GfÖ
GfÖ Ecological Society of Germany, Austria and Switzerland
Basic and Applied Ecology 9 (2008) 422–432
Basic and Applied Ecology
www.elsevier.de/baae

Can allelopathically active submerged macrophytes stabilise clear-water states in shallow lakes?

Sabine Hilt[a,*], Elisabeth M. Gross[b]

[a]Leibniz-Institute of Freshwater Ecology and Inland Fisheries Berlin, Müggelseedamm 301, 12587 Berlin, Germany
[b]Limnological Institute, University of Konstanz, P.O. Box 5560 M659, D-78457 Konstanz, Germany

Received 28 November 2006; accepted 27 April 2007

Abstract

Inhibition of phytoplankton by allelochemicals released by submerged macrophytes is supposed to be one of the mechanisms that contribute to the stabilisation of clear-water states in shallow lakes. The relevance of this process at ecosystem level, however, is debated because *in situ* evidence is difficult to achieve. Our literature review indicates that allelopathically active species such as *Myriophyllum*, *Ceratophyllum*, *Elodea* and *Najas* or certain charophytes are among the most frequent submerged macrophytes in temperate shallow lakes. The most common experimental approach for allelopathic interference between macrophytes and phytoplankton has been the use of plant extracts or purified plant compounds. Final evidence, however, requires combination with more realistic *in situ* experiments. Such investigations have successfully been performed with selected species. *In situ* allelopathic activity is also influenced by the fact that phytoplankton species exhibit differential sensitivity against allelochemicals both between and within major taxonomic groups such as diatoms, cyanobacteria and chlorophytes. In general, epiphytic species apparently are less sensitive towards allelochemicals than phytoplankton despite living closely attached to the plants and being of key importance for macrophyte growth due to their shading. Light and nutrient availability potentially influence the sensitivity of target algae and cyanobacteria. Whether or not additional stressors such as nutrient limitation enhance or dampen allelopathic interactions still has to be clarified. We strongly propose allelopathy as an important mechanism in the interaction between submerged macrophytes and phytoplankton in shallow lakes based on the frequent occurrence of active species and the knowledge of potential target species. The role of allelopathy interfering with epiphyton development is less well understood. Including further levels of complexity, such as nutrient interference, grazing and climate, will extend this ecosystem-based view of *in situ* allelopathy.

Zusammenfassung

Die Inhibition von Phytoplankton durch Allelochemikalien aus submersen Makrophyten ist einer der potentiellen Mechanismen, die zur Stabilisierung von Klarwasserzuständen in Makrophyten-dominierten Flachseen beitragen. Die Relevanz dieses Prozesses auf Ökosystemebene ist jedoch umstritten, da der *in situ* Nachweis schwierig ist. Unsere Literaturübersicht zeigt, dass allelopathisch aktive Arten wie *Myriophyllum*, *Ceratophyllum*, *Elodea* und *Najas* sowie bestimmte Characeen zu den häufigsten submersen Makrophyten in Flachseen der gemäßigten Breiten gehören. Der experimentelle Nachweis allelopathischer Effekte auf Phytoplankton erfolgte bisher überwiegend durch Pflanzenextrakte oder aufgereinigte Substanzen. Ein endgültiger Beweis erfordert jedoch zusätzlich Experimente unter *in situ* Bedingungen,

*Corresponding author. Tel.: +49 30 64181677; fax: +49 30 64181682.
E-mail addresses: hilt@igb-berlin.de (S. Hilt, nee Körner), Elisabeth.gross@uni-konstanz.de (E.M. Gross).

1439-1791/$ - see front matter
doi:10.1016/j.baae.2007.04.003

die bisher nur für einige Arten verfügbar sind. Die allelopathische Aktivität *in situ* wird auch durch die differentielle Sensitivität der Phytoplanktonarten gegenüber Allelochemikalien beeinflusst, die sowohl zwischen als auch innerhalb verschiedener Gruppen wie Diatomeen, Grünalgen und Cyanobakterien nachgewiesen wurde. Epiphytische Arten erscheinen im Allgemeinen weniger durch Allelochemikalien beeinflusst als planktische, obwohl sie direkt auf der Pflanzenoberfläche leben und durch ihre Beschattung eine Schlüsselrolle für das Wachstum der Makrophyten spielen. Licht- und Nährstoffverfügbarkeit können die Sensitivität des Phytoplanktons beeinflussen. Ob zusätzlicher Stress z.B. durch Phosphatlimitation allelopathische Interaktionen verstärkt oder abschwächt, muss noch geklärt werden. Aufgrund des derzeitigen Wissensstandes zur Häufigkeit allelopathisch aktiver submerser Makrophytenarten sowie der Sensitivität der Zielorganismen halten wir Allelopathie für einen wichtigen Mechanismus in der Interaktion zwischen submersen Makrophyten und Phytoplankton in Flachseen. Die Rolle der Allelopathie bei der Beeinflussung der Epiphytonentwicklung ist dagegen bisher weniger gut verstanden. Die Einbeziehung weiterer komplexer Ebenen wie Nährstoffinteraktionen, Grazing und Klimaänderungen wird unsere Ökosystem-basierte Sicht allelopathischer *in situ* Aktivität weiter vertiefen.

Keywords: Allelopathy; Shallow lakes; Bistability; Alternative stable states; Submerged macrophytes; *In situ* evidence; Phytoplankton; Epiphytes

Introduction

Most of the world's lakes are small and shallow (Wetzel, 1990), and many of them display two strongly contrasting states: a clear state dominated by aquatic vegetation, and a turbid state characterised by a high phytoplankton biomass. These states represent alternative equilibria due to stabilising mechanisms that tend to keep the system in either the vegetation dominated or the phytoplankton-dominated state. Shifts between these equilibria are generally abrupt and difficult to reverse (Scheffer, Hosper, Meijer, Moss, & Jeppesen, 1993). A loss of submerged vegetation and a switch to the turbid state have often been documented in temperate shallow lakes in response to eutrophication (Blindow, 1992; Körner, 2002; Sand-Jensen, Riis, Vestergaard, & Larsen, 2000). Both shading by phytoplankton and/or epiphyton (attached algae growing on the plants' surfaces) seem to be responsible for the disappearance of submerged macrophytes. Phillips, Eminson, and Moss (1978) already argued that a nutrient-mediated increase in the density of epiphyton rather than an increase of phytoplankton is the most important factor for the loss of submerged macrophytes. The detrimental role of epiphyton (Jones & Sayer, 2003) may be due to competition for light and carbon dioxide (Jones, Eaton, & Hardwick, 2000). Reduced macrophyte growth then results in less negative effects on phytoplankton and ultimately in turbid conditions.

The negative effect of submerged macrophytes on phytoplankton may depend on various mechanisms: provision of refuge for phytoplankton-grazing zooplankton against predation by planktivorous fish, reduced nutrient availability, increased sinking losses, reduced light availability, and the release of allelopathically active substances (Scheffer et al., 1993). The latter is subject of much debate because final proof for allelopathy *in situ* is difficult or even inaccessible (Gross, Hilt, Lombardo, & Mulderij, 2007). Several authors independently suggested a possible involvement of allelopathy behind observed phytoplankton patterns in whole-lake studies of vegetated, shallow lakes (Blindow et al., 2002; Lombardo, 2005; Mjelde & Faafeng, 1997). However, none could provide any evidence in favour of or against allelopathy, and the debate on the role of allelopathy at ecosystem level remains open.

We reviewed the available literature in order to assess the ability of submerged macrophytes to significantly suppress phytoplankton growth through the production and release of allelopathically active substances and the possible prevalence of this mechanism in eutrophic shallow lakes. The major focus is on community and ecosystem level effects. We specifically address the following questions:

(1) Which submerged macrophyte species exhibit allelopathic activity against phytoplankton, how frequent do they occur in shallow lakes and what macrophyte coverage is required for an effective phytoplankton inhibition?
(2) Are allelopathically active substances produced and released by aquatic macrophytes in sufficient quantity?
(3) Are the relevant phytoplankton (and epiphyton) species significantly inhibited by these substances?
(4) Which environmental factors may influence the allelopathic interference between submerged macrophytes and algae or cyanobacteria?

Allelopathically active submerged macrophytes in shallow lakes

Active species

Allelopathic effects of submerged macrophytes on phytoplankton have been shown for at least 37 species (Mulderij, 2006). Studies directly comparing the activity