

Allelopathy of Aquatic Autotrophs

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ABSTRACT: Allelopathy in aquatic environments may provide a competitive advantage to angiosperms, algae, or cyanobacteria in their interaction with other primary producers. Allelopathy can influence the competition between different photoautotrophs for resources and change the succession of species, for example, in phytoplankton communities. Field evidence and laboratory studies indicate that allelopathy occurs in all aquatic habitats (marine and freshwater), and that all primary producing organisms (cyanobacteria, micro- and macroalgae as well as angiosperms) are capable of producing and releasing allelopathically active compounds. Although allelopathy also includes positive (stimulating) interactions, the majority of studies describe the inhibitory activity of allelopathically active compounds. Different mechanisms operate depending on whether allelopathy takes place in the open water (pelagic zone) or is substrate associated (benthic habitats). Allelopathical interactions are especially common in fully aquatic species, such as submersed macrophytes or benthic algae and cyanobacteria. The prevention of shading by epiphytic and planktonic primary producers and the competition for space may be the ultimate cause for allelopathical interactions. Aquatic allelochemicals often target multiple physiological processes. The inhibition of photosynthesis of competing primary producers seems to be a frequent mode of action. Multiple biotic and abiotic factors determine the strength of allelopathic interactions. Bacteria associated with the donor or target organism can metabolize excreted allelochemicals. Frequently, the impact of surplus or limiting nutrients has been shown to affect the overall production of allelochemicals and their effect on target species. Similarities and differences of allelopathic interactions in marine and freshwater habitats as well as between the different types of producing organisms are discussed.

KEY WORDS: marine ecosystem, freshwater ecosystem, algae, cyanobacteria, angiosperms, coral, ecology.

I. INTRODUCTION

Aquatic photoautotrophs often face severe competition for resources, either space, light, or nutrients. The release of allelopathically active compounds interfering with settlement and/or growth of competitors in their vicinity is an adaptive trait developed by primary producers against competitors. According to Molisch (1937), allelopathy covers biochemical interactions, both stimulatory and inhibitory, among different primary producers or between primary producers and microorganisms. Similar to terrestrial habitats, final proof for allelopathic interactions in aquatic systems is almost impossible. Most aquatic studies cover only a few of the six requirements demanded by Willis (1985), often neglecting eco-

logical aspects of allelopathy. Even so, many studies point toward allelopathic interactions among aquatic photoautotrophs, sometimes substantiated by both field and laboratory evidence.

This review has the following objectives: (1) to summarize current knowledge of allelopathic interactions in all aquatic systems, (2) to name factors and constraints for allelopathy in these environments, and (3) to emphasize common patterns in both freshwater and marine habitats. The main attention was given to studies published within the last decade, and reference was made to general reviews of this topic (Gopal and Goel, 1993; Inderjit and Dakshini, 1994; Gross, 1999). First, the article covers current knowledge on allelopathically active primary producers in marine and freshwater habitats. Within these habitats, different groups of

primary producers involved (angiosperms, macro- and microalgae, cyanobacteria) have been distinguished. Cyanobacteria were separated from other microalgae because they are prokaryotes and are generally known to produce a vast array of novel secondary metabolites. Secondly, general aspects of allelopathy, such as the mode of action of allelopathically active compounds and environmental and biotic factors acting on the production of allelochemicals, are discussed. This part bridges insights from different habitats and producing organisms. Apparently there are general principles to all aquatic habitats and most primary producers.

A. Differences between Terrestrial and Aquatic Habitats

Generally, allelopathic interactions in aquatic habitats resemble those in terrestrial systems, although some fundamental differences exist. One major difference is that most aquatic photoautotrophs are surrounded by water instead of air. Allelochemicals released by donor organisms into the water need to be sufficiently hydrophilic and reach their target organisms in effective concentrations despite considerable dilution. We might expect less lipophilic allelochemicals in this habitat compared with terrestrial sites where transfer through the air is possible. Further, algae, cyanobacteria, and fully aquatic angiosperms are 'leaky', maybe even more than terrestrial plants. Submersed leaves of aquatic angiosperms have no stomata, a reduced cuticula, and less tight cell connections compared with emergent or floating leaves (Hutchinson, 1975), all of which should facilitate the release of organic compounds. Leaves of terrestrial plants are generally protected by a thick cuticula. However, leakage through open stomata or from epidermal cells may occur. To my knowledge, a direct comparison between aquatic and terrestrial photoautotrophs for qualitative and/or quantitative differences in organic leachates was never done. Both algae (Sieburth, 1968; Wood et al., 1992), and higher plants (Wetzel, 1969; Wetzel and Manny, 1972; Søndergaard, 1981; Nalewajko and Godmaire, 1993) release organic compounds, usually referred to as DOC (dissolved organic carbon/compounds)

or EOC (extracellular organic carbon/compounds). Leachates contain mainly carbon-based organic compounds, considered to be surplus photosynthates (Wetzel, 1969; Hough and Filbin, 1990). Besides pure carbon-based compounds, dissolved organic nitrogen compounds are also found (Wetzel and Manny, 1972).

Allelopathic interactions of aquatic photoautotrophs may also occur via root exudation. Commonly, simplified model systems are used to evaluate allelopathic root exudates (Gallardo et al., 1998b; Kato-Noguchi and Ino, 2001). Yet, physico-chemical processes in root compartments (of terrestrial plants) are diverse and may be complex. Their effect on various interactions, among them allelopathy, was discussed recently by El-Shatnawi and Makhadmeh (2001). The importance of soil processes in terrestrial systems for allelopathic interactions involving phenolic compounds were analyzed in detail by Blum et al. (1999). A major difference in aquatic habitats compared with terrestrial systems is that the sediment is waterlogged, creating anaerobic environments. Most aquatic macrophytes manage to create small oxygenic boundary layers around their roots (Christensen et al., 1994; Flessa, 1994; Sorrell and Armstrong, 1994; Brix and Sorrell, 1996; Wigand et al., 1997; Jackson and Armstrong, 1999). Aerobic microzones around roots of aquatic angiosperms are small (approx. 1 mm), but may significantly alter the redox potential of the soil (Flessa, 1994). Certainly, these microzones have an impact on the transfer of allelopathically active compounds, although few direct studies have been performed so far. The relevance of aquatic bioactive metabolites in the rhizosphere and around roots was discussed recently by Neori et al. (2000).

Two different types of allelopathic interactions occur in aquatic habitats. First, pelagic algae and cyanobacteria may use allelopathically active compounds to outcompete other species, to gain dominance over predecessors, or influence the type of conspecifics and successors. Fundamental studies have been done by Keating (1977, 1978) on allelopathy and the cyanobacterial dominance in eutrophic lakes. Allelopathy in pelagic environments depends on sufficient production and excretion of allelopathically active compounds

into the water and their effective distribution to reach target species at active concentrations. Dilution is the major problem in this type of allelopathic interaction (Lewis, 1986). We may consider the pelagic zone as a three-dimensional habitat compared with littoral or benthic zones, where the competition for space is more severe and the colonized surface represents rather a two-dimensional habitat. Thus, secondly, in aquatic environments we are dealing with allelopathic interactions between organisms living adjacent to each other, sometimes even touching other species in littoral or benthic zones. In these habitats angiosperms and macroalgae, so-called 'macrophytes' (see Wetzel, 2001), compete with other macrophytes, epiphytes, and/or phytoplankton. Allelopathically active compounds produced by benthic photoautotrophs that affect phytoplankton rely on similar mechanisms than described for the pelagic habitat. When macrophytes excrete allelochemicals targeting epiphytes, these compounds may be passed along either via the water or by direct contact, that is, compounds located in secretory trichomes, epidermal glands, or otherwise associated with the surface of the plant. In this case we can assume high local concentrations of allelochemicals directly acting on target species. We may consider more hydrophilic compounds acting on plankton species, whereas compounds translocated by direct contact should be more lipophilic. Leaf washings, as used with terrestrial plants to remove lipophilic substances from the surface, are difficult with aquatic angiosperms. Surface concentrations of natural products on marine macroalgae have been quantified using short hexane washings (de Nys et al., 1998; Dworjany et al., 1999).

The presence of surface-associated allelochemicals does not exclude allelochemicals with low water solubility in pelagic allelochemical interactions, since lipophilic compounds may bind to small particles or form micelles (Fischer and Quijano, 1985; Perez, 1999; Perez and Martin, 2001). Micelle formation as a means of increasing the solubility of lipophilic allelochemicals in water, however, has been debated, and other mechanisms may also be involved (Fischer et al., 1994).

Some studies report allelopathic interactions between terrestrial and aquatic photoautotrophs.

In the last decade, many studies have investigated the algicidal effect of (deciduous) leaf litter and (barley) straw (i.e., Dasneves and Gaspar, 1990; Newman and Barrett, 1993; Pillinger et al., 1994; Lege et al., 1995; Martin and Ridge, 1999; Ridge et al., 1999; Al Hamdi et al., 2001). Especially in small lakes and rivers, leaf litter may strongly influence algal communities. The use of straw to prevent cyanobacterial blooms represents, however, an artificial coupling of terrestrial and aquatic organisms. Wetland plants are at the interface of terrestrial and aquatic systems. Some of them have allelopathic properties (Elakovich and Wooten, 1989; Rojo et al., 2000). Rice, an important wetland crop, was affected by allelopathic interference from cyanobacteria (Inderjit and Dakshini, 1997) or aquatic plants (Quayyum et al., 1999a, 1999b).

B. Suitable Target Organisms and Impact of Stressors on Allelopathy

The debate on the existence of allelopathy *in situ* and how to transfer laboratory results to field situations is ongoing for both terrestrial and aquatic systems and will not be settled on in the near future, as already mentioned. Much controversy arises from the use of adequate bioassays, above normal concentrations of inhibitors, or wrong target organisms. Reviews on laboratory bioassays are available by Inderjit and Dakshini (1995) and Inderjit (this issue). Some of the constraints of allelopathy occurring *in situ* have been discussed recently by Reigosa et al. (1999).

Allelopathic interactions apparently are enhanced under abiotic or biotic stress (Lovett et al., 1989; Tang et al., 1995; Reigosa et al., 1999). This is corroborated by many studies showing the impact of nutrient limitation of both donor and target organisms on the outcome of allelopathic interactions (see Section VI.A). Complex field situations may have one or multiple stressors acting at the same time, a facet not yet much reflected in aquatic allelopathy research. Further, temporal and spatial changes in stressors acting on competing primary producers occur. Inorganic phosphorus is the major limiting nutrient for algae and cyanobacteria in summertime (Schindler,

1977). Ultraviolet radiation is strongest in summer; the depth reached in aquatic systems strongly depends on the clarity of the water (Haeder et al., 1998). Generally, UV-stress seems less important for most freshwater systems (Williamson, 1995) but has strong impacts on many marine habitats (Suzuki et al., 1998; Farjalla et al., 2001). Water stress (i.e., drought) is seldom a stressor in aquatic systems. It is not unlikely that the presence or absence of allelopathic interactions in a given system is related to changes in stressors acting on the organisms. There is some potential that studies incorporating common stressors may resolve contradicting results on allelopathic activity.

The question of whether target species have to be from the same habitat than the donor organism is also discussed as controversial. It seems obvious that aquatic allelochemicals should not be tested on terrestrial plants since there is no ecological relevance. The argument that proper ecological studies should use donor and target species from the same habitat refers mainly to the use of artificial systems for allelopathic studies. In spite of that, terrestrial plants or plant parts are sometimes used additionally to aquatic target organisms because they may provide the better model systems for a detailed investigation of the mode of action (e.g., spinach chloroplasts for photosynthesis inhibition [see Section IV.B.]). The use of cultured algae or cyanobacteria in aquatic allelopathy is frequent because they allow bioassays to be run under controlled and replicated conditions. Reigosa et al. (1999) argued that organisms within one habitat should be adapted to allelochemicals in this system. Therefore, allelopathic interactions should only be expected between organisms from different habitats. Allelopathic interactions among aquatic photoautotrophs would consequently be more likely if the organisms originate from different lakes or streams, maybe even from different geographical regions. Unfortunately, we are lacking studies directly addressing this aspect. It would be interesting to see if Reigosa's hypothesis (Reigosa et al., 1999) is also generally applicable for aquatic ecosystems. More insight could arise from a comparison of the allelopathical potential of aquatic neophytes and their native relatives. Nevertheless, allelopathy may act between organisms of one habitat or

between those from different sites. Considering that some allelochemicals are inducible and their production controlled by stress or other environmental factors (see Sections I.A and V.A), we should expect a changing susceptibility of target organisms to allelopathically active species within one habitat. Further, the studies by Keating (1977, 1978) showed that allelopathy might explain phytoplankton succession within one lake. Thus, not only spatial concerns (same or different original habitat of interfering species) but also temporal aspects (climax of stressors, seasonal succession of species) need reference.

II. MARINE SYSTEMS

Allelopathy in marine ecosystems may occur between phytoplankton species or in benthic areas where macroalgae, corals, and a few species of angiosperms are present. Benthic zones are small compared with the vast pelagic zones in the sea. Phytoplankton densities are extremely low in mid ocean, but may increase considerably along the shores as a result of eutrophication. Angiosperms, macroalgae, and corals produce inhibitory compounds interfering with epiphytes and other epibionts, competing for light and/or space (Harrison and Chan, 1980; Harlin, 1987; Endean et al., 1997; Jeong et al., 2000). Allelochemical interactions among planktonic algae have been described, mainly when bloom-forming microalgae were involved (Smayda, 1997).

A. Angiosperms

Only few aquatic angiosperms live in marine littoral areas. Their distribution depends on sediment characteristics (sandy, not rocky shore) and turbidity caused by biotic or abiotic factors (see, e.g., Orth et al., 2000). *Zostera marina* often dominates worldwide seagrass communities. Water-soluble extracts from both green and dead leaves of *Z. marina* inhibited algae and bacteria (Harrison and Chan, 1980; Harrison and Durance, 1985). Dead leaves were active only shortly after senescence. It is likely that phenolic allelochemicals were responsible for the observed effect

(Quackenbush et al., 1986; Harrison and Durance, 1989). The highest concentrations of phenolic compounds (1.5% based on dry mass) were found in September, at the end of the active growing season (Harrison and Durance, 1989). One might expect algicidal compounds to be highest during maximum phytoplankton or epiphyte development, but in this case phenolic allelochemicals were not correlated to maximum densities of microalgae or cyanobacteria. Whether antimicrobial phenolic acid sulfate esters (Todd et al., 1993) also act on epiphytic algae or cyanobacteria has not yet been elucidated. *Ruppia maritima* (Potamogetonaceae) growing in brackish or salt water produces antialgal diterpenes (Della Greca et al., 2000a). To my knowledge, no other marine angiosperms produce allelopathically active compounds.

B. Macroalgae

Macroalgae in marine environments belong to various groups, predominantly to the phaeophytes, chlorophytes, and rhodophytes. Depending on their growth form (crustose or erect, sometimes canopy forming), they experience different interactions with other photoautotrophs, and also sometimes with heterotrophs. Allelochemical interference of macroalgae with microalgae has long been known (Shapiro, 1957; McLachlan and Craigie, 1964; Sieburth, 1968).

Prevention of epiphyte growth on macroalgal tissue by allelopathic mechanisms occurs frequently (Harlin, 1987). Extracts of various macroalgae inhibited the settlement and growth of the chlorophyte *Enteromorpha prolifera* (Young Cho et al., 2001), a common epiphyte on other macroalgae. Antifouling activity of macroalgae against bacteria and fungi was shown by Hellio et al. (2000). In their study, some macroalgae possessed antifungal activity, others antibacterial, and only *Laurencia pinnatifida* (Rhodomelaceae) exhibited both antifungal and antibacterial activity. Extracts from this rhodophyte also exhibited a strong antifouling activity against microalgae, comparable to that of heavy metals and biocides currently used in antifouling paints (Hellio et al., 2002). Several extracts from other macroalgae

were also active. Allelopathy was apparently not involved in the prevention of epiphyte growth on the siphonaceous macroalgae *Avrainvillea* (Bryopsidales, Chlorophyta). The major cause for low epiphyte densities was identified as the reallocation of protoplasm for new growth through protoplasmic streaming, subsequent blade abandonment and proliferation (Littler and Littler, 1999). Exuded phlorotannins apparently were not allelopathically active since they did not affect the abundance and distribution of epiphytes on the phaeophyte *Ecklonia radiata* (Jennings and Steinberg, 1994; Jennings and Steinberg, 1997).

Crustose algae are prone to shading by canopy-forming macroalgae. Allelopathy may be an effective defensive trait preventing severe light limitation. Crustose coralline algae of the genus *Lithophyllum* (Rhodophyceae) produced a lipophilic allelopathic substance of low molecular weight that destroyed zoospores of the phaeophyte *Laminaria religiosa* (Suzuki et al., 1998). *Plocamium hamatum* (Rhodophyceae) produces allelopathically active monoterpenes affecting both microalgae (König et al., 1999) and adjacently growing soft corals (de Nys et al., 1991). Certain marine macroalgae (*Corallina pilulifera*, *Ulva pertusa*, *Ishige foliacea*, and *Enderachne binghamiae*) exuded allelochemicals into the culture medium that inhibited toxic bloom-forming microalgae, such as *Cochlodinium polykrikoides* (Jeong et al., 2000). No seasonal variation was found for the algicidal activity, and extracts of *C. pilulifera* did not inhibit other, nontoxic microalgae.

C. Microalgae

Most of the 60 to 80 harmful marine phytoplankton species are flagellates, particularly dinoflagellates. To counteract low nutrient uptake affinities compared with diatoms, four major adaptations, among them allelopathy and grazing deterrence, have evolved in harmful flagellates (Smayda, 1997). Dominance of harmful dinoflagellate blooms in marine phytoplankton communities is considered to be mediated by the production of poisoning toxins, okadaic acid (OA), and dinophysistoxin-1 (DTX-1) (Lewis and

Holmes, 1993; Windust et al., 1996; Plumley, 1997). Some studies suggested that OA and DTX-1 derived from *Prorocentrum lima* may have allelopathic properties and inhibit microalgae not forming toxins (Windust et al., 1996). However, a refined study showed that although OA had growth inhibitory activity, it was not the major allelopathically active compound present in *P. lima*. Three co-occurring dinoflagellates of *P. lima* exhibited reduced growth by another, yet unidentified allelochemical than OA (Sugg and van Dolah, 1999). Similar evidence that bloom-forming microalgae may dominate phytoplankton, not only because they have feeding deterrents, but also because of allelopathic interactions with other phytoplankton species, has been reported recently. Culture filtrates of two raphidophytes (*Heterosigma akashiwo* and *Chattonella antiqua*) from the late logarithmic growth phase strongly inhibited the growth of the diatom *Skeletonema costatum* (Matsuyama et al., 2000). Three toxin-producing *Alexandrium* species exuded allelopathically active compounds inhibiting other microalgae (*Chaetoceros gracile*, *Gymnodinium mikimotoi*, and *Scrippsiella trochoidea*), both in the exponential and stationary growth phase (Arzul et al., 1999). Recent evidence indicates, however, that also bacteria might be involved in both induction and inhibition of cyst formation in the toxic *A. tamarense* (Adachi et al., 1999; Adachi et al., 2002), thus influencing the life cycle and bloom formation in this bloom-forming dinoflagellate.

D. Cyanobacteria

Despite the plethora of novel bioactive secondary metabolites isolated from marine cyanobacteria (e.g., Fish and Codd, 1994a; Moore, 1996; Abarzua et al., 1999; Nagle and Paul, 1999), almost nothing is known about allelopathic interactions. The production of grazer deterrents or antifouling metabolites (antifungal, antibacterial activity) is generally considered to determine competitive strength and allow toxin-producing strains to outcompete others. Many dominant species, for example, *Lyngbya majuscula*, produce a vast array of bioactive compounds (Nagle and Paul, 1999), but no allelopathically active com-

pounds were isolated so far. Recently, it was shown that *Nodularia harveyana*, a nitrogen-fixing cyanobacterium isolated from the Mediterranean Sea, exhibited strong allelopathic activity against other axenic cyanobacteria, antibiotic activity against Gram-positive pathogenic bacteria, and antifungal activity against two plant pathogens (Pushparaj et al., 1998). Since many freshwater cyanobacteria (see below), especially benthic forms, produce allelopathically active compounds, we should expect similar activities in marine (benthic) cyanobacteria.

E. Corals

Corals were included in this review because anthozoa usually live in symbiosis with primary producers, zooxanthellae. The sessile nature of corals makes them vulnerable, being overgrown by macroalgae, especially under conditions of nutrient enrichment along reefs. In addition, competition for space with other corals exists. Therefore, it seems adaptive for corals to produce and release allelopathically active compounds deterring epibionts or adjacent organisms. Competition between scleractinian corals and benthic algae has been considered important for the structuring of coral reef communities (McCook et al., 2001). The regular spacing of massive coral blocks can be a result of allelopathic interference (Endean et al., 1997). The absence of higher plants at the Great Barrier Reef led to a screening for plant growth inhibitors. Specific inhibitors of C₄ plants were found in exudates of coral reef organisms by Jim Burnell and Lyndon Llewellyn (Thwaites, 2000). Nothing is yet known about the producing organisms, the chemical nature of the allelochemicals, and their ecological function.

Soft corals (e.g., *Sinularia flexibilis*, *Lobophytum hedleyi*) inhibited growth and produced tissue necrosis in neighboring scleractinian corals due to the exudation of inhibitory terpenes (Aceret et al., 1995). The competition for space among some scleractinian corals seems to depend on allelopathy. Lipophilic extracts containing indole alkaloids isolated from *Tubastrea faulkneri* inhibited other scleractinians (Koh and Sweatman, 2000). Allelochemicals from alcyonacean octocorals (soft corals) have multiple

functions; they may enhance reproductive success or act as antipredator, antifouling, and antialgal compounds (Sammarco, 1996; Griffith, 1997). Even antarctic soft corals produced allelopathically active compounds (as in the broader sense of allelopathy including animals) that prevented the growth of sponges on their surface (Slattery and McClintock, 1997).

Compounds active against fouling by epibionts may also interfere with other organisms colonizing neighboring space and therefore be adaptive for the coral. Corals are sometimes susceptible to allelochemicals released by neighboring sponges. The liver sponge *Plakortis halichondroides* caused necrosis of *Agaricia lamarcki*, a sheet coral (Porter and Targett, 1988). In addition, stimulating allelopathic effects have been observed. Allelochemicals released by alcyonacean corals enhanced the settlement and growth of scleractinian corals adapted to these compounds (Maida et al., 1995a,b).

However, often corals are target and not donor organisms, that is, they are susceptible to (inhibitory) allelochemicals released by co-occurring algae (McCook et al., 2001). Algae exerted allelopathic effects on both soft (de Nys et al., 1991) and hard corals (Littler and Littler, 1997).

III. FRESHWATER SYSTEMS

In freshwater systems we find allelopathic interactions among photoautotrophs both in pelagic zones and in benthic or littoral zones. In contrast to marine benthic areas, freshwater littoral zones are generally dominated by diverse aquatic angiosperms of different growth form, but only few macroalgae occur. Phytoplankton density may be high as a result of lake morphology and trophic state (Wetzel, 2001). Different types of interaction among those primary producers occur, as illustrated below. Members of all groups of primary producers in freshwater have been shown to be involved in allelopathic interactions (Gopal and Goel, 1993; Inderjit and Dakshini, 1994; Gross, 1999). Apart from stagnant waters, primary producers grow also in running waters. In rivers and streams, the current would rapidly carry exuded allelochemicals away. With the ex-

ception of benthic macroalgae (Dodds, 1991), no reports on allelopathy have been reported for this system.

A. Angiosperms

A comprehensive review of competition and allelopathy in aquatic plant communities was presented by Gopal and Goel (1993). Further references on allelopathy or secondary metabolites in aquatic angiosperms can be found in McClure (1970), Ostrofsky and Zettler (1986), Wium-Andersen (1987), and Gross (1999). Therefore, I do not extensively cover all literature given there, but rather focus on more recent publications and selected macrophytes. Aquatic angiosperms are presented in three sections — emergent, floating-leaved, and submerged macrophytes — because of differences in habitat characteristics and growth form. Emergent plants seldom face competition with epiphytes or phytoplankton. However, these largely clonally dispersing species may compete with other emergents for nutrients and space. Floating leaved macrophytes cause shading for submerged growing macrophytes and phytoplankton. Rooted floating-leaved plants also compete for space because they predominantly spread vegetatively. True aquatic angiosperms living fully submerged face the strongest light and space competition with other primary producers, both higher plants and microalgae. Allelopathic interaction should be an efficient counteractive strategy for many of them. Sudden switches between phytoplankton or macrophyte dominance in many shallow eutrophic lakes occur frequently (Scheffer et al., 1993; Jeppesen et al., 1998). These changes are influenced by many abiotic and biotic factors, among them allelopathic interference of macrophytes with phytoplankton development (Crawford, 1977; Phillips et al., 1978; Gross, 1999; Scheffer, 1999).

1. Emergent Macrophytes

Allelopathic interactions in helophytes were reviewed by Szczepanska (1987). She focussed on interspecific effects of emergent macrophytes,

such as *Phragmites australis* and *Typha latifolia*, both growing frequently in the same littoral area. Much is known about common reed species, such as *Typha* or *Juncus*, and only few studies deal with other emergent macrophytes. *Acorus gramineus* (Araceae) contains several phenylpropanoids with antialgal and anticyanobacterial activity (Della Greca et al., 1989).

Juncus effusus, a cosmopolitan clonal angiosperm, is highly competitive and possesses allelopathic activity. The algicidal activity was related to dihydrophenanthrene and tetrahydropyrene aglycones (Della Greca et al., 1996) and stereochemical requirements for inhibition were elucidated by synthesis of these and related compounds (Della Greca et al., 2000b, 2001b). Similar compounds are found in *J. acutus* (Della Greca et al., 2002a, 2002b), suggesting that this class of compounds is widespread in this genus. Additionally, antialgal phenylpropane glycerides were isolated from *J. effusus* (Della Greca et al., 1998). Leachates of dead, aboveground tissue of adult plants are autotoxic to seedlings (Ervin and Wetzel, 2000). Whether autotoxicity is based on the above-mentioned algicidal compounds or other secondary metabolites present in this species (Corsaro et al., 1994; Della Greca et al., 1992a, 1993a, 1993b, 1994, 1995, 1996) remains to be elucidated. Autotoxicity toward seedlings in this otherwise vegetatively spreading plant may benefit temporal dispersal of seedling establishment and population regeneration after disturbance (Ervin and Wetzel, 2000). A very detailed review on autotoxicity, mainly in terrestrial plants, and its ecological significance was presented recently in this journal (Singh et al., 1999).

Autotoxicity was also reported for *Typha latifolia* (McNaughton, 1968). Phenolic compounds present in aqueous leachates from leaves completely inhibited seed germination in this species. However, autotoxicity was reevaluated 15 years later by Grace (1983), who could not confirm the earlier findings. Similar to *J. effusus*, antialgal secondary metabolites (sterols, fatty acids) have been isolated from *T. latifolia* (Aliotta et al., 1990; Della Greca et al., 1990). Aqueous extracts of leaves, stems, and roots of *T. domingensis* inhibited the growth of the water fern *Salvinia minima* in bioassays (Gallardo et al.,

1998b). The most active phenolic compounds were 2-chlorophenol and salicylaldehyde, especially when extracted from roots. The concentration of these compounds was several micrograms per gram fresh mass of plant tissue (Gallardo et al., 1999). Recently, Gallardo-Williams et al. (2002) isolated several compounds from aqueous extracts and leachates of *T. domingensis*, among them linoleic and α -linolenic acids and trace amounts of various phenolic acids. Linoleic and α -linolenic acids have also been found in *T. latifolia* (Aliotta et al., 1990). These compounds are generally recognized to be phytotoxic; however, in the study by Gallardo-Williams et al. (2002) no bioassays with ecologically relevant concentrations were made. An annotated literature review of *Typha*, including citations on competitive abilities of this species, was provided by Gallardo et al. (1998a).

2. Floating Leaved Macrophytes

Both rooted and free-floating macrophytes have been included in this section. Rooted species obtain their nutrients predominantly from the sediment, and generally no nutrient competition with algae or epiphytes takes place. In contrast, free-floating macrophytes get all nutrients from the water, and may compete with phytoplankton or epiphytes. Floating leaved macrophytes grow only in stagnant waters, protected from wind or wave exposure. Few seedlings of other species can establish in extensive stands of rooted floating leaved macrophytes. Aqueous extracts of *Nuphar lutea* inhibited the growth of lettuce seedlings at low concentrations compared with 16 other macrophytes (Elakovich and Wooten, 1991; Elakovich and Wooten, 1995). Osmotic effects or changes in pH due to extract addition were ruled out in these assays. Alkaloids were considered responsible for the allelopathic activity (Elakovich and Yang, 1996). However, active concentrations used in the *Lemna* bioassay were too high for ecological relevance (2 ppm equivalent to approx. 4 mM). Aqueous leaf extracts and whole seedlings of *Nelumbo lutea* exhibited no allelopathic activity against the submerged macrophytes *Myriophyllum spicatum* and *Potamogeton pectinatus* (Vance and

Francko, 1997). In exudates of *Nuphar lutea*, resorcinol was found in relatively high concentrations (Sütfeld et al., 1996). Some cryptophycean algae apparently polymerized resorcinol, but died after prolonged exposure (Sütfeld, 1998). Cyanobacteria and chlorophytes were not inhibited (Sütfeld et al., 1996).

Eichhornia crassipes is a dominant free-floating macrophyte in many tropical and subtropical lakes and waterways. *Eichhornia* may spread very fast and cause deleterious effects to lakes and waterways (Center et al., 1989; Mehra et al., 1999). Low phytoplankton densities may occur in these systems, either due to nutrient or light competition or the exudation of allelopathically active compounds. An axenic culture of *Eichhornia* was established, which allowed a controlled testing of exudates. Water, in which *E. crassipes* seedlings were cultivated, inhibited the growth of *Chlamydomonas reinhardtii* (Sun et al., 1990). Axenic as well as nonaxenic root exudates contained *N*-phenyl-1-naphthylamine and *N*-phenyl-2-naphthylamine; both highly algicidal compounds (Sun et al., 1993). Additionally, several phenalene metabolites have been isolated (Della Greca et al., 1992b; 1992c). However, their allelopathic activity *in vitro* against several algae was low. A benzoinone isolated from plant tissue was shown to inhibit *Candida albicans* (Della Greca et al., 1991). *Eichhornia* itself was susceptible to allelopathic inhibition by residues and aqueous extracts of *Parthenium hysterophorus* (Asteraceae) (Pandey et al., 1993a; 1993b; Pandey, 1996). However, the concentrations of *Parthenium* allelochemicals needed for a deleterious effect *in situ* have been very high. Aqueous leachates of the terrestrial plant *Lantana camara* (Verbenaceae) killed *Eichhornia* when added to the culture medium (Saxena, 2000).

Pistia stratiotes is another free-floating macrophyte causing severe problems in many inland waters. Water lettuce, as it is also called, contains lipophilic algicidal compounds, among them α -asarone, various fatty acids, and steroid derivatives (Aliotta et al., 1991). Two unusual hydroxy fatty acids were especially inhibitory. They may have originated from lipoxygenase oxidation of α -linolenic acid. The inhibitory activity of linoleic and γ -linolenic acid; however, is probably due to

the formation of hydroperoxide derivatives in the bioassay (Aliotta et al., 1990; Aliotta et al., 1991).

Potamogeton natans, a species with both floating-leaved and submersed leaves, produces various diterpenes with antialgal activity (Cangiano et al., 2001; Della Greca et al., 2001a; Cangiano et al., 2002). These studies are not explicit whether only floating leaves were used; such leaves emerge only after submersed leaves are decomposed. Most other Potamogetonaceae live fully submersed and exhibit no or only very weak allelopathic activity (personal observation). Hasler and Jones (1949) are sometimes cited for allelopathy in *Potamogeton*; however, in this study only small amounts of *P. foliosus* grew together with *Elodea (Anacharis) canadensis*. The latter exhibits allelopathic activity (Erhard and Gross, unpublished results).

3. Submersed Macrophytes

The major limiting resource for submersed macrophytes is shading by epiphytes and phytoplankton, or turbidity caused by sediment resuspension or humic compounds (Sand-Jensen, 1990). Effective defensive traits may include fast apical growth, canopy formation and the release of allelopathically active compounds. Evidence from field studies shows that allelopathy may be involved in macrophyte-microphyte interactions (Phillips et al., 1978; Scheffer et al., 1993). However, *in situ* no direct proof has been possible so far. Thus, we have to extrapolate from laboratory and mesocosm studies to investigate the ecological and evolutionary impact of allelopathy in this system.

Ceratophyllum demersum, a nonrooting, canopy-forming submersed angiosperm, showed allelopathic activity toward phytoplankton (Kogan and Chinnova, 1972; Wium-Andersen et al., 1983; Jasser, 1994; Jasser, 1995). Sulfur or a lipophilic, labile sulfur compound have been described as the major algicides in lipophilic extracts (Wium-Andersen et al., 1983). Later studies showed that intact *C. demersum* released allelopathically active compounds inhibiting especially cyanobacteria (Jasser, 1994). Exudates caused species-specific allelopathic effects on various freshwater algae and cyanobacteria (Körner and Nicklisch, 2002). In a

series of shallow eutrophic Norwegian lakes, *C. demersum* hampered phytoplankton development (Mjelde and Faafeng, 1997). The dominance of *C. demersum* in these lakes could best be explained by competition for nitrogen with phytoplankton. *Ceratophyllum* spp. appeared to be sensitive to allelopathic interference by *Hydrilla verticillata* (Kulshretha and Gopal, 1983). However, the active compounds of this interaction have not been identified.

Members of the genus *Myriophyllum* (Haloragaceae) are highly competitive submersed macrophytes (Grace and Wetzel, 1978; Smith and Barko, 1990; Madsen et al., 1991; Weisner et al., 1997). Many studies report their allelopathic activity against algae and cyanobacteria (Fitzgerald, 1969; Planas et al., 1981; Agami and Waisel, 1985; Saito et al., 1989; Aliotta et al., 1992; Gross et al., 1996; Nakai et al., 2000). Several phenolic compounds with algicidal activity against cultured algae and natural phytoplankton assemblages have been isolated from *M. spicatum* (Planas et al., 1981). The cyanobacterium *Synechocystis* [*Anacystis*] *nidulans* was most sensitive compared with the chlorophytes *Selenastrum* and *Scenedesmus*. In a later study *M. spicatum*, grown in mesocosms, stimulated phytoplankton growth (Godmaire and Planas, 1986). Nutrients or light did not account for higher phytoplankton productivity, suggesting that other, not yet identified factors caused this effect. Whether this is an example of stimulatory allelopathy remains to be elucidated.

Gallic, ellagic, and tannic acid were isolated from *M. spicatum* tissue after acid hydrolysis and shown to inhibit phytoplankton species (Planas et al., 1981). The presence of these phenolic compounds already indicated that hydrolyzable polyphenols might be responsible for the allelopathic interaction. Tellimagrandin II and other hydrolyzable polyphenols were later identified as the major algicidal compounds (Gross and Sütfield, 1994; Gross et al., 1996). *M. spicatum* contains 10 to 25% polyphenols based on dry weight in leaves or apical meristem (Gross, 2000; Gross, unpublished results). This is much higher than concentrations of phenolic compounds observed in submersed macrophytes of other families (Gross, 1999; Smolders et al., 2000; Choi et al., 2002). Tellimagrandin II, also known as eugenin

(see Haslam, 1989; Gross, 1999), is also the major algicidal compound with strong activity against bloom-forming cyanobacteria in *M. brasiliense*, a South American partly emergent aquatic angiosperm (Saito et al., 1989). Planas (1981) described 3,5-dimethoxy-4-hydroxycinnamic acid (sinapic or sinapinic acid) to be present in high concentrations in *M. spicatum*. Algicidal esters of sinapic (sinapinic) acid, other phenylpropanoic acids and gallic acid were isolated from *M. verticillatum* by Aliotta et al. (1992). Extracts of *M. spicatum* exhibited the strongest inhibitory activity toward *Selenastrum capricornutum* and *Microcystis aeruginosa* compared with extracts from *Egeria densa* and *Cabomba caroliniana* (Nakai et al., 1996). *M. spicatum* actively releases allelochemicals to the environment (Gross et al., 1996), but the allelochemicals are readily metabolized after exudation (Gross et al., 1996; Gross, 1999), and a continuous release is required for the algicidal activity (Nakai et al., 1999). Tellimagrandin II, ellagic acid, and several other not yet identified low molecular polyphenols have been found in exudates of this plant (Gross and Sütfield, 1994). Similar results have been reported by Nakai et al. (2000), who found gallic, pyrogalllic, and ellagic acid as well as (+)-catechin in exudates. Gallic and pyrogalllic acids were more inhibitory toward *Microcystis aeruginosa* than ellagic acid and (+)-catechin. Glomski et al. (2002) recently doubted that exudation of polyphenols by *M. spicatum* occurs to any significant amount. However, their method was not adjusted to optimal trapping of polyphenols, and no exact concentrations of plants used in the exudation experiment were provided.

B. Macroalgae

The most prominent macroalgae in freshwater (and brackish) systems are charophytes (Characeae, Nitellaceae). *Chara*-dominated lakes are generally clear and exhibit low phytoplankton densities (Crawford, 1977; van den Berg et al., 1998). Multiple factors may account for this, for example, reduced sediment resuspension, competition for nutrients, and refuge for herbivorous zooplankton (Scheffer et al., 1993; van Donk and

van de Bund, 2002). In addition, allelopathy was frequently considered as an adaptive trait of *Chara* to prevent dense phytoplankton and epiphyte development. Bioactive cyclic sulfur compounds have been isolated from *Chara globularis* (Anthoni et al., 1980) and other brackish and freshwater *Chara* species (Wium-Andersen et al., 1982). These compounds are very labile and may release sulfur after decay. Whether the cyclic sulfur compounds, their presumed precursors in the plant, or sulfur itself caused the inhibition of photosynthesis in phytoplanktonic algae has never been resolved (Wium-Andersen et al., 1982; Wium-Andersen, 1987). The ecological significance of these laboratory findings with extracted material has been debated. Based on the relation of phytoplankton chlorophyll to phosphorus concentration in *Chara*-dominated and *Chara*-free lakes, Forsberg et al. (1990) argued that allelopathy is unlikely to be of ecological importance *in situ*. Lack of allelopathic activity might be due to nonallelopathic *Chara* species present in these lakes. *Ch. globularis*, the only species with prominent allelopathic activity (Wium-Andersen et al., 1982), was not dominant but *Ch. tomentosa* (Forsberg et al., 1990); other occurring species were *Ch. contraria*, *Ch. vulgaris*, and *Ch. aspera*. Laboratory studies revealed that only exudates of *Chara globularis* significantly limited microalgal growth, exudates of *Ch. tomentosa*, *Ch. delicatula*, or *Ch. hispida* either had no or stimulatory effects on *Scenedesmus* (Hootsmans and Blindow, 1994). These findings indicate that the release of allelopathically active compounds in *Chara* is species specific. They further point out that such effects might be possible *in situ*. However, we are still lacking conclusive field evidence for the proposed allelopathic activity of *Chara*. New evidence for allelopathy in *Chara* was provided recently by van Donk and van de Bund (2002).

Tuft-forming *Cladophora* species are frequent both in running and stagnant waters. They can form big mats, competing with other macroalgae or macrophytes for light and space. They also suffer from dense epiphyte cover. Extracts of *C. glomerata* lowered the photosynthetic rates of epiphytic *Nitzschia* sp. (Dodds, 1991). Low epiphyte densities were also found on *Spirogyra* and may be related to tannin-like compounds present

in viable cells of this macroalga (Pankow, 1961; also see Section IV.A). Furthermore, positive allelopathic interactions were described for *Spirogyra*. Aqueous extracts stimulated growth and microcystin production in *Oscillatoria agardhii* (Mohamed, 2002). *Oscillatoria* formed only blooms in irrigation channels when *Spirogyra* was present.

C. Microalgae

Only few recent studies reveal allelopathic interactions of freshwater microalgae. Inderjit and Dakshini (1994) published a review on algal allelopathy. Many algae or cyanobacteria produce a distinct pattern of volatile organic compounds (VOC). Their ecological role is largely unknown. To test whether they are allelopathically active, various VOC commonly found in cyanobacteria and algae were used as synthetic compounds in an agar diffusion assay, and they inhibited *Chlorella pyrenoidosa* (Ikawa et al., 2001). However, the concentrations needed were extremely high (up to 10 mg/ml, equivalent to the mM range), and the bioassay design does rather implicate a direct effect on the cells and not via airborne chemicals.

In contrast to marine dinoflagellates, those living in freshwater are generally considered to be nontoxic and harmless algae. *Peridinium gatunense*, a bloom-forming dinoflagellate in Lake Kinneret, Israel, influences toxin production in *Microcystis* sp., bloom-forming cyanobacteria in this lake (Vardi et al., 2002, and see Section III.D). *P. bipes* was also shown to have an algicidal effect on *M. aeruginosa* (Wu et al., 1998). *P. aciculiferum* caused cell lysis of the cryptophyte *Rhodomonas lacustris* (Rengefors and Legrand, 2001). This cryptophyte is a naturally co-occurring competitor for *P. aciculiferum*. The authors suggest that allelopathy in this dinoflagellate is an adaptive strategy to outcompete other winter phytoplankton.

D. Cyanobacteria

Cyanobacteria may be dominant in both pelagic and benthic freshwater habitats. They can

produce effective allelochemicals interfering with the growth of competing cyanobacteria and algae. The control of photoautotrophic biofilms by allelopathic interactions was recently reviewed by Jüttner (1999), with special emphasis on benthic cyanobacteria. Further references are given in Gross (1999). Bloom-forming pelagic cyanobacteria are well known for their neuro- or hepatotoxic metabolites (Ostensvik et al., 1998; Skulberg, 2000; Kaebnick and Neilan, 2001). The ecological role of these cyanotoxins, especially with regard to allelopathy, is debated. The dominance of a colonial cyanobacterium in an acidic Swedish lake, *Merismopedia tenuissima*, was thought to depend on allelopathical control of other phytoplankton species (Blomqvist, 1996). Because not much is known on allelopathic interactions of bloom-forming cyanobacteria, I have included all available studies on the potential allelopathic activity of cyanotoxins in this review. Reference to allelopathically active nonbloom-forming or benthic cyanobacteria is provided in this section and in Section IV.B.

The benthic cyanobacterium *Scytonema hofmannii* produces cyanobacterin, an effective allelochemical-inhibiting cyanobacteria (Gleason and Paulson, 1984), eukaryotic algae (Gleason and Baxa, 1986), and higher plants (Gleason and Case, 1986). A second chlorinated aromatic compound with algicidal activity was later isolated from this cyanobacterium (Lee and Gleason, 1994). No further reports on halogenated secondary metabolites in freshwater cyanobacteria exist to date. The mode of action of these lipophilic, low-molecular-weight secondary metabolites is inhibition of photosystem II (see Section IV.B). Cyanobacterin is toxic to a variety of higher plants when applied as spray on the leaves but not via root uptake (Gleason and Case, 1986). The floating macrophyte *Lemna gibba* was severely inhibited when cyanobacterin was added in concentrations as low as 2.3 μM to the cultivation medium (Gleason and Case, 1986).

Members of the genus *Fischerella* (especially *F. ambigua* and *F. muscicola*), benthic cyanobacteria, exhibit allelopathic activity toward many cyanobacteria and eukaryotic algae, but almost none against bacteria. *F. muscicola* UTEX 1829 was the most active strain in a screening of 65

filamentous, nitrogen-fixing cyanobacteria for cyanobactericidal compounds (Flores and Wolk, 1986). *Fischerella* strains were also the most active species in a screening of new cyanobacterial isolates from Australia and Asia for allelopathy against chlorophytes and cyanobacteria (Schlegel et al., 1998). *F. muscicola* apparently produces cyanobactericidal metabolites at all growth stages (Srivastava et al., 1999). The major inhibitor fischerellin A was isolated (Gross et al., 1991), and its structure identified to contain an enediyne moiety and two heterocyclic ring systems (Hagmann and Jüttner, 1996). Other minor compounds with similar chemical and physiological characteristics are present in *Fischerella* (e.g., fischerellin B), which has only one heterocyclic ring and a similar side chain as fischerellin A (Papke et al., 1997). The alkaloids 12-epihapalindole E isonitrile from *Fischerella* and calothrixin A from *Calothrix* inhibited RNA synthesis of various organisms (Doan et al., 2000), indicating another mode of action for allelopathically active secondary metabolites in cyanobacteria.

Exudates of the filamentous cyanobacterium *Trichormus doliolum* inhibited other cyanobacteria and some chlorophytes (von Elert and Jüttner, 1996). The inhibition was enhanced when the donor species was kept in phosphorus limitation, and target species were more susceptible to inhibition under light limitation. Allelochemicals in exudates from phosphorus-limited *T. doliolum* cultures inhibited *Anabaena variabilis* ATCC 29413 even when the biomass of this target species was 20-fold greater (von Elert and Jüttner, 1997).

Oscillatoria sp. produced and released allelopathically active compounds inhibiting other cyanobacteria and chlorophytes but not heterotrophic organisms (Chauhan et al., 1992; Bagchi et al., 1993). Later, a lipophilic low molecular inhibitor of photosystem II from *Oscillatoria late-virens* was isolated (Bagchi et al., 1993; Bagchi, 1995). Nutrients interfered with the production of these allelopathically active compounds (Ray and Bagchi, 2001). *Nostoc linckia* produced and released another allelochemical named cyanobacterin LU-1 that inhibited the growth of many cyanobacteria and eu-

karyotic algae but not heterotrophic bacteria and fungi (Gromov et al., 1991). *Nostoc* strain 31 produces cyclic heptapeptides, nostocyclamide and nostocyclamide M, which are allelopathically active against cyanobacteria and algae (Todorova and Jüttner, 1995; Jüttner et al., 2001).

Several bloom-forming, pelagic cyanobacteria produce cyanotoxins, neurotoxins such as anatoxin and hepatotoxins such as microcystins (see Carmichael, 1992; Skulberg, 2000). These toxins act primarily on vertebrates, and there is little evidence that intact cells release these compounds in significant concentrations to the surrounding medium. The physiological, ecological, and evolutionary aspects of cyanotoxin production for the producing cyanobacteria is not well known (Kaebernick and Neilan, 2001), although some reports indicate allelopathic activity in *Microcystis* (Lam and Silvester, 1979), and see Maestrini and Bonin (1981) for discussion. *Chlorella pyrenoidosa* was inhibited by lipids from *Microcystis aeruginosa* (Ikawa et al., 1996). The compounds responsible for the observed allelopathic effect were linoleic and linolenic acid. Other studies caution against the bioactivity of these fatty acids, since they may oxidize during the bioassay procedure (Aliotta et al., 1990; Aliotta et al., 1991).

Recently, anatoxin and microcystin LR from *Anabaena flos-aquae* were reported to be involved in chemical signaling between competing phytoplankton organisms, that is, *A. flos-aquae* and *Chlamydomonas reinhardtii*, a flagellated unicellular chlorophyte (Kearns and Hunter, 2000; Kearns and Hunter, 2001). Extracellular products of *A. flos-aquae* inhibited the growth of *C. reinhardtii* but not *vice versa*. Microcystin LR but not anatoxin used as purified compound inhibited growth of the chlorophyte. *C. reinhardtii* and the extracellular products of this chlorophyte had no impact on microcystin LR, but significantly increased the anatoxin content in *A. flos-aquae* (Kearns and Hunter, 2000). Motility and settling rate of *C. reinhardtii* were temporarily increased in the presence of purified cyanotoxins or extracellular products from *A. flos-aquae* (Kearns and Hunter, 2001). However, there is some inconsistency in the two studies concerning the extracellular concentration of the cyanotoxins, and at present it may as well be that other, not yet

identified allelochemicals in the exudates of *A. flos-aquae* are responsible for the inhibition of motility and growth in *C. reinhardtii*. Exudates from *C. reinhardtii* inhibited heterocyst formation in *A. flos-aquae* (Kearns and Hunter, 2002).

Allelopathic activity of an unidentified microcystin was suggested by Singh et al. (2001). Photosynthetic oxygen evolution, $^{14}\text{CO}_2$ -carbon uptake and nitrogenase activity of *Nostoc muscorum* and *Anabaena* BT1 were inhibited in concentrations of 25 to 300 μM by a compound strongly resembling microcystin LR based on TLC and HPLC findings. No final identification of the active compound was made. The concentration of the microcystin-like compound used was, however, at the upper limit of or even above microcystin concentrations found in German lakes (Fastner et al., 1999). Microcystin LR was considered allelopathically active against various submersed macrophytes (Pflugmacher, 2002). Kasumigamide, a tetrapeptide isolated from *M. aeruginosa*, inhibited green algae at concentrations of approx. 2.5 mM (MIC), thus also well above possible natural concentrations (Ishida and Murakami, 2000).

A novel allelopathic mode of action was discovered recently whereby exudates from *Microcystis* inhibited photosynthesis of the dinoflagellate *Peridinium gatunense* by interference with its internal carbonic anhydrase activity (Sukenic et al., 2002). Microcystin LR is apparently not responsible for this action, since this mechanism occurred also with strains not producing this heptapeptide. Exudates also induced oxidative stress in *P. gatunense* and activated certain protein kinases (Vardi et al., 2002). Interestingly, both *Microcystis* and *P. gatunense* exerted reciprocal, density-dependent allelopathic activity. In the presence of *P. gatunensis*, *Microcystis* cells lost buoyancy, followed by cell lysis and a dramatic increase of McyB, a subunit of the peptide synthetase complex involved in microcystin biosynthesis (Vardi et al., 2002). These two species might be a highly interesting model system for aquatic allelopathy: both occur in the same lake, exudates exerted the allelopathic activity, and the modes of action could be identified using modern physiological and molecular techniques.

IV. MODES OF ACTION

Allelochemicals can interfere with many processes of target organisms (see, e.g., Reigosa et al., 1999; Einhellig, 2001). From the above-mentioned studies it is apparent that allelopathically active compounds are often directed at two physiological processes, photosynthesis and enzyme activity. Only those are considered in detail in the following.

A. Inhibition of Enzymes

Enzyme function is essential for all organisms. Many aquatic organisms produce extracellular enzymes that enable them to use complex substrates or are involved in the colonization of surfaces (Chróst, 1991; Wetzel, 1991). Interference with these enzymes can alter competitive interactions among organisms, change the settling of organisms, and interfere with biofilm formation and/or epiphyte growth.

Many microalgae and cyanobacteria produce glycosidase (Cannell et al., 1987) and protease inhibitors (Cannell et al., 1988b), some are released into the culture medium. Approximately 20% of all isolates of filamentous cyanobacteria from biofilms in Taiwan possessed α -glucosidase inhibitory activity, as well as allelopathic activity and grazer toxicity (Jüttner and Wu, 2000). Pentagalloylglucose was identified as the major inhibitor of α -glucosidase from the chlorophyte *Spirogyra varians* (Cannell et al., 1988a). Further, tetra- to undecagalotannins were isolated from *Spirogyra* at concentrations of 2 to 6% of the dry mass (Nishizawa et al., 1985). Most hydrolyzable polyphenols effectively complex proteins, and thus might inhibit enzymes (Haslam, 1989). The occurrence of hydrolyzable polyphenols in chlorophytes is limited to species belonging to the 'phragmoplast' group (see Sawitzky and Grolig, 1995; Pickett-Heaps et al., 1999) such as *Spirogyra*. Tannins are stored in vacuoles of this filamentous chlorophyte, comparable to higher plants. Another extracellular, low-molecular-weight α -amylase inhibitor was isolated from *Anabaena flos-aquae* (Winder et al., 1989).

Tellimagrandin II and other hydrolyzable polyphenols present in and released by the freshwater submersed angiosperm *Myriophyllum spicatum* are effective inhibitors of alkaline phosphatase (Gross and Sütfield, 1994; Gross et al., 1996; Gross, 1999). The inhibitory activity of complex polyphenols was much larger than comparable amounts of the simple phenolic compound gallic acid (Gross et al., 1996).

B. Allelochemicals Affecting Photosynthesis

The inhibition of photosynthesis, the central physiological process of competing primary producers, is an effective defense strategy of many aquatic angiosperms, algae, and cyanobacteria. Methods used by several authors to investigate the impact of allelochemicals on photosynthesis focus either on measuring oxygen evolution with Clark-type electrodes, or carbon incorporation with the radiocarbon method. The former allows a more detailed study of the site of inhibition because artificial electron acceptors and donors allow a decoupling of photosystem I and II (PSI and PSII), and comparison with known synthetic herbicides. These studies indicate that the majority of the allelochemicals interfere with PSII. However, in most cases they act at different sites than most synthetic herbicides, whose primary target is the quinone-B binding site (Trebst et al., 1984; Ohad and Hirschberg, 1990; Huppatz, 1996). This confirms that natural herbicides exhibit a wider range of target sites than synthetic inhibitors (Duke et al., 2001).

1. Cyanobacteria

A recent review summarized allelochemicals affecting photosynthesis produced by cyanobacteria (Smith and Doan, 1999), indicating that this mode of action is widespread among cyanobacteria. Conversely, in a large screening of cyanobacteria, Schlegel et al. (1998) concluded that bioactivity directed against algal photosynthesis might be relatively rare because of differential effects observed under photoautotrophic or heterotrophic conditions.

Yet, no direct measurements of photosynthetic electron transport were made in this study. Lipophilic inhibitors produced by benthic cyanobacteria are best investigated for their impact on photosystem II of other cyanobacteria and algae. Cyanobacterin from *Scytonema hofmannii* (Pignatello et al., 1983) inhibits PSII at the oxidizing site of the quinone-B electron acceptor, but not at the site where DCMU (3-(3,4-dichlorophenyl)-1,1-dimethylurea) interacts with PSII (Gleason and Paulson, 1984; Gleason and Baxa, 1986; Gleason and Case, 1986; Gleason et al., 1986). Electron microscope studies revealed that cyanobacterin also specifically disrupted the thylakoid membrane structure in *Euglena gracilis* (Gleason, 1990). These findings show that allelopathically active compounds may have multiple modes of action, as was postulated before (Einhellig, 1995; Einhellig, 2001).

Fischerellin A isolated from *Fischerella muscicola* inhibited PSII (Gross et al., 1991; Srivastava et al., 1998) and acted at four different sites in PSII with different times of interaction (Srivastava et al., 1998). PSII of cyanobacteria and eukaryotic algae but not of purple bacteria was affected by fischerellin A. Many other cyanobacteria inhibit photosynthesis, and some of the allelochemicals involved act specifically on PSII. Examples are allelochemicals released by *Trichormus doliolum* (von Elert and Jüttner, 1997) or the inhibitor isolated from *Oscillatoria late-virens* (Bagchi, 1995).

2. Macrophytes

Aqueous extracts, possibly including phenolic allelochemicals, from the marine angiosperm *Zostera marina* decreased the primary production of epiphytic diatoms (Harrison and Durance, 1985). For freshwater systems, the cyclic sulfur compounds dithiolane and trithiane from *Chara globularis* are the best known allelochemicals affecting carbon uptake by cultured diatoms and natural phytoplankton assemblages (Wium-Andersen et al., 1982). In a later study, the same author proposed that a labile sulfur compound in *Ceratophyllum demersum* was responsible for the observed reduction in primary productivity and concluded that elemental sulfur released from these

labile compounds might be the ultimate cause (Wium-Andersen et al., 1983). Whether sulfur is also the effective allelochemical in *Chara* has never been investigated. Exudates of *C. demersum* inhibited PSII but not growth of algae and cyanobacteria (Körner and Nicklisch, 2002).

Extracts and exudates from *Myriophyllum spicatum* inhibit photosynthesis of various cyanobacteria, chlorophytes, and diatoms (Körner and Nicklisch, 2002; Leu et al., 2002). Using dialysis membranes and controlling for nutrient competition, Körner and Nicklisch (2002) showed that *M. spicatum* causes species-specific effects in a range of cyanobacteria, chlorophytes, and diatoms and inhibits both growth and PSII in natural relevant concentrations. The mechanism of interference with PSII was studied in detail by Leu et al. (2002). Lipophilic extracts and purified tellimagrandin II interfered with photosynthetic electron transport of the cyanobacterium *Anabaena* sp. PCC 7120. Tellimagrandin II and/or other polyphenols in *M. spicatum* probably cause a higher redox midpoint potential for the non-heme iron, located between the primary and the secondary quinone electron acceptors, Q_A and Q_B in PSII. This mode of action is different from those of synthetic herbicides, apparently a common characteristic of many natural herbicides (Duke et al., 2000).

V. BACTERIAL MEDIATION/BIOFILM

From the above-mentioned studies it is apparent that many allelopathic interactions in aquatic systems occur surface-associated, either in benthic communities or between photoautotrophs and their epiphytes. Benthic algal or cyanobacterial mats and epiphytic communities are complex systems, differing, for example, in stratification or recycling capacity (Peterson and Tuchman, 1992; Wetzel, 1993). Biofilms are formed through a complex succession of organisms, usually starting with carbohydrates, followed by bacteria, photoautotrophs, and animals (Wahl, 1989). Microorganisms, thus bacteria and fungi, are explicitly incorporated in the original definition of allelopathy by Molisch (1937). However, we have only little insight into the role of bacteria

in allelopathic interactions of aquatic primary producers. The following section presents some information on allelopathic interference between bacteria and aquatic photoautotrophs.

Several cyanobacteria produce antibiotic compounds against heterotrophic bacteria (Borowitzka, 1995; Ostensvik et al., 1998; Kreitlow et al., 1999; Skulberg, 2000). Some planktonic cyanobacteria (*Aphanizomenon flos-aquae*, *Cylindrospermopsis raciborskii*, *Microcystis aeruginosa*, *Tychonema bourrellyi*) exhibited extractable antibiotic activity in various bioassay systems (Ostensvik et al., 1998). A strain of *Phormidium* produced extracellular antimicrobial compounds inhibiting a wide range of Gram-positive and Gram-negative heterotrophic bacteria (Fish and Codd, 1994b).

Although bacteria do not compete with cyanobacteria for light or most nutrients, they may enhance attachment of other primary producing microalgae on benthic cyanobacterial mats. *Nostoc muscorum* produced antibiotic and antifungal compounds of medium molecular weight (M_r 2000 to 3000) (Bloor and England, 1989). The release of these compounds into the culture medium was controlled by nitrate and iron (Bloor and England, 1991). However, it has never been investigated whether these antibiotic compounds are ecologically relevant in preventing or delaying the development of biofilms. Direct interactions between bacteria and certain cyanobacteria have been described. Bacteria co-occurring with *Microcystis aeruginosa* exhibited a higher attractance to this cyanobacterium than to other cyanobacteria and were less inhibited by exudates (Casamatta and Wickstrom, 2000). The marine bacterium *Pseudoalteromonas tunicata* effectively inhibited algal spore germination through extracellular inhibitors (Egan et al., 2001a; Egan et al., 2001b). Some marine fungi growing epiphytically on the surface of macroalgae produce algicidal compounds inhibiting the growth of microalgae (Chen et al., 1996; Jenkins et al., 1998). Hence, in some instances not the host plant itself but associated microorganisms account for allelopathic effects.

To avoid bacterial metabolization of allelochemicals, many studies use axenic organisms. Axenic [Greek] meaning "without strangers" was originally coined as term by Baker and

Ferguson (1942). Bacterial metabolization of allelochemicals released by plants happens frequently. Juglone would not be active without the glycosidase activity of soil bacteria. Non-axenic *Fischerella tisserantii* (Cyanobacteria) contained lower concentrations of fischerellin A compared with the axenic strains *F. ambigua* and *F. muscicola* (Gross et al., 1991; Gross, unpublished results). Exudates of *Myriophyllum spicatum* lose their inhibitory activity on algae and cyanobacteria over time, indicating bacterial degradation (Gross et al., 1996; Nakai et al., 1999).

VI. ABIOTIC INTERFERENCE

A. Nutrient Stress

Allelopathy is considered to be especially effective in stress situations (Reigosa et al., 1999), for example, under nutrient limitation. Target organisms might be more susceptible to allelochemicals under stress, and/or donor organisms might induce or augment the production of allelopathically active compounds under such conditions.

In the soft coral *Sarcophyton ehrenbergi* (Octocorallia: Acyonaceae) the ratio of allelochemicals to lipids was strongly influenced by the nutrient status of the tissue (Fleury et al., 2000). The active compounds are cembranoid diterpenes, some of which are ichthyotoxic and others may be involved in allelopathic interactions (see Section II.E). Increased nitrogen availability leads to higher ratios, whereas under surplus phosphorus the ratio declined compared with nutrient saturation. At times of greatest coral growth, more nitrogen resulted in more biomass production of the zooxanthellae and less transfer of metabolites to the coral. In response, the terpenoid biosynthesis of the latter increased (Fleury et al., 2000).

Fitzgerald (1969) recognized that nitrogen limitation but not phosphorus limitation caused a decline in epiphyte growth on various macroalgae and aquatic angiosperms. He considered either a "nitrogen sink" effect or antagonistic (allelopathic) interference to be responsible for the inhibition of epiphytes in cultures of *Myriophyllum* sp., *Ceratophyllum* sp., *Lemna minor*, *Cladophora* sp., and *Pithophthora oedogonium*. *Myriophyllum*, the

only rooted species in this list, can take up nitrogen both with shoots and roots, depending on the concentrations in the respective compartments (Nichols and Keeney, 1976a). All others obtain nitrogen primarily from the water. *Ceratophyllum demersum* appeared to act as a nitrogen sink, especially in spring (Mjelde and Faafeng, 1997): Many clearwater shallow Norwegian lakes exhibiting low phytoplankton densities, high phosphorus concentrations but indication of nitrogen limitations were dominated by *C. demersum*. Unfortunately, allelopathy was not investigated in this study.

Nutrients frequently interfere with the allelopathic activity of cyanobacteria (von Elert and Jüttner, 1996; von Elert and Jüttner, 1997; Ray and Bagchi, 2001). Phosphorus limitation of phytoplankton and epiphytes during summer is common in many freshwater lakes, even when the lake is eutrophic (Vrba et al., 1993). Polyphenolic allelochemicals present in *Myriophyllum spicatum* interfere with alkaline phosphatase, an exoenzyme used by many algae and cyanobacteria to overcome inorganic phosphorus limitation (Gross et al., 1996; Gross, 1999). The macrophyte obtains phosphorus predominantly through the roots (Best and Mantai, 1978; Carignan and Kalff, 1980; Barko and Smart, 1981), but phytoplankton and epiphytes (Carignan and Kalff, 1982) rely on phosphorus in the water. Thus, the inhibition of alkaline phosphatase provides a competitive advantage for this submersed macrophyte. In contrast to marine systems, freshwater phytoplankton is seldom nitrogen limited (Weithoff and Walz, 1999; Wetzel, 2001). *M. spicatum*, yet, was frequently reported to be nitrogen limited (Nichols and Keeney, 1976b; Barko and Smart, 1986; Sytsma and Anderson, 1993). Algicidal polyphenols in *M. spicatum* are inversely related to tissue nitrogen (Gross, 1999; Gross, unpublished results). Especially active growing tissues (apical meristems) have high spring and summer levels of polyphenols, whereas in fall polyphenols decline and nitrogen tissue concentration increases. The differential responses of the donor organism (*M. spicatum*) and target organisms (phytoplankton, epiphytes) to phosphorus and nitrogen limitation strongly affects the allelopathic interactions in this system. Because nutrients often

interfere with allelopathic interactions, Inderjit (1997) recently asked whether it is realistic to separate resource competition from allelopathy.

B. Other Environmental Impacts

The soft coral *Sinularia flexibilis* produces allelochemicals preventing the growth of bacteria and algae on its surface (Aceret et al., 1998). Bleaching caused a loss of zooxanthellae in this coral, and resulted in a short-term loss of the principal algicidal terpenoid sinulariolide to 8% compared with controls (Michalek-Wagner and Bowden, 2000). In contrast, the levels of the antibacterial secondary metabolite flexibilid more than doubled. Surprisingly, low levels of algicide did not result in increased algal growth on the surface of *Sinularia* (Michalek-Wagner and Bowden, 2000). Considering the succession of epibionts (see above Wahl, 1989), bacteria have to colonize first before algae will attach. In this context, stressed *S. flexibilis* would reallocate the secondary metabolites to the primary target of epibiosis (bacteria) and still get sufficient protection against algal overgrowth. More studies are needed to investigate the mutual effect of bacteria and algae in aquatic biofilms. Important insights are currently emerging from the study of the rhodophyte *Delisea pulchra* and its secondary metabolites that interfere with bacterial quorum-sensing signals (Kjelleberg et al., 1997; Rice et al., 1999; Charlton et al., 2001; Steinberg et al., 2001).

Terrestrial humic compounds are frequently reported to disturb aquatic communities (phytoplankton, macroalgae, higher plants) both in marine and freshwater systems (Inderjit and Gross, 2002). Precipitation run-off from land to water is one possibility how terrestrial vegetation can impact aquatic primary producers. Lower run-off of forest humic compounds caused a shift in the macroalgal community structure from phaeophytes to crustose coralline rhodophytes on the coast of Japan. Laboratory experiments showed that allochthonous humic compounds inhibit crustose coralline spore germination and promoted phaeophyte oogonium formation, the latter probably through complexation of iron by fulvic acids (Matsunaga et al., 1999).

After release, allelochemicals are subjected not only to biotic metabolism but also to abiotic factors. Light, oxygen, and redox conditions might influence the stability of allelochemicals. Transformations such as oxidation, polymerization, or cleavage can take place. Ultraviolet radiation caused a different photoreactivity of leachates from two freshwater macrophytes (Farjalla et al., 2001).

VII. MATHEMATICAL MODELING

Few authors have been modeling allelopathic interactions based on field or experimental data (Chao and Levin, 1981; Antonelli et al., 1993; Cheng, 1995; Mukhopadhyay et al., 1998; Tapaswi and Mukhopadhyay, 1999; An et al., 2002; An et al., 2003). Such studies generally have to simplify processes, which may not always be satisfactory. However, models can help to clarify patterns of species interactions and guide further experiments. Allelopathy among bacteria, that is, antibiotic activity, strongly differed whether they were grown in liquid culture or on agar, a two-dimensional, structured habitat (Chao and Levin, 1981; Wiener, 2000). On agar, allelochemical-producing *Escherichia coli* had an advantage over competing bacteria even at low initial densities (Chao and Levin, 1981). Allelopathic interactions in phytoplankton communities were modeled by Mukhopadhyay et al. (1998) and Tapaswi and Mukhopadhyay (1999). Their models are based on two species Lotka-Volterra competitive systems where both species had competitive and allelopathic interactions. Allelopathic interference between soft and scleractinian corals was described based on the mathematical theory of Volterra-Hamilton systems (Antonelli et al., 1993). Scleractinians had the highest survival when they took refuge in space and evaded direct toxic effects of soft corals. The model predicted no co-evolution leading to the neutralization of the allelopathically active terpenes by the target organisms. This outcome is remarkable in the context of Reigosa et al. (1999), who hypothesized that allelopathy between species in one habitat is rare because of tolerance toward allelochemicals present in this system (see Section I.B).

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