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Allelopathic inhibition of phytoplankton by exudates from *Stratiotes aloides*

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Abstract

The allelopathic potential of exudates from the aquatic macrophyte *Stratiotes aloides* on the growth of phytoplankton was investigated. A selection of phytoplankton species, occurring in habitats similar to that of *Stratiotes*, was used: two cyanobacterial strains (toxic and non-toxic *Microcystis aeruginosa*), one green alga (*Scenedesmus obliquus*) and one eustigmatophyte (*Nannochloropsis limnetica*). The results indicate allelopathic effects of *Stratiotes* on phytoplankton in six of the eight cases, expressed in an extended duration of the initial biovolume doubling time. The overall inhibitory effect (8–51%) was strain-specific for the two cyanobacteria. We also studied the effect of irradiance on the allelopathic potential of exudates from *Stratiotes*. Irradiance influenced the response of *Scenedesmus* only. The inhibitory effect of *Stratiotes* exudates on the growth of this green alga was stronger at 35 μmol m^{-2} s^{-1} than at 105 μmol m^{-2} s^{-1}. We conclude that *Stratiotes* has allelopathic effects on phytoplankton, and that irradiance can, but does not always determine the extent of the allelopathic inhibition. In our experiments, the sensitivity of cyanobacteria to *Stratiotes* exudates was not higher than for other phytoplankton strains, but within cyanobacteria, the toxic strain was more sensitive than the non-toxic one.

Keywords: Allelopathy; Exudate; Growth inhibition; Initial biovolume doubling time; Irradiance; Lag phase

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1. Introduction

The presence of submerged macrophytes is considered to be of great importance for maintaining the clear water state in shallow lakes (e.g. Jeppesen et al., 1998a). Submerged macrophytes play different roles in shallow aquatic ecosystems. They fix substantial amounts of nutrients in their biomass (e.g. Kufel and Ozimek, 1994; Van Donk and Van de Bund, 2002) and thus compete for these nutrients with other autotrophic organisms, such as phytoplankton, and limit the latter's growth so that water transparency improves. The macrophytes may also contribute to an increase in water transparency by providing a refuge for zooplankton (Jeppesen et al., 1998b) and by the excretion of allelopathic substances that inhibit phytoplankton growth (Gross, 2003).

Molisch (1937) originally defined allelopathy as both stimulatory and inhibitory biochemical interactions between classes of plants (including microorganisms). Most recent studies, however, have focussed on the inhibitory effect of allelopathic substances (Gross, 2003). Allelopathy may be a useful strategy for macrophytes against other phototrophic organisms in aquatic food webs. There are several reported cases of allelopathic activity of macrophytes, e.g. *Chara* (Wium-Andersen et al., 1982; Blindow and Hootsmans, 1991; Mulderij et al., 2005), *Ceratophyllum* (Jasser, 1995; Mjelde and Faafeng, 1997) and *Myriophyllum* (Jasser, 1995; Gross et al., 1996), resulting in changes in phytoplankton biomass, phytoplankton composition or both.

In the present study we focussed on allelopathic interactions between the macrophyte *Stratiotes aloides* and several phytoplankton species. *S. aloides* is one of the characteristic species in the waters of peaty lowlands in the Netherlands. It is a dioecious, perennial aquatic macrophyte that shows vigorous clonal branching by means of tillers and turions and may form very dense stands (Smolders et al., 1996). In spring, the plants rise to the water surface (Smolders et al., 2003), where they float, flower and produce new tillers and turions. In autumn, all plants (with tillers and turions) sink to the sediment, where they stay until next spring. For growth and reproduction, *Stratiotes* needs moderately high nutrient concentrations and is, therefore, absent in oligotrophic waters (Smolders et al., 2003).

Brammer (1979) and Brammer and Wetzel (1984) observed that *Stratiotes* markedly changes the in situ concentrations of K^+, Na^+ and Ca^{2+}. Also lake water phosphorus and nitrogen levels decreased, suggesting that the dominant *Stratiotes* might withdraw nutrients not only from the sediment but also from the surrounding water (Brammer, 1979). Co-precipitation of phosphorus with calcium on *Stratiotes* leaves was also discussed as alternative explanation for clear water around *Stratiotes* plants (Brammer, 1979; Brammer and Wetzel, 1984). Rather than allelopathy, competition for essential nutrients and changes in the ionic composition of the water seemed to be more likely explanations for low phytoplankton density (Brammer, 1979; Brammer and Wetzel, 1984). Waterbodies dominated by *S. aloides* are, however, usually very clear despite the moderately high nutrient concentrations. Therefore, nutrient limitation may not be the critical growth limiting factor for phytoplankton. Jasser (1995) showed that extracts of *S. aloides* significantly inhibited three cyanobacteria. This study does not rule out competition for nutrients, but it implies another possible mechanism. It suggests that allelopathic substances were present in the extracts.