

Alien vs. native plants in a Patagonian wetland: elemental ratios and ecosystem stoichiometric impacts

Florencia Cuassolo · Esteban Balseiro ·
Beatriz Modenutti

Received: 19 November 2010 / Accepted: 4 April 2011 / Published online: 19 April 2011
© Springer Science+Business Media B.V. 2011

Abstract Wetlands are subject to invasion by exotic plant species, especially during the dry season when they resemble terrestrial systems; therefore, terrestrial plants could exploit this situation to colonize this environment. We analyzed *P. anserina* invading Patagonian wetlands in terms of elemental ratios that would modify wetland stoichiometry due to organic matter inputs. We studied the elemental relationship (carbon/nitrogen/phosphorus) of *P. anserina* in comparison with native emergent macrophytes (*Eleocharis pachicarpa* and *Carex aematorrhyncha*). These plant species are common and dominant in the wetland. Additionally, we analyzed the presence of mycorrhizal fungi in the roots and their proportion of root infection. Our study reveals that the invasive species presented nutrient (especially phosphorus) allocation in roots and differences in mycorrhizal infection, with a predominance of arbuscular mycorrhiza, compared with native species. During flooded periods with the decay of aerial parts, *P. anserina* stores phosphorus in the roots and releases dissolved organic matter of high molecular weight molecules, high color, and a high C-to-nutrient ratio in comparison with native macrophytes. These results show the strategy of an invasive terrestrial plant in temporary aquatic systems, and how the elemental relationships

of the invasive plant can modify the stoichiometry of the environment.

Keywords Invasion ecology · Wetland · Mycorrhizal fungi · Stoichiometric strategies · Leachates · Dissolved organic matter release

Introduction

Wetlands are characterized by seasonal fluctuations in water level, with alternating wet and dry periods. These ecosystems are especially vulnerable to alien weed invasions (Zedler and Kercher 2004); therefore, many wetland plants fit the definition of invasive plants, which are species or strains that rapidly increase their spatial distribution by expanding into native plant communities (Richardson et al. 2000). The susceptibility of communities to invasion requires more attention (Prieur-Richard and Lavorel 2000) because native plants are now uncommon or endangered due to wetland invaders that form monotypes (Champion et al. 2009), and they can cause substantial changes in organic matter accumulation and carbon sequestration (Zedler and Kercher 2004, 2005).

In aquatic systems, nutrient supply could be an important factor in the competitive balance between plant species, e.g. rapid nutrient uptake allowed a

F. Cuassolo (✉) · E. Balseiro · B. Modenutti
Laboratorio de Limnología, INIBIOMA-CONICET-
UNComahue, Quintral 1250, 8400 Bariloche, Argentina
e-mail: cuassolof@comahue-conicet.gob.ar

rapid growth (Zedler and Kercher 2004). In submerged plants, at high fertility, the invasive *Hydrilla verticillata* was a stronger competitor relative to *Vallisneria americana*, whereas under low nutrient conditions, native species outperform invasive ones (Van et al. 1999). Other studies also indicated that emergent species better adapted to high nutrient environment (e.g. *Typha dominguensis*) can effectively invade with greater competitive capability under high nutrient conditions (Davis 1991).

Temporary or semi-temporary wetlands represent a particular situation, because during the dry season, the environment remains without water resembling a terrestrial system. The water table fluctuation is a natural disturbance that these systems can tolerate, which causes changes in both plant diversity and carbon cycling. However, due to alternation between dry and flooded periods, plant species that can tolerate a wide range of water levels are more successful (Raffaele 2004). During dry periods, some of these species develop their whole growing cycle and become an important source of decaying organic matter during the flooded period (Díaz Villanueva and Trochine 2005; Roehm 2005). In this case, the elemental composition of the plant tissue would play a crucial role in the resulting organic matter quality (Osborne et al. 2007). The differences in macrophyte tissue nutrient concentrations were observed to be species specific with a strict C:N:P (carbon:nitrogen:phosphorous) stoichiometric ratios (Demars and Edwards 2007). The elemental composition (N and P) in plant tissues is determined by several factors such as (1) the balance of nutrient uptake and carbon (C) assimilation (Aerts and Chapin 2000; Sterner and Elser 2002), (2) losses through leaching, respiration, exudation, and herbivory (Ventura et al. 2008; Wong et al. 2010), and (3) the presence of mycorrhizal fungi since mycorrhizal associations favor nutrient uptake in wetland plants (Cornwell et al. 2001; Dunham et al. 2003). In the Andean temperate lacustrine district (41°S), there are large and deep lakes, along with small lakes and wetlands (Modenutti et al. 1998). In comparison with deep lakes, shallow lakes and wetlands present a higher concentration of dissolved organic matter (DOM) (Morris et al. 1995). This high content of DOM can be associated with the presence of macrophytes and external watershed contributions (Bastidas Navarro et al. 2009a). Leachates of macrophytes can contribute significantly to

the DOM water content mainly during senescence because of the decomposition of tissue and subsequent leachates (Bertilsson and Jones 2003). Moreover, they are an important source and reservoir of essential nutrients, such as phosphorus (Bastidas Navarro and Modenutti 2010), and contribute nutrients for heterotrophic production (Bastidas Navarro et al. 2009b). These results may imply that variations in the composition of macrophytes could generate changes in DOM quality, both in terms of elemental composition and in terms of optical features.

Potentilla anserina is an exotic species that is widely distributed in wet soils in Patagonia (Correa 1984; Ezcurra and Brion 2005). In Patagonia wetlands, this hemicriptophyte exotic species may cover almost the entire bottom and restrict the distribution of native macrophytes (Díaz Villanueva and Trochine 2005; Naiman and Melillo 1984). Recent studies in Chile (Hauenstein et al. 2008) have indicated that *P. anserina* has intermediate N requirements, which could create beneficial colonizing environments. We have hypothesized that invasive (*P. anserina*) and native macrophytes (*Eleocharis pachycarpa* and *Carex aematorrhyncha*) co-occurring in the same wetland exhibit different strategies in terms of nutrient allocation. In that sense, we also propose that the elemental composition of leachates and tissues of native and invasive macrophytes may distinctively affect the dissolved organic matter (DOM) source of the wetland. For that purpose, we analyzed the elemental relationships (C:N:P) in the plant tissues (aerial and radicular parts) and the leachates of the different species. Additionally, we analyzed the presence of mycorrhizal fungi because this type of interaction could be differentially used by exotic and native plants as a strategy for colonizing temporary environments and obtaining the necessary nutrients for growth.

Materials and methods

Study area

This study was conducted in Laguna Fantasma, which is a temporary pond located at 41°07'S, 71°27'W, 780 m above sea level in North Patagonia, Argentina. The pond has an area of 1 ha (170 m length and 80 m

wide approximately), with a maximum depth of 2 m during the autumn–winter period. Precipitation during autumn and winter (May–August 2009) averaged 208.3 ± 91 mm per month when the flooded area reached a maximum of 1 ha and was reduced to 24.2 ± 15 mm per month during late spring and summer (September–January 2009). The pond was colonized by two native macrophytes, *Eleocharis pachycarpa* and *Carex aematorrhyncha*, and by the exotic plant *Potentilla anserina*. These plant species are common and dominant in the wetland. Riparian vegetation was scarce, so other inputs of allochthonous particulate organic matter to the pond were negligible.

Field study

The wetland was sampled on six different occasions from April 2009 to January 2010. Water temperature and pH were measured using a thermometer (YSI 85 Yellow Spring Instruments, USA) and a pH meter (HI 8424 Hanna Instruments, USA), respectively. Water and sediment samples were taken, along two orthogonal permanent transects of 105 and 48 m in length, with a limnological bottle (2L) and a core of 5 cm in diameter in the upper 5 cm, respectively. The three plant species were sampled every 3 m along the transect lines on each sampling occasion. Plants were collected at each sampling point, and roots were dug out of the ground at a depth of 30 cm. Thus, on each sampling occasion, we sampled each species in dry and flooded plots. The plants were immediately carried in polyethylene bags to the laboratory. In addition, the vegetation coverage of each species was estimated at the beginning and at the end of the hydroperiod (May and December 2009) for 55 points chosen at random with a 50×50 -cm plot.

Laboratory procedures

Lake water was filtered with pre-combusted (450°C , 2 h) GF/F filters and analyzed for dissolved organic carbon (DOC) with a carbon analyzer (TOC-VCSH Shimadzu) and for total dissolved phosphorus (TDP) and total dissolved nitrogen (TDN). TDP was determined after digestion with persulfate at 1.5 atm for 1 h, followed by the ascorbate-reduced molybdenum method (APHA 2005). TDN was determined

following Valderrama (1981). Sediment samples were dried at 60°C and were analyzed for particulate carbon (C), nitrogen (N), and phosphorous (P) content. C and N concentrations were measured with a CN analyzer (Thermo Finingan Flash EA 1112). Phosphorus was measured after combustion of 2 mg of sediment at 450°C for 1 h, followed by the ascorbate-reduced molybdenum method (APHA 2005).

The elemental analysis of vegetal tissue was carried out by carefully washing the plants with tap water and then with distilled water. The aerial and root parts were separated and dried at 60°C for 48 h up to constant weight. Afterward, each part was crushed to powder with a clean mortar, and approximately 2 mg of dry weight (DW) was destined for elemental analysis. Carbon (C) and nitrogen (N) concentrations in the tissues were measured with a CN analyzer (Thermo Finingan Flash EA 1112). Phosphorus was measured after combustion of 2 mg of tissue at 450°C for 1 h, followed by the ascorbate-reduced molybdenum method (APHA 2005).

The mycorrhizal analysis was conducted on ten young roots of each plant preserved in 50% ethanol. The roots were cleared in KOH 10% (w/v) acidified with HCl 5% (v/v) and stained with trypan blue (Brundrett et al. 1994); they were then cut into 1-cm pieces. Typical structures of arbuscular mycorrhizal (AM) colonization (hyphae, arbuscules, vesicles, coils) and of dark septate fungi (DSF) (dark hyphae, microsclerotia, hyaline hyphae) were identified and quantified according to their presence–absence in the microscope field (Cardoso et al. 2010) using a direct microscope Olympus BX50 at $400\times$.

The elemental analysis of leachates was conducted using the aerial parts of the three species. To obtain leachates, aerial parts were carefully washed with distilled water and dried at room temperature, and then 1 g (DW) of each plant was placed in 100 mL of MilliQ water and left at 4°C for 48 h following Anesio et al. (2000). The resulting water was filtered through a pre-combusted GF/F filter (Osmonics). In all cases, leachates were obtained in four replicates. All glassware was previously acid-washed and combusted at 450°C for 1 h. TDP, TDN, and DOC were determined as previously explained for the lake water analyses. Additionally, we obtained spectrophotometric scans from 250 to 790 nm for each leachate in 5-cm quartz cuvettes using a double-beam spectrophotometric Shimadzu UV2450.

Statistical analysis

To determine significant differences between C, N, and P in the different parts (aerial and radicular) of plant tissues and in two different wetland situations (dry and flooded plots), a two-way ANOVA was applied. Differences between C, N, and P in leachates for the three species were analyzed with one-way ANOVA. The percentage of root infection by AM or DSF in each species was analyzed with one-way ANOVA. An a posteriori Tukey's test was applied where the ANOVA model was significant. ANOVA was performed with SigmaPlot (version 11.0, software package). The analysis of covariance (ANCOVA) was used to evaluate whether P concentration differs between *E. pachycarpa* (native) and *P. anserina* (exotic) using the parts (aerial vs. radicular) and plots (dry vs. flooded) as treatments and time as a covariate, to avoid its effect in the variable. P concentration was log-transformed, and time was used as a categorical variable (each sampling date). ANCOVA was performed using the STATISTICA for Windows software package (Stat—Soft 1998). Homogeneity of variance was tested through Levene's test with a statistical significance $\alpha = 0.05$. When this assumption was not fulfilled after data transformation (log), Kruskal–Wallis test was applied instead of one-way ANOVA.

Finally, the absorbance units from the leachate scans (A) were converted to absorption coefficients (a) as $a = \ln(10^A)/cl$, where cl is the cuvette length in m. Relative molecular weight was estimated using the $a_{250}:a_{365}$ ratio (Perez and Sommaruga 2006), and water color was determined as the absorbance at 440 nm (a_{440}) in a 10-cm quartz cuvette according to Pace and Cole (Pace and Cole 2002).

Results

Lake water temperature ranged from 4.81 ± 2.88 in autumn–winter (May–August) to $14.47 \pm 2.95^\circ\text{C}$ in spring–summer (September–January). Nutrient concentrations in water and sediments (Fig. 1) did not show significant differences. However, DOC concentration in the water varied significantly between the two periods (Kruskal–Wallis, $H_{(1,10)} = 7.500$, $P = 0.004$), with the highest values observed in spring–summer (Fig. 1). The distribution of the three plant

species was uneven in the wetland. *C. aematorrhyncha* occupied an outer ring, whereas the inner part of the ring was occupied by both the native *E. pachycarpa* and the exotic *P. anserina*. The vegetation coverage at the beginning and at the end of the hydroperiod in 2009–2010 was estimated to be 60% *E. pachycarpa*, 30% *P. anserina*, and 10% *C. aematorrhyncha*. However, during the flooded period, the aerial part of *P. anserina* decayed and left the roots in the flooded sediments.

We observed differences in the elemental relationships in vegetal tissue when comparing the plants collected in flooded and dry plots. Under flooded conditions, the C:P ratio varied significantly between species (two-way ANOVA; $F_{(2,33)} = 14.513$, $P < 0.001$) and parts (two-way ANOVA; $F_{(1,33)} = 7.342$, $P = 0.011$). In the a posteriori Tukey's test between parts within species, there were significant differences for the exotic *P. anserina* (Tukey's test, $q_{\text{aerial vs. radicular}} = 3.754$, $P = 0.013$), and the C:P ratio was highest in the aerial parts (Fig. 2a). The C:P ratio in the roots of the exotic plant was two to three times lower (more P concentration in root) than in the two native emergent macrophytes (Tukey's test, $q_{\text{Potentilla vs. Carex}} = 5.798$, $P = 0.001$; $q_{\text{Potentilla vs. Eleocharis}} = 3.829$, $P = 0.030$, Fig. 2a). On the contrary, the aerial part of *C. aematorrhyncha* had a higher C:P ratio (less P concentration in aerial parts) than the other two plants (Tukey's test, $q_{\text{Carex vs. Potentilla}} = 4.945$, $P = 0.004$; $q_{\text{Carex vs. Eleocharis}} = 3.616$, $P = 0.042$, Fig. 2a). We observed significant differences in the C:N ratio between species (two-way ANOVA; $F_{(2,35)} = 19.039$, $P < 0.001$). In particular, *C. aematorrhyncha* exhibited the highest C:N ratio, with no differences between the other two (Tukey's test, $q_{\text{Carex vs. Potentilla}} = 7.938$, $P < 0.001$, and $q_{\text{Carex vs. Eleocharis}} = 7.078$, $P < 0.001$, Fig. 2b).

In the dry plots, we found a statistical interaction between parts and species for the C:P ratio (two-way ANOVA, $F_{(2,20)} = 6.341$, $P = 0.010$). We found that *E. pachycarpa* exhibited the lowest C:P ratio in the roots, but the differences were only significant compared to the other native species *C. aematorrhyncha* (Tukey's test, $q_{\text{Eleocharis vs. Carex}} = 4.590$, $P = 0.014$, Fig. 2c) and not to the exotic species (Tukey's test, $q_{\text{Eleocharis vs. Potentilla}} = 2.999$, $P = 0.119$, Fig. 2c). No significant differences were found between species concerning aerial parts (Tukey's test, $P > 0.05$, Fig. 2c). Only marginal differences in the C:N ratio

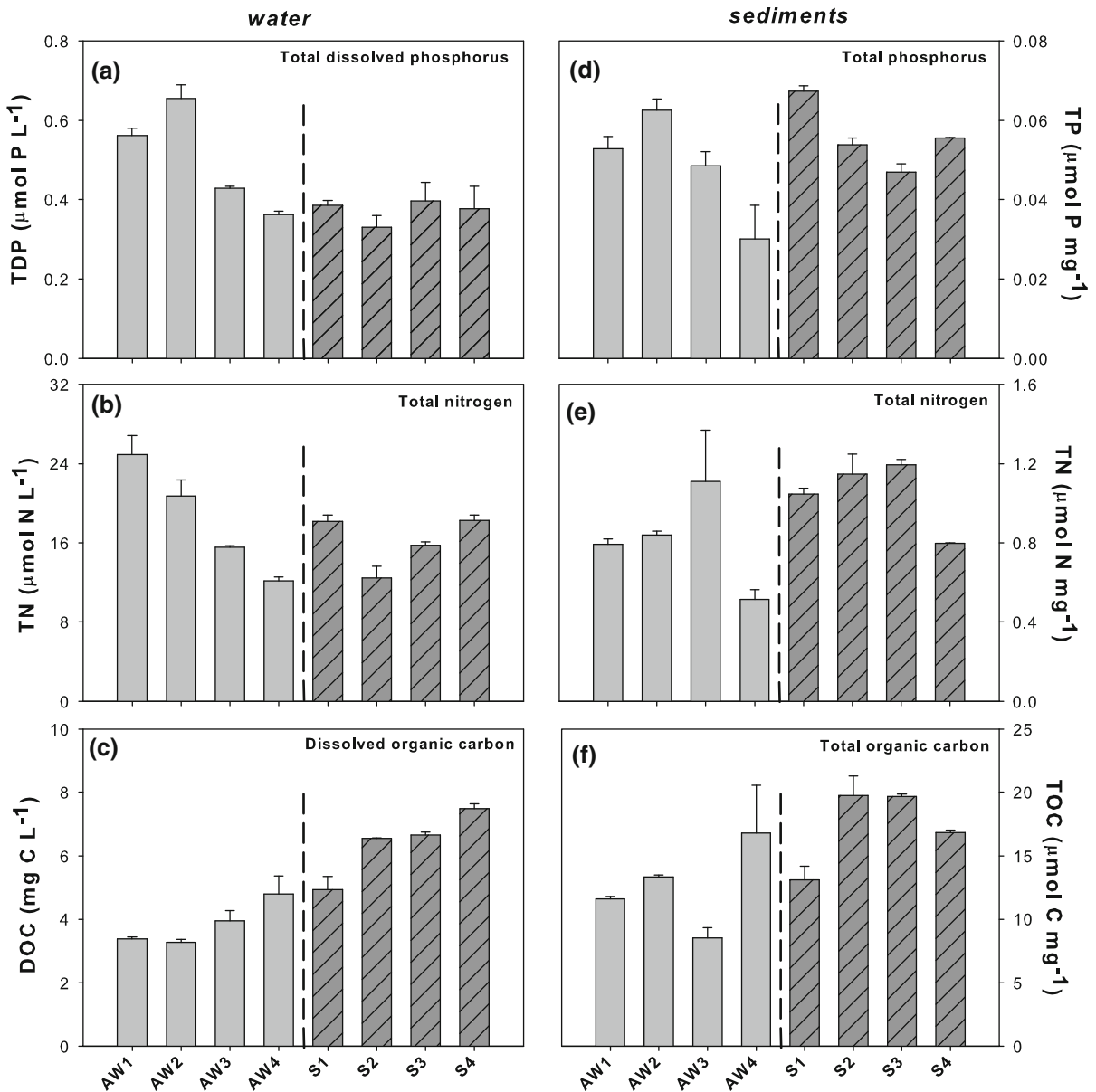


Fig. 1 (a) Total dissolved phosphorous (*TDP*), (b) total nitrogen (*TN*), and (c) dissolved organic carbon (*DOC*) in the water. (d) Total phosphorous (*TP*), (e) total nitrogen (*TN*), and (f) total carbon (*TC*) in sediments. Values are given as

average \pm standard error. AW1, AW2, AW3, and AW4 are samples from autumn–winter (flooded period), and S1, S2, S3, and S4 are samples from spring–summer (dry period). The dotted lines divide both periods

were found between parts (aerial and roots) (two-way ANOVA, $F_{(1,20)} = 4.547$, $P = 0.050$) (Fig. 2d). Regarding P concentrations, we found an interaction between plots and parts, in which the aerial parts of the exotic *P. anserina* had a P concentration more than twofold higher in the dry plots compared to the flooded plots (ANCOVA $F_{(1,77)} = 15.597$, $P < 0.001$)

(Fig. 3a). On the other hand, the P concentration in roots in the flooded plots was significantly higher than in the dry ones. For the native *E. pachycarpa*, there were significant differences only for the plots (dry vs. flooded) (ANCOVA, $F_{(1,42)} = 12.778$, $P < 0.001$, Fig. 3b). In the two cases, we found no interaction between the covariate time and treatment (ANCOVA,

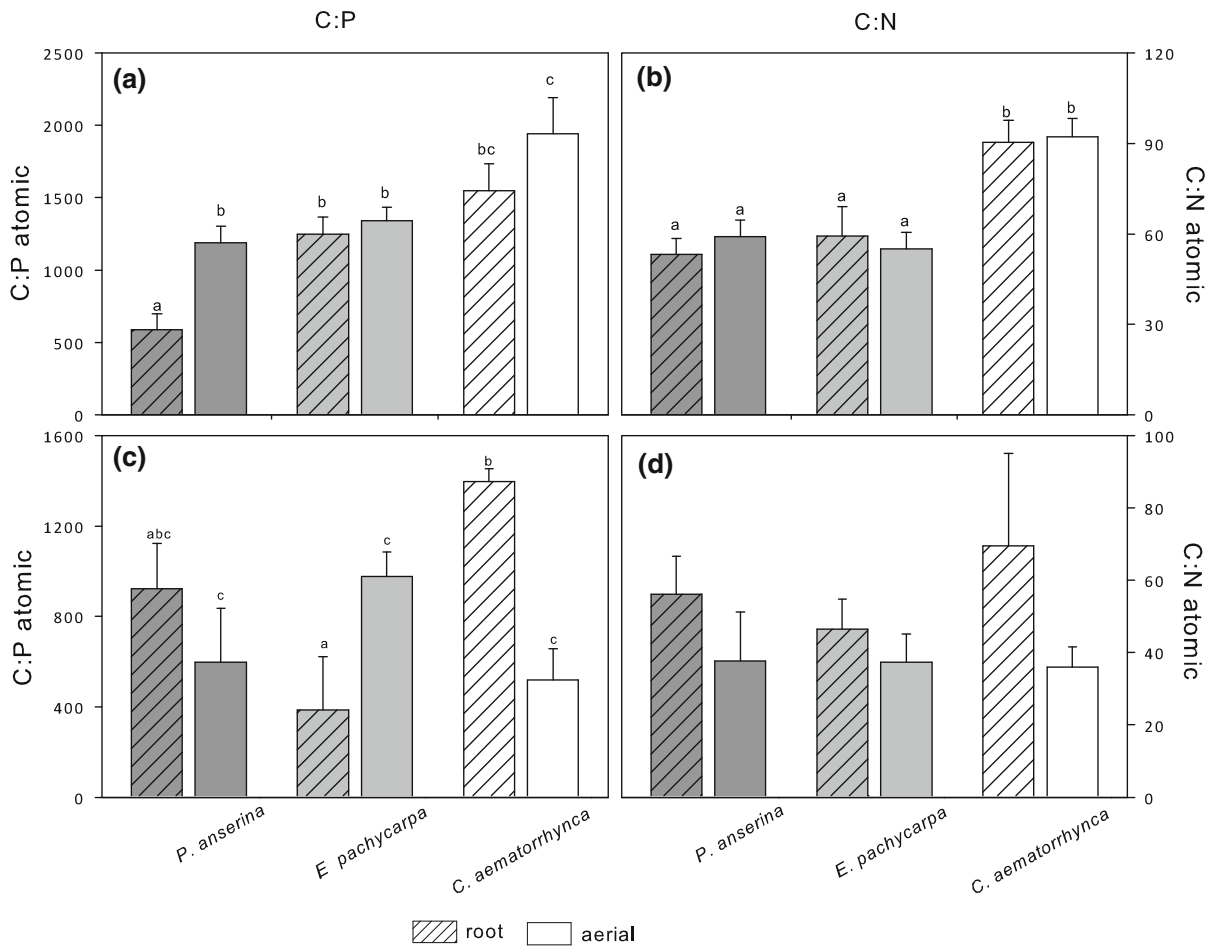
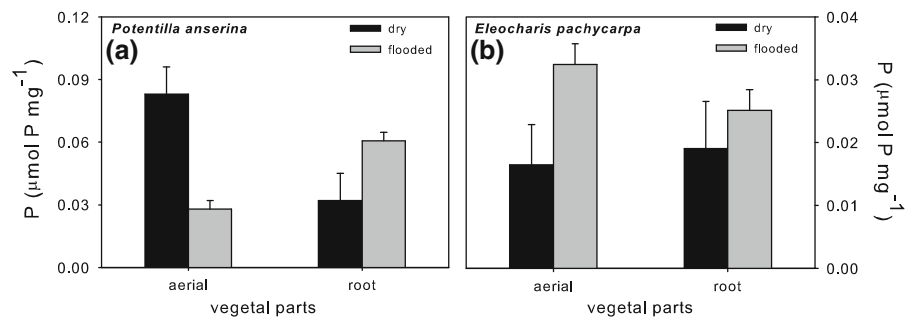


Fig. 2 Elemental relationships (C:P and C:N ratios) in roots and aerial parts in the three studied plant species (*P. anserina*, *E. pachycarpa*, and *C. aematorrhyncha*); (a) and (b) plants in

flooded plots; (c) and (d) plants in dry plots. The letters on the bars indicate significant differences ($P < 0.05$) between plant parts and species

Fig. 3 Phosphorus concentration in the exotic plant *P. anserina* (a) and in the native *Eleocharis pachycarpa* (b) in the dry (dark bar) and flooded plots (white bar) and in the plant parts (aerial vs. roots)



E. pachycarpa $F_{(1,42)} = 1.978$, $P < 0.167$; *P. anserina* $F_{(1,77)} = 0.733$ $P = 0.394$).

We also observed differences in the mycorrhizal colonization, with a significant interaction between plant species and mycorrhiza type (two-way ANOVA,

$F_{(2,12)} = 26.030$, $P < 0.001$). The infection with AM was higher in *P. anserina* compared with *C. aematorrhyncha* (Tukey's test, $q_{Potentilla \text{ vs. } Carex} = 5.784$, $P = 0.011$), while DSF infections were dominant in the two native species compared with the exotic

plant (Tukey's test, $q_{Potentilla \text{ vs. } Eleocharis} = 6.357$, $P = 0.007$, $q_{Potentilla \text{ vs. } Carex} = 8.564$, $P = 0.001$, Fig. 4). Considering the type of infection in each species, *E. pachycarpa* did not present any significant differences between AM and DSF infection (Tukey's test, $q_{AM \text{ vs } DSF} = 2.087$, $P = 0.184$, Fig. 4).

The composition of leachates from *E. pachycarpa* exhibited the highest nutrient (P and N) concentrations in comparison with the other two species (one-way ANOVA, $F_{(2,11)} = 198.113$, $P < 0.001$, and $F_{(2,11)} = 80.766$, $P < 0.001$, respectively; Fig. 5a, b). However, *P. anserina* presented the highest C concentration in the leachates (one-way ANOVA, $F_{(2,11)} = 80.766$, $P < 0.001$, Fig. 5c). Accordingly, the C:P and C:N ratios were lower in the leachates of *E. pachycarpa* than in the other two species (one-way ANOVA, $F_{(2,4)} = 7.538$, $P = 0.011$, one-way ANOVA, $F_{(2,4)} = 9.269$, $P = 0.011$ for P and N, Fig. 6a and b). The absorbance spectra of the leachates exhibited a unimodal pattern in the three species. *E. pachycarpa* and *C. aematorrhyncha* exhibited a maximum absorbance of approximately 250 nm, whereas *P. anserina* had the highest absorbance between 250 and 450 nm (Fig. 7a). The mean molecular weight of DOM leachates showed significant differences between the species (one-way ANOVA, $F_{(2,11)} = 60.899$, $P < 0.001$). The $a_{250}:a_{365}$ ratio indicated that *E. pachycarpa* leachates were composed of lower molecular weight molecules, while *P. anserina* showed intermediate values in comparison with the native species (Fig. 7b). Water color, measured as a_{440} ,

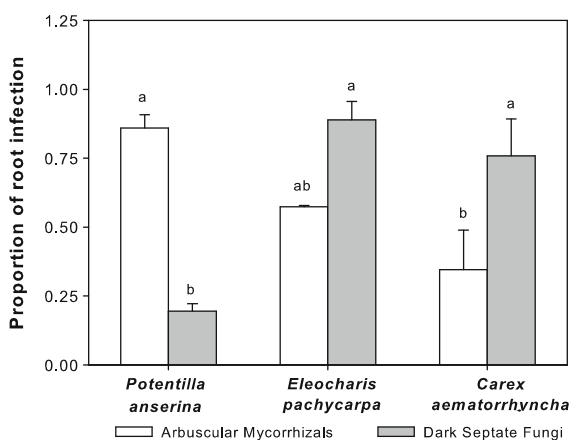


Fig. 4 Proportion of root infection in each plant species with two types of radicular symbionts. The letters on the bars indicate significant differences ($P < 0.05$) between types of mycorrhiza colonizing the plant species

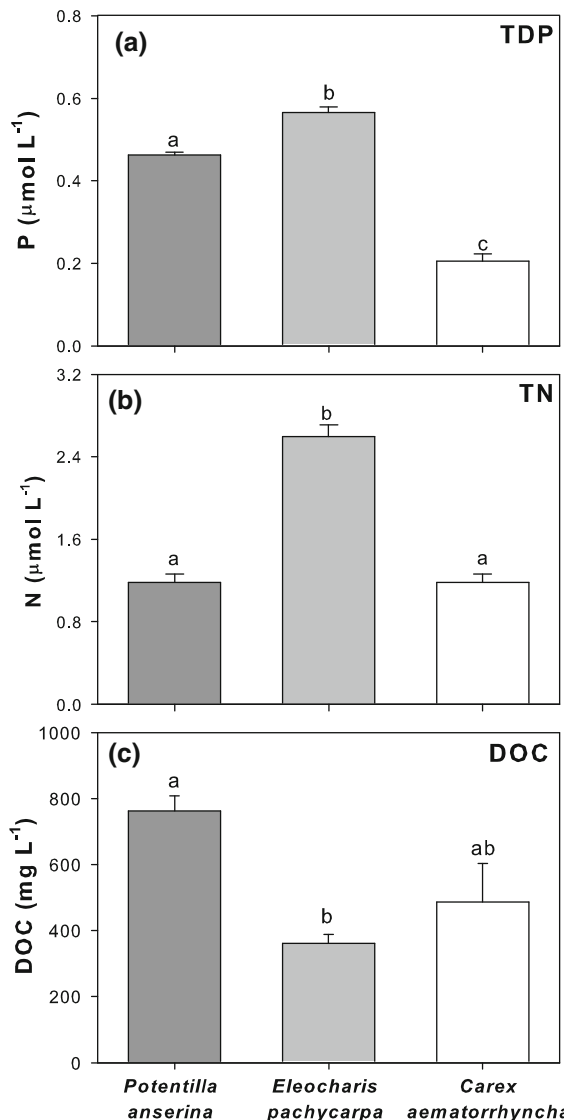


Fig. 5 Phosphorus (a), nitrogen (b), and carbon (c) in the leachates from the three studied plant species (*P. anserina*, *E. pachycarpa*, and *C. aematorrhyncha*). The letters on the bars indicate significant differences ($P < 0.05$) between species

was higher in *P. anserina* leachates than in the two native species (Fig. 7b), indicating a darker color for the DOM released.

Discussion

The three studied species, dominant in the wetland, show that the elemental composition of their tissues and leachates were markedly different. The C:P ratio

Fig. 6 Elemental relationships C:P ratio (a) and C:N ratio (b) in the leachates from the three studied plant species (*P. anserina*, *E. pachycarpa*, and *C. aematorrhyncha*). The letters on the bars indicate significant differences ($P < 0.05$) between species

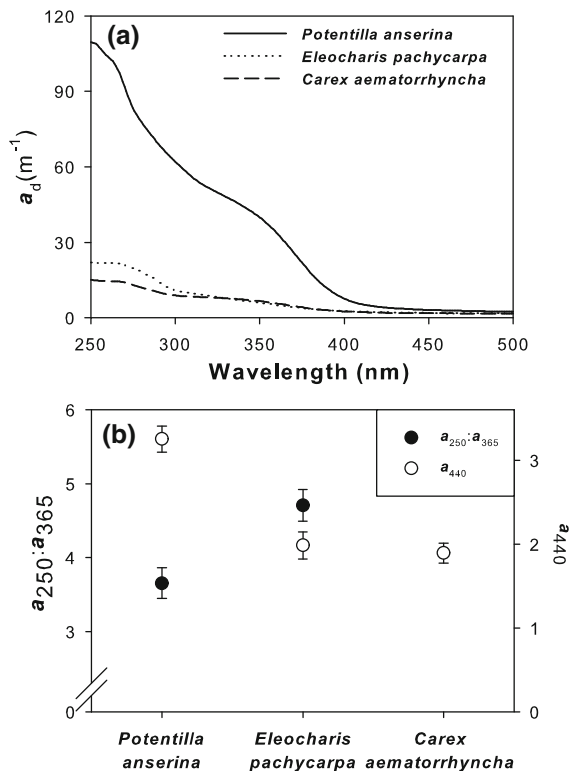
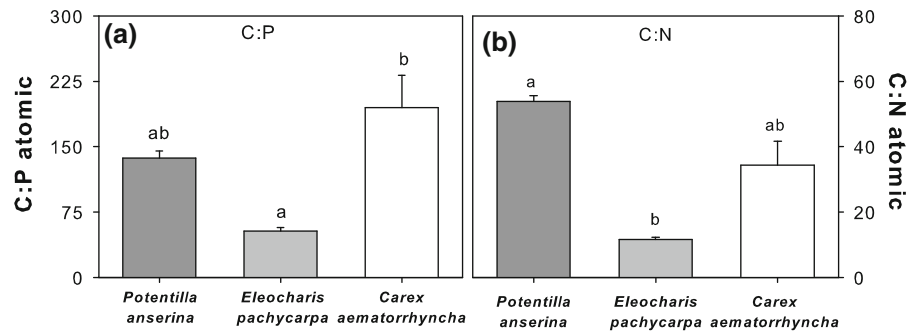


Fig. 7 Spectrophotometric absorbance curves (a) and $a_{250}:a_{365}$ ratio and a_{440} (b) in the leachates from the three studied plant species (*P. anserina*, *E. pachycarpa*, and *C. aematorrhyncha*)

in the roots of the exotic *P. anserina* was two to three times lower than the native emergent macrophytes in the flooded plot. These differences in plant tissue nutrient concentrations could be explained by basic species-specific relationships (Demars and Edwards 2007; Osborne et al. 2007; Sterner and Elser 2002). However, the presence of mycorrhizal fungi in the roots favoring nutrient uptake (Cornwell et al. 2001) is a factor that would change the elemental ratio.

In that sense, AM favors P uptake (Raffaele 1996), and its dominance in the exotic *P. anserina* roots would explain the low C:P ratio observed in the tissue of this species. On the contrary, the effects of DSF are uncertain because they could be either beneficial or damaging to plants (Jumpponen 2001). It is likely the case that the comparatively higher C-to-nutrient ratios observed in the two native species are related to the dominance of DSF among mycorrhizal fungi in the roots. On the other hand, Dunham and colleagues (Dunham et al. 2003) suggested that mycorrhizal plants have higher concentrations of N in their roots. However, we observed that the C:N ratio did not change significantly in dry and flooded plots nor among species, suggesting that N is a nutrient relatively constant in the three studied plant tissues. Our study revealed that mutualisms between mycorrhizal fungi and plants could be used by exotic plants, such as *P. anserina*, as a strategy for obtaining the nutrients necessary for growth, in particular P.

A recent study of the biological invasions related to ecological stoichiometry (González et al. 2010) proposes that under low nutrient conditions, the efficiency in the use of resources is higher, and under high nutrient conditions, a higher growth and reproductive rate could be expected with a lower C-to-nutrient ratio in the tissues. Our results indicate that the exotic *P. anserina* success under low nutrient conditions achieving a lower C:P ratio. This situation is probably due to the AM dominance in the roots and suggests that mycorrhizal mutualism is an important strategy for invasive plants in temporary aquatic systems that could result in high reproductive rates. Furthermore, we found that this invasive species makes a translocation of phosphorus during the flooding period, probably by storing P of the aerial parts in the roots. This is also supported by the fact

that *P. anserina* presented leachates with comparatively low P concentrations, but high C concentrations. The stoichiometric strategy of this invasive plant seemed to be as follows: when the wetland is dry, *P. anserina* begins to sprout; the phosphorus stored in the roots is sent to the new shoots, reducing the P in the roots (Fig. 3) and increasing their C:P ratio (Fig. 2), but when the wetland is flooded, P is sent to the roots and lowers the C:P ratio (Figs. 3 and 2). This strategy gives this species the advantage of being P enriched when the growing season begins. The nutrient concentration in the sediments did not vary along the hydroperiod; therefore, the plants had similar nutrient concentrations for growth.

Regarding the potential impact of terrestrial plant invasions in wetlands, it is important to consider the plant elemental release into the environment during flooded periods when aerial parts decay. Following cell death, a pulse of dissolved organic matter (DOM) is released from macrophytes to the aquatic environment (Bertilsson and Jones 2003). This DOM coming from leachates is one of the most important sources for bacterial community growth (Anesio et al. 1999; Bastidas Navarro et al. 2009a), and it is crucial in the transfer of matter and energy in aquatic food webs (Osborne et al. 2007). In our study, the results obtained on the composition of leachates revealed that *P. anserina* release a DOM of high molecular weight with high color and a high C-to-nutrient ratio in comparison with native macrophytes (Figs. 6 and 7). The higher absorbance detected for *P. anserina* in the range of UV (between 250 and 350 nm) indicates a higher proportion of colored organic matter released in the leachates, in contrast to natives (Fig. 7). In a recent study, Caceres and colleagues (Caceres et al. 2008) observed that an increase in nutrient supply due to the seasonal tree leaf-out causes a decrease in light availability, upsetting the balance of nutrients for primary producers, and producing a shading effect that reduces chlorophyll concentration. Because the leachates of the exotic *P. anserina* are dark in color, with a maximum absorption in the UV range, we can predict that the input of these leachates would affect phytoplanktonic algae and other algae in the wetland. At the same time, this type of DOM constitutes a UVR shield for planktonic communities (Souza et al. 2010).

On the other hand, the low molecular weight (high $a_{250}:a_{365}$ ratio) observed in the leachates of *Eleocharis pachycarpa* highlights the importance of the effect of this native species on the microbial community. The molecular weight and size of the DOM have often been considered to be an important factor influencing microbial activities, such as growth and carbon and nutrients utilization (Anesio et al. 2000; Bastidas Navarro et al. 2009a; Bastidas Navarro and Modenutti 2010). Considering the C-to-nutrient ratios, it has been suggested (Del Giorgio and Cole 1998) that the bacterial growth efficiency decreases when the C:N ratio of the substrate is greater than 10. The C:N atomic ratio in the leachate of the native *E. pachycarpa* was on average 10, while in the exotic plant and in the other native were on average 55 and 35, respectively. Consequently, changes in this ratio due to increases in *P. anserina* would affect the bacterial community by increasing N limitation. Plant community structure may be a significant modulator of DOM quality and quantity due to species-specific contributions of characteristically different DOM (Osborne et al. 2007). In this sense, the comparison of leachates and tissues of native and invasive plant species in Patagonia suggests that the differences in the elemental ratio of the plant tissues reveal distinctive strategies of the invasive species that would cause a direct impact in the wetland through the input of DOM.

In conclusion, this study points out that invasive *P. anserina* and the natives *Eleocharis pachycarpa* and *Carex aematorrhyncha* presented notable differences in plant nutrient allocation and senescence strategy. Our study reveals that *P. anserina* presented nutrient (especially phosphorus) allocation in roots and differences in mycorrhizal infection, with a predominance of arbuscular mycorrhiza, compared with native species. During flooded periods with the decay of aerial parts, the invasive plant releases dissolved organic matter of high molecular weight, high color, and a high C-to-nutrient ratio in comparison with native macrophytes. Thus, the invasion of the terrestrial plant during drought periods would, in the flooded periods, affect DOM quality release and sediment enrichment. As a consequence, significant ecological impacts would be expected that might affect planktonic and benthic communities of the

environment, including the facilitation of new invasive species.

Acknowledgments This work was supported by FONCyT PICT 2007-01256 and FONCyT PICT 2007-01258 and UNComahue B-141. FC is a CONICET fellowship and EB and BM are CONICET researchers. We also thank Marcela Bastidas Navarro, Marta Cabello and Nora Baccalá for their help in laboratory analysis, mycorrhizal identification and statistical analysis respectively.

References

- Aerts R, Chapin FSI (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Adv Ecol Res* 30:1–67
- Anesio MA, Denward CMT, Tranvik LJ, Graneli W (1999) Decrease bacterial growth on vascular plant detritus due to photochemical modification. *Aquat Microb Ecol* 17: 159–165
- Anesio AM, Theil-Nielsen J, Graneli W (2000) Bacterial growth on photochemically transformed leachates from aquatic and terrestrial primary producers. *Microb Ecol* 40:200–208
- APHA (2005) Standard methods for the examination of water and wastewater. American Public Health Association, AWWA, Washington
- Bastidas Navarro M, Modenutti BE (2010) UVR induce optical changes and phosphorous release of lake water and macrophyte leachates in shallow Andean lakes. *J Limnol* 69:112–119
- Bastidas Navarro M, Balseiro E, Modenutti B (2009a) Effect of UVR on lake water and macrophyte leachates in shallow andean-patagonian lakes: bacterial response to changes in optical features. *Photochem Photobiol* 85:332–340
- Bastidas Navarro M, Modenutti B, Callieri C, Bertoni R, Balseiro E (2009b) Balance between primary and bacterial production in North Patagonian shallow lakes. *Aquat Ecol* 43:867–878
- Bertilsson S, Jones JB (2003) Supply of dissolved organic matter to aquatic ecosystem: autochthonous sources. In: Findlay SEG, Sinsabaugh RL (eds) *Aquatic ecosystems: interactivity of dissolved organic matter*. Academic Press, San Diego, pp 3–24
- Brundrett M, Melville L, Peterson L (1994) Isolating and propagating Glomalean fungi. In: Brundrett M, Melville L, Peterson L (eds) *Practical methods in mycorrhizal research*. Mycologue Publications, Waterloo
- Caceres CE, Tessier AJ, Andreou A, Duffy MA (2008) Stoichiometric relationships in vernal pond plankton communities. *Freshw Biol* 53:1291–1302
- Cardoso BM, Chaia EE, Raffaele E (2010) Are Northwestern Patagonian “mallín” wetland meadows reservoirs of *Ochetophila trinervis* infective *Frankia*? *Symbiosis* 52:11–19
- Champion PD, Reeves P, Zealand N (2009) Factors causing dune ephemeral wetlands to be vulnerable to weed invasion. Publishing Team, Department of Conservation
- Cornwell WK, Bedford BL, Chapin CT (2001) Occurrence of arbuscular mycorrhizal fungi in a phosphorus-poor wetland and mycorrhizal response to phosphorus fertilization. *Am J Bot* 88:1824–1829
- Correa MN (ed) (1984) Escalloniaceae, Dicoliledoneae dialipétalas (Rosaceae a Leguminosae). Flora Patagónica. Colección Científica, INTA, Buenos Aires, pp 77–73
- Davis SM (1991) Growth, decomposition, and nutrient retention of *Cladium jamaicense* Crantz and *Typha domingensis* Pers. in the Florida Everglades. *Aquat Bot* 40:203–224
- Del Giorgio PA, Cole JJ (1998) Bacterial growth efficiency in natural aquatic systems. *Annu Rev Ecol Syst* 29:503–541
- Demars BOL, Edwards AC (2007) Tissue nutrient concentrations in freshwater aquatic macrophytes: high inter-taxon differences and low phenotypic response to nutrient supply. *Freshw Biol* 52:2073–2086
- Díaz Villanueva V, Trochine C (2005) The role of microorganisms in the diet of *Verger cf. limnophilus* (Trichoptera: Limnephilidae) larvae in a Patagonian Andean temporary pond. *Wetlands* 25:473–479
- Dunham RM, Ray AM, Inouye RS (2003) Growth, physiology, and chemistry of mycorrhizal and nonmycorrhizal *Typha latifolia* seedlings. *Wetlands* 23:890–896
- Ezcurra C, Brion C (2005) Plantas del Nahuel huapi. Universidad Nacional del Comahue and Red Latinoamericana de Botánica, San Carlos de Bariloche
- González AL, Kominoski JS, Danger M, Ishida S, Iwai N, Rubach A (2010) Can ecological stoichiometry help explain patterns of biological invasions? *Oikos* 119:779–790
- Hauenstein E, Paña-Cortés F, Bertrán C, Tapia J, Schlatter R (2008) Floristic comparison and trophic condition based on indicator species in coastal lagoons of the Araucanian region, Chile. *Ecología Austral* 18:43–53
- Jumpponen A (2001) Dark septate endophytes—are they mycorrhizal? *Mycorrhiza* 11:207–211
- Modenutti BE, Balseiro E, Dieguez MC, Queimaliños C, Albariño R (1998) Heterogeneity of fresh-water Patagonian ecosystems. *Ecología Austral* 8:155–165
- Morris DP, Zagarese H, Williamson CE et al (1995) The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. *Limnol Oceanogr* 40:1381–1391
- Naiman RJ, Melillo JM (1984) Nitrogen budget of a subarctic stream altered by beaver (*Castor canadensis*). *Oecologia* 62:150–155
- Osborne TZ, Inglett PW, Reddy KR (2007) The use of senescent plant biomass to investigate relationships between potential particulate and dissolved organic matter in a wetland ecosystem. *Aquat Bot* 86:53–61
- Pace ML, Cole JJ (2002) Synchronous variation of dissolved organic carbon and color in lakes. *Limnol Oceanogr* 47:333–342
- Perez MT, Sommaruga R (2006) Differential effect of algal- and soil-derived dissolved organic matter on alpine lake bacterial community composition and activity. *Limnol Oceanogr* 51:2527–2537
- Prieur-Richard AH, Lavorel S (2000) Invasions: the perspective of diverse plant communities. *Austral Ecology* 25:1–7
- Raffaele E (1996) Relationship between seed and spore banks and vegetation of a mountain flood meadow (Mallín) in Patagonia, Argentina. *Wetlands* 16:1–9

- Raffaele E (2004) Susceptibility of a Patagonian mallín flooded meadow to invasion by exotic species. *Biol Invasions* 6: 473–481
- Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Dane Panetta F, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. *Divers Distrib* 6: 93–107
- Roehm CL (2005) Respiration in wetland ecosystems. In: del Giorgio P, Williams P (eds) *Respiration in aquatic ecosystems*. Oxford University Press, Montreal, pp 83–102
- Souza MS, Balseiro E, Laspoumaderes C, Modenutti B (2010) Effect of ultraviolet radiation on acetylcholinesterase activity in freshwater copepods. *Photochem Photobiol* 86: 367–373
- Sterner RW, Elser JJ (2002) *Ecological stoichiometry. The biology of elements from molecules to the biosphere*. Princeton University Press, Princeton
- Valderrama JC (1981) The simultaneous analysis of total nitrogen and total phosphorus in natural waters. *Mar Chem* 10:109–122
- Van TK, Wheeler GS, Center TD (1999) Competition between *Hydrilla verticillata* and *Vallisneria americana* as influenced by soil fertility. *Aquat Bot* 62:225–233
- Ventura M, Liboriussen L, Lauridsen T, SØndergaard M, Jeppesen E (2008) Effects of increased temperature and nutrient enrichment on the stoichiometry of primary producers and consumers in temperate shallow lakes. *Freshw Biol* 53:1434–1452
- Wong PK, Liang Y, Liu NY, Qiu JW (2010) Palatability of macrophytes to the invasive freshwater snail *Pomacea canaliculata*: differential effects of multiple plant traits. *Freshw Biol* 55:2023–2031
- Zedler JB, Kercher S (2004) Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. *Crit Rev Plant Sci* 23:431–452
- Zedler JB, Kercher S (2005) Wetland resources: status, trends, ecosystem services, and restorability. *Ann Rev Environ Res* 30:39–74