.* 1995); *Pinus radiata* and *Eucalyptus globulus*, dominant exotic species in the ChMZ (CONAF 2011). The mixture of leaf litter from these species was also studied. The foliar material was collected by means of leaf traps and dried at 60°C (Memmert ULM-600 oven) for 24 hours until constant weight was obtained. Groups of leaves were formed with a standardized weight of 3 ± 0.1 g, determined through a digital scale (Precisa 240; 0.0001 g sensitivity).

The treatments used in the experiments were as follows: temu (T), pitra (Pit), eucalyptus (E), pine (Pin), temu-pitra (TPit) and pine-eucalyptus (PinE) (n=4 replicates per treatment). All samples were stored in containers (20 x 20 cm) with 1 cm pore opening (mesh, n= 96) for colonization by BMI. On the other hand, a pore opening of 55 µm (bags, n= 96) were used to allow colonization only by BF. All replicas were submerged and randomly distributed throughout the wetland.

The experiment lasted 60 days and the decomposition of the leaf litter was measured at 15 day intervals during the autumn season of 2011. In each collection period, 4 replicates per treatment and type of containers were collected.

Extracted samples were washed (in order to eliminate the accumulated sediment), dried and weighted, according to the initial described treatment. For the calculation of the degradation of total leaf litter (k) the negative exponential model was used (Hladyz *et al.* 2010): $W_t = W_i e^{-kt}$, where t corresponds to time, W_t corresponds to the dry weight at t time measured in percentage respect to initial weight, W_i is the initial dry mass of the leaf fixed in 100% and k (days⁻¹) is the slope of the plot of the natural logarithm of the mass of the leaf in relation to time, and it corresponds to the only decomposition rate that allows performing the comparative analyses.

In order to have a complementary measure of the foliar material degradation, the toughness of the leaves of each

species was determined in each sampling period using a Leaf Toughness Tester (Woodcock & Huryn 2005). This was conducted on 5 leaves or fragments randomly selected from the replicas of each treatment. Results were expressed in penetrance (g) that corresponds to the minimum strength applied on a surface of 0.29 mm², necessary to penetrate the leaf.

In order to determine the physicochemical characteristics of the water column, temperature (°C), pH, conductivity (μS cm⁻¹), turbidity (NTU) and dissolved oxygen (mg L⁻¹) were measured in each period, using a YSI-30 sensor (Wetzel & Likens 1991).

STATISTICAL ANALYSES

After verifying the normality of data in order to evaluate the individual effect and the interactions of the factors on the quantitative dependent variable, a covariance analysis was carried out (ANCOVA). The quantitative independent

variables were: colonizing community (BF and BF-BMI) and treatment (T, Pit, E, Pin, TPit and EPin). The covariable was exposure time (15, 30, 45 and 60 days), whereas the dependent variable was the degradation rate (amount of mass lost over time). All analyses were performed with the following software: Statistica 7 (StatSoft Inc. 2004) y PAST-Palaeontological Statistics 2.10 (Hammer *et al.* 2001).

RESULTS

The degradation of the foliar detritus was faster in the treatments with non-native species (Pin, E) in comparison to native species (T, Pit) (Fig. 2a, 2b). Leaves of *E. globulus* presented the highest degradation rate, leaving 61.9% of the leaves exposed to BF and 58.8% of the leaves exposed to BF and BMI at the end of the exposure period (60 days). The lowest degradation rate among native species was presented

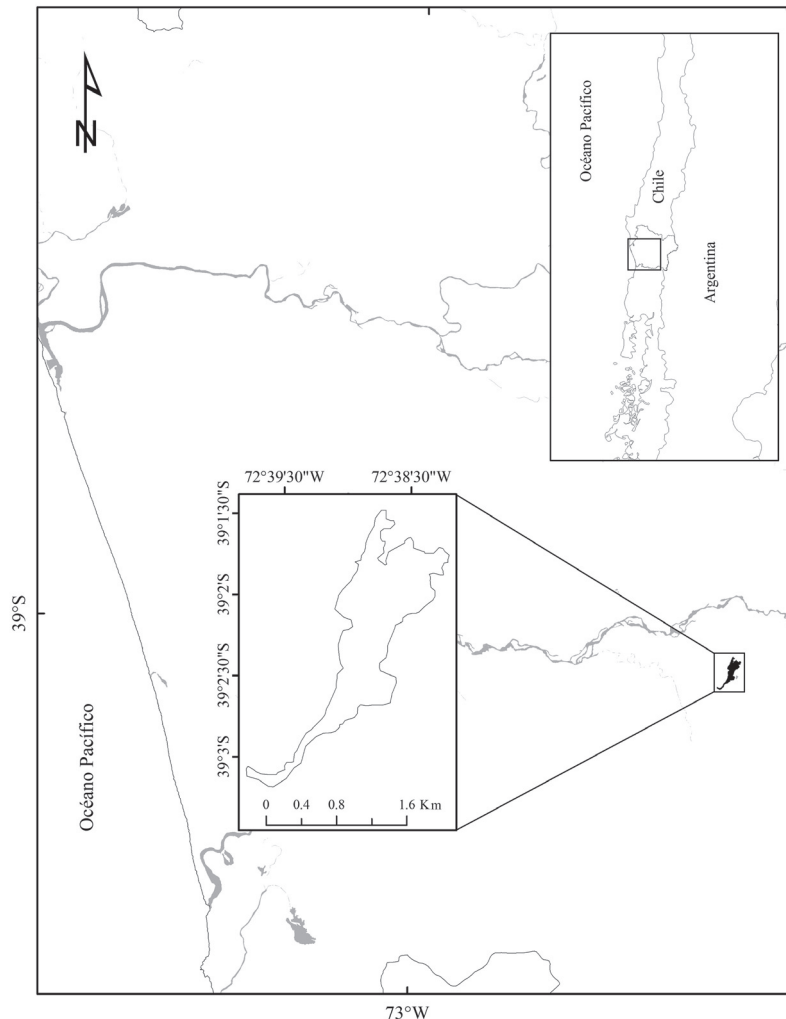


FIGURE 1. Location of the study area corresponding at the wetland Petrencia located in the commune of Pitrufuén, Araucanía Region, Chile. / Ubicación del área de estudio correspondiente al humedal Petrencia de la comuna de Pitrufuén, región De la Araucanía, Chile.

by Temu (*B. cruckshanksii*), where 86.9% of the leaves exposed to BF remained and 79.6% of the leaves exposed to BF and BMI. The greatest degradation of leaf litter was registered during the first 15 days for both non-native and native species (Fig. 2c, 2d).

Covariance analyses (ANCOVA) for the degraded plant species indicates that there are statistically significant differences ($p < 0.05$) between the exposure to BF and BF-BMI, as well as between types of leaf litter, but there is no

co-variation between the types of tree of came from and the exposure of the different communities (Table 1).

Regarding the toughness of the leaves, the average of the initial toughness of the experiment was 387 g in *M. exsucca*, 219 g in *B. cruckshanksii*, 251 g in *E.globulus* and 293 g in *P. radiata*. No clear pattern of increase or decrease over time was observed (Fig. 3). Indeed, this pattern tended to maintain constant, without significant differences ($p > 0.05$).

TABLE 1. ANCOVA analysis from the variables of time (covariate), type of container and type of leaves respect to degradation rate. / Análisis de ANCOVA de las variables de tiempo (covariable), tipo de contenedor y tipo de hoja respecto a la tasa de descomposición.

	g.l.	MS	F	p
Time	3	0.003	232.1	0.001*
Container	1	0	005.3	0.022*
Fallen leaves	5	0.001	052.5	0.001*
Container – fallen leaves	5	0	1.1	0.364

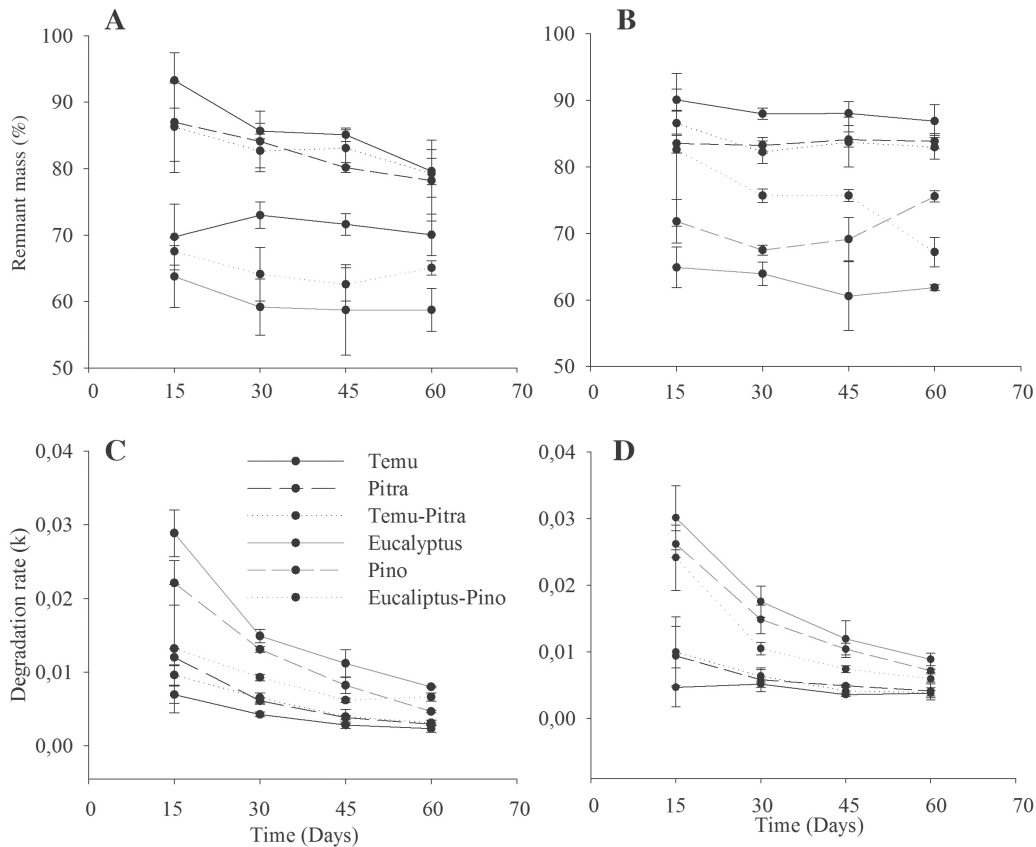


FIGURE 2. Temporal variation of remnant mass rate of the different species exposed to colonization by BF (A) and BF-BMI (B), and the degradation rate of the different species exposed to colonization by BF (C) and BF-BMI (D) during their 60 day exposure in the water column. / Variación temporal de la masa remanente de las diferentes especies expuestas a la colonización por BF (A) y BF-BMI (B) y tasa de degradación de las diferentes especies expuestas a la colonización por BF (C) y BF-BMI (D) durante los 60 días de exposición en la columna de agua.

However, this variable did presented significant differences between type of leaves (native- exotic) ($p = 0.002$). The Tuckey HSD test for toughness indicated that the differences between types of leaves are mostly given by the leaves of exotic origin, specifically of the species *E. globulus* (EPit vs EPin, $p < 0.05$).

Physicochemical variables measured in the water column presented a strong direct correlation between

conductivity, dissolved oxygen and turbidity, as well as between temperature and pH. Only turbidity showed a clear trend to decrease at temporal scale ($T_0 = 75.2$ NTU - $T_1 = 1.8$ NTU). However, all variables presented a high dispersion respect to their mean value (C.V. > 0.05) (Table 2) all the variables with correlation, show significant differences ($p < 0.05$) less the correlation between turbidity and O.D.

TABLE 2. Values of the physicochemical variables of the water column in the different sampling days, Coefficient of variation (CV) and correlation analyses between variables. Cond. = Conductivity ($\mu\text{S}/\text{cm}$), Temp. = Temperature ($^{\circ}\text{C}$), O.D. = Dissolved oxygen (mg L^{-1}), * = strong correlation. / Valores de las variables fisicoquímicas de la columna de agua en los diferentes días de muestreo, coeficiente de variación (CV) y análisis de correlación entre las variables. Cond. = Conductividad ($\mu\text{S}/\text{cm}$), Temp. = Temperatura ($^{\circ}\text{C}$), O.D. = Oxígeno disuelto (mg L^{-1}), * = Correlación fuerte.

	T ₀	T ₁	T ₂	T ₃	T ₄	Mean	C.V.	Cond.	pH	Temp.	O.D.
Cond.	54.4	36	30	27.8	39.9	37.6±9.4	0.28				
pH	6.18	6.32	6.29	5.13	6.6	6.1±0.5	0.09	0.18			
Temp.	8	9.25	7.45	5.9	9.3	7.7±1.4	0.17	0.19	0.80*		
O.D.	3.9	5.8	7.9	7.3	6.1	6.2±1.4	0.24	0.90*	0.09	0.20	
Turbidity	75.2	1.73	3.55	2.4	1.8	16.9±29.1	1.92	0.78*	0.01	0.00	0.67*

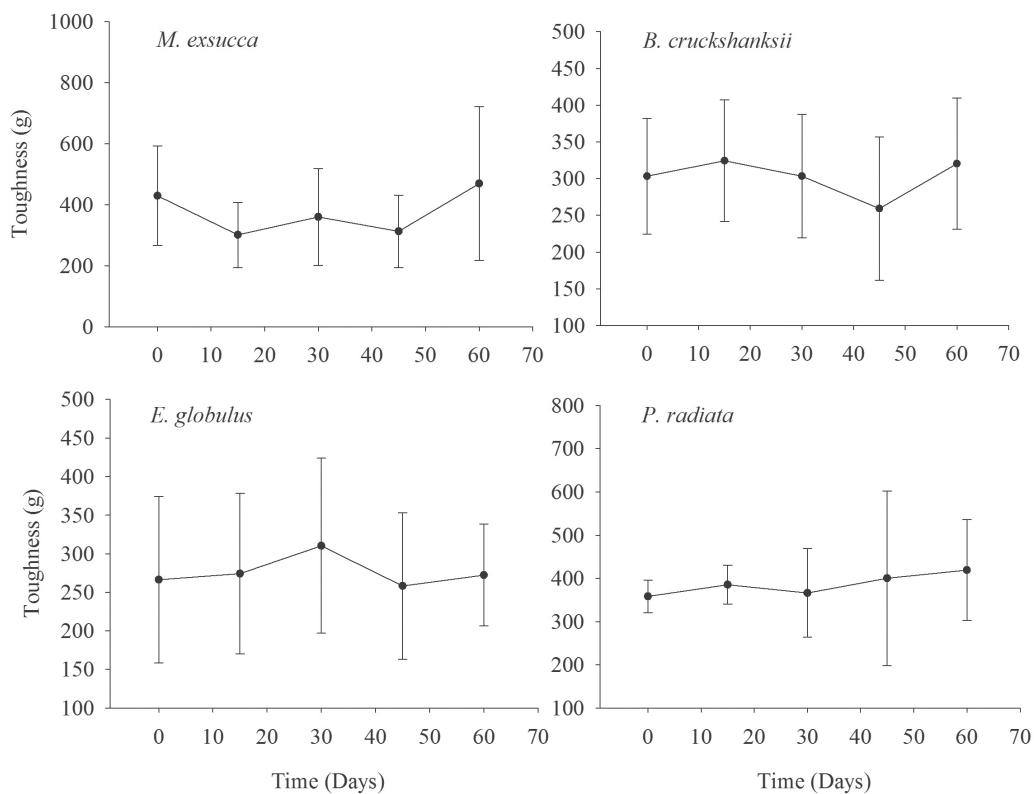


FIGURE 3. Temporal variation of the toughness (g) in the leaves of native (*M. exsucca* and *B. cruckshanksii*) and non-native species (*E. globulus* and *P. radiata*). / Variación temporal de la dureza (g) en las hojas de especies nativas (*M. exsucca* and *B. cruckshanksii*) y exóticas (*E. globulus* and *P. radiata*).

DISCUSSION

The general phases of the degradation of the foliar material in aquatic ecosystems have been described as sequential, initiated by a lixiviation process of the soluble compounds, followed by a colonization of BF which facilitates the arrival of the BMI, especially shredders (Cheshire *et al.* 2005). Our results showed that the greatest weight loss was registered during the first 15 days for both native and exotic species. This coincides with liberation phase of soluble compounds, described as the phase of greater weight loss in the foliar material (Solada *et al.* 1996).

In the heads of the mountain lotic environments like in the wetlands, light penetration is scarce and they receive a high load of fallen leaves (Lugo *et al.* 1990), and the decomposition process is mainly given by BMI (Vannote *et al.* 1980). In forested wetlands BMI would also be a determinant factor in the processing of organic matter, because in containers with presence of these organisms together with communities of bacteria and fungi (BF) was observed a significantly higher decomposition than in the case where only BF were present. This is in agreement with what was reported in tropical forested wetlands by Del Valle (2003), where the macroinvertebrate community was also relevant in the processing of organic matter. However, forested wetlands present important differences respect to mountain river environments, as well as in other lentic environments (*e.g.* freshwater marshes and exposed lagoons), both in physical, chemical and biological characteristics. The fact that there is no mechanical effect produced by the water movement and the benthic components must be highlighted (Casas *et al.* 2000), because this would explain the high non-degraded percentage of organic material in these ecosystems. This implies that the total degradation of the plant material would last twice the time considered for the current study or even more. It is interesting to mention that the shredding organisms not showed preference by native or non-native leaf litter, so that differences registered in the decomposition rate were mostly influenced by species-specific features. This is the case of the toughness of the leaves which in native species was higher compared to exotic species, as reported by Ramírez *et al.* (1980), who indicated that these species have a leathery nature. In addition, none of the species presented significant differences in toughness at timescale, contrary to was observed in mountain river environments from the ChMZ, where these were negatively correlated to the exposure time (Ovalle 2012). In the latter case, the mechanical effect that takes place in these environments was a determinant factor on the variations of the toughness of leaves. The presence of chemical compounds such as waxes or oils secreted by the leaves, described for *B. cruckshanksii* (Tucker *et al.* 1993), would provide hydrophobicity to the leaf, affecting the capacity of the BF community to penetrate the tissue. This implies that the decomposition process by

these microorganisms is dependent on the individual features of each leaf.

An interesting case about the interaction between BF, BMI and the physicochemical characteristics of the leaves is presented by the species *E. globulus*, which has phenolic compounds whose anaerobic degradation can initiate an increment in compounds such as quinones, which are highly toxic for BMI from aerobic systems. This would not occur equally in forested wetlands, given the low concentration of oxygen registered (Canhoto *et al.* 2013). but compounds like quinones not be affecting the bacterial degradation, causing that forested wetlands eucalyptus are degraded faster than native species. Hence, under these conditions the BF community would be more relevant on the degradation of organic matter of forested wetlands in comparison to BMI. Another variable that can affect the degradation rate, though not assessed in the present study is the surface area of the leaves, which can be affecting the size of fungi colonies associated to the degradation of organic matter (Allen *et al.* 1991). It would be interesting to incorporate this issue in further studies.

In most aquatic ecosystems, physicochemical variables such as temperature, conductivity, amount of dissolved oxygen and nutrients are fundamental to the development of the organisms (Haapala *et al.* 2001). In this regard, the environmental variables measured in the water column presented timescale variations, as well as direct relations between conductivity, dissolved oxygen and turbidity; this would be associated to the rainfall events that decrease turbidity and the concentration of ionic compounds responsible for the conductivity (Arle 2002). This is an indicator of the buffer effect that would be produced by the forest cover, intercepting the water to enter the system by means of streamflow, which decreases the contribution and re-suspension of fine sediments (McIvor *et al.* 2012), implying a lower perturbation of the water column (FAO 2005).

Dissolved oxygen is one of the most relevant variables for aquatic life. This level was registered in low concentrations in the forested wetlands ($6.2 \pm 1.38 \text{ mg L}^{-1}$), in comparison to that observed in aquatic environments of the same area ($8.7 - 11.6 \text{ mg L}^{-1}$; Habit *et al.* 2003; Figueroa *et al.* 2003; Correa-Araneda *et al.* 2010, 2014), which implies the dominance of resident and generalist organism, such as the BF community (Bärlocher & Kendrick 1974; Figueroa *et al.* 2003). Such organisms would be the main responsible of the degradation and changes in the toughness of the fallen trees in this kind of aquatic ecosystems.

Regarding the temperature, this variable affects the dissolution of oxygen in the water (Alvarado & Aguilar 2009), the metabolism of the organisms and many other factors are directly or indirectly related to the processing of organic matter (Hauer & Hill 2007). The low temperatures recorded ($5.9 - 9.3^\circ\text{C}$), prevent the descent of the levels of oxygen to hypoxic levels and foster an ideal environment

to the development of psychrophilic bacteria (0 - 30°C) (Morita 1975), which have a slower reproduction rate respect to mesophilic or thermophilic bacteria (Elliot & Michener 1965).

Forested wetlands present differential characteristics with other types of wetlands, highlighting the low penetration of light and explaining the low temperatures of the water, the constant supply of fallen leaves and the low degradation rate of organic matter. These features make forested wetlands particularly vulnerable against the excessive input of organic matter as a result of the diverse productive activities carried out in the area. In addition, the loss of forest material as a result of its extraction for human consumption (Correa-Araneda *et al.* 2011) can facilitate the input of light, generating changes in the thermal regime and in the related variables (Döll & Zhang 2010). The synergistic effect of these modifications might lead to a greater bacterial colonization (Molinerio *et al.* 1996), accelerating biological processes (Cortes 1992, Belovsky & Slade 2000) and in turn, causing a greater consumption of oxygen. This would modify many of the physical and chemical characteristics of these ecosystems. These processes have not been yet clarified and the interest on them from a limnological point of view is emerging. Therefore, delving into these processes is of great importance to encourage and support future actions of both restoration and preservation.

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