GfÖ
GfÖ Ecological Society of Germany, Austria and Switzerland
Basic and Applied Ecology 15 (2014) 219–228
Basic and Applied Ecology
www.elsevier.com/locate/baae

Effects of experimental warming and nitrogen enrichment on leaf and litter chemistry of a wetland grass, *Phragmites australis*

Sabine Flury[a,b,c,*], Mark O. Gessner[a,b,d,e]

[a]*Department of Aquatic Ecology, Eawag: Swiss Federal Institute of Aquatic Science and Technology, Seestrasse 79, Kastanienbaum, Switzerland*
[b]*Institute of Integrative Biology (IBZ), ETH Zürich, Universitätsstrasse 16, Zürich, Switzerland*
[c]*Department of Chemical Analytics and Biogeochemistry, Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Müggelseedamm 310, Berlin, Germany*
[d]*Department of Experimental Limnology, Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Alte Fischerhütte 2, Stechlin, Germany*
[e]*Department of Ecology, Berlin Institute of Technology (TU Berlin), Ernst-Reuter-Platz 1, Berlin, Germany*

Received 10 November 2013; accepted 12 April 2014
Available online 21 April 2014

Abstract

As global climate is warming and the nitrogen cycle accelerates, plants are likely to respond not only by shifting community composition, but also by adjusting traits such as tissue chemistry. We subjected a widespread wetland plant, *Phragmites australis*, to increased nitrate supply and elevated temperature in enclosures that were established in a littoral permanently submerged freshwater marsh. The nitrogen (N) and phosphorus (P) concentrations in green leaves ranged from 11.4 to 13.8 mg N and from 1.5 to 2.0 mg P g^{-1} dry mass. While the N concentration changed little in brown litter, the P concentration decreased to 0.53–0.65 mg P g^{-1} litter dry mass. Neither experimental warming of the water and sediment surface, nor nitrate enrichment during the growing season affected nitrogen or phosphorus concentrations in green leaves. Concentrations of the two major structural carbon compounds in plant litter, cellulose and lignin, were also unaffected, ranging from 32.1 to 34.2% of dry mass for cellulose and from 16.3 to 17.7% of dry mass for lignin. Warming, however, significantly increased the nitrogen concentration of fully brown leaf litter. Thus, temperature appears to be more important than the supply of dissolved N in the water, especially in affecting leaf litter N concentrations in *P. australis*, even when only water but not air temperature is increased. This result may have implications for decomposition processes and decomposer food webs, which both depend on the quality of plant litter.

Zusammenfassung

Im Zuge der globalen Klimaerwärmung und der Beschleunigung des Stickstoffkreislaufs ist es wahrscheinlich, dass die Vegetation nicht nur durch Veränderungen der derzeit etablierten Artengemeinschaften, sondern auch durch Verschiebung von Pflanzenmerkmalen wie der chemischen Gewebezusammensetzung reagieren. In einem permanent überfluteten natürlichen Uferröhricht errichteten wir Mesokosmen, um die Reaktion einer weit verbreiteten Feuchtgebietspflanze (*Phragmites australis*)

*Corresponding author. Present address: Department of Chemical Analytics and Biogeochemistry, Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Müggelseedamm 310, 12587 Berlin, Germany. Tel.: +49 30 6418 1960; fax: +49 30 6418 1700.
E-mail addresses: sabine.flury@yahoo.com (S. Flury), gessner@igb-berlin.de (M.O. Gessner).

http://dx.doi.org/10.1016/j.baae.2014.04.002
1439-1791/

auf erhöhte Nitratverfügbarkeit und erhöhte Wassertemperaturen zu testen. Die Stickstoff- und Phosphorkonzentrationen der grünen Blätter variierten zwischen 11.4 und 13.8 mg N bzw. zwischen 1.5 und 2.0 mg P g^{-1} Trockenmasse. Während sich der P-Gehalt in den braunen Blättern auf 0.53–0.65 mg P g^{-1} Trockenmasse verringerte, blieb der N Gehalt während der Seneszenz weitgehend unverändert. Weder die experimentelle Erwärmung des Wassers noch die Erhöhung des Nitratangebots während der Wachstumsperiode hatte einen Einfluss auf die Stickstoff- oder Phosphorkonzentrationen grüner Blätter. Ebenfalls unbeeinflusst war der Gehalt der wichtigsten Kohlenstoffverbindungen – Cellulose und Lignin – in der Blattstreu, wobei der Cellulose- und Ligningehalt zwischen 32.1 und 34.2% bzw. 16.3 und 17.7% der Trockenmasse schwankte. Erwärmung des Wassers führte dagegen zu einem signifikanten Anstieg des Stickstoffgehalts der Blattstreu. Diese Ergebnisse weisen darauf hin, dass die Temperatur eine wichtigere Rolle für die Stickstoffkonzentration in Blattstreu spielt als die Verfügbarkeit von gelöstem Stickstoff im Wasser, selbst wenn nur die Wasser-, nicht aber die Lufttemperatur direkt erhöht ist. Daraus ergeben sich mögliche Konsequenzen für Abbauprozesse und Nahrungsnetze von Destruenten, die beide maßgeblich von der Qualität der Pflanzenstreu abhängen.

Keywords: Climate change; Field experiment; Fertilization; Common reed; Plant tissue quality; Nutrient stoichiometry; Lignin; Mesocosm experiment

Introduction

Increased emissions of greenhouse gases by human activities have led to warming of the Earth's atmosphere by approximately 0.13–0.33 °C per decade over the past century (Trenberth, Jones, Ambenje, Bojariu, & Easterling et al. 2007). Scenarios for this century anticipate further warming by about 1.8–3.4 °C (Meehl, Stocker, Collins, Friedlingstein, & Gaye et al. 2007), a projected trend that is paralleled by increasing water temperatures of lakes, rivers and wetlands (North, Livingstone, Hari, Koester, & Niederhauser et al. 2013). Local thermal pollution by cooling-water discharge from power plants and manufactories also increases temperatures of the receiving water bodies (Kirillin, Shatwell, & Kasprzak 2013; Prats, Val, Armengol, & Dolz 2010). Simultaneously, humans have greatly altered the global nitrogen cycle by producing industrial fertilizer, intensifying agriculture, and releasing geologically fixed N by combusting fossil fuels (Galloway, Townsend, Erisman, Bekunda, & Cai et al. 2008). As a result, global NO_3^- and NH_4^+ deposition (wet and dry) has approximately doubled from pre-industrial times (7.4×10^9 kg NO_3^- yr^{-1}, 11.6×10^9 kg NH_4^+ yr^{-1}) to the present (14.8×10^9 kg NO_3^- yr^{-1}, 24.6×10^9 kg NH_4^+ yr^{-1}) and is predicted to increase further, reaching about $19–25 \times 10^9$ kg NO_3^- yr^{-1} and $15–18 \times 10^9$ kg NH_4^+ yr^{-1} by 2100 (Luo, Zender, Bian, & Metzger 2007).

Alterations in temperature, nitrogen supply and other factors of environmental change can affect ecosystems through effects on plant community composition and traits such as tissue chemistry (Chapin, Shaver, Giblin, Nadelhoffer, & Laundre 1995; Lü, Reed, Yu, He, & Wang, et al. 2013; Macek & Rejmánková 2007; Macek, Rejmánková, & Lepś, 2010). For example, litter nutrient content of wetland species is increased by exposure to elevated N and P concentrations during shoot growth (Macek & Rejmánková 2007; Macek et al. 2010). Such variation in plant tissue chemistry can have knock-on effects on trophic relationships in ecosystems (Chapin et al. 1995; Hines, Megonigal, & Denno 2006). Both herbivore (Treydte, Heitkonig, & Ludwig 2009) and detritivore food webs (Hines et al. 2006) can be affected, because differences in the tissue chemistry of life plants tend to persist after plant death (*e.g.* Garten, Brice, Castro, Graham, & Mayes et al. 2011) in spite of important chemical changes during plant senescence. Ecosystem processes such as litter decomposition can also be influenced because decomposition rates depend on litter chemistry, particularly concentrations of lignin (Rahman, Tsukamoto, Yoneyama, & Mostafa 2013), nutrients (Aerts & deCaluwe 1997; Enriquez, Duarte, & Sand-Jensen 1993; Rejmánková & Houdková 2006) and secondary metabolites (Li, Zeng, Yu, Fan, & Yang et al. 2011).

The aim of this study was to assess the effect of simulated increases in water temperature and N deposition on the tissue chemistry of a widespread wetland plant (*Phragmites australis* (Cav.) Trin. ex Steud.) that often assumes the role of a foundation species in freshwater and brackish marshes. We hypothesized that N concentrations would increase in green leaves and leaf litter of plants subject to elevated NO_3^- supply (Macek & Rejmánková 2007; Ruiz & Velasco 2010). Furthermore, we expected a decrease in the lignin content of plants exposed to increased N supply and elevated temperature due to a reduced investment in sclerenchyma by rapidly growing shoots exposed to high nutrient supplies (Engloner 2009) and warming (Henry, Cleland, Field, & Vitousek 2005). We tested these hypotheses by collecting leaves of *P. australis* naturally established in a permanently flooded littoral reed stand and subjected, or not, to experimental warming and/or nitrogen enrichment *in situ*. Green leaves collected in the middle of the growing season and fully brown leaf litter collected from standing-dead shoots after plant senescence and partial decomposition (Gessner 2001) were subsequently analyzed for nutrients (N and P in both green and brown leaves) and