

Allelopathic Inhibition by Exudates from Autotrophs - A Review

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ABSTRACT

Allelopathy is the release of chemicals by one species that affect other species in its vicinity, usually to their detriment. The allelopathic potential of exudates from plants has been known as early as 370 B.C. Field evidence and laboratory studies indicate that allelopathy occurs in all aquatic habitats and that all primary producing organisms are capable of producing allelopathically active compounds. Allelochemicals may inhibit photosynthesis or protein activity of target species, modify or activate its other physiological functions, damage cell membranes, kill the competitor or exclude it from donor vicinity. The present work highlights allelopathy as an important process in ecology.

Key words: Allelopathy, exudates, allelochemicals, photosynthesis, membrane, competitor, donor

INTRODUCTION

The term 'allelopathy', originating from the Greek words allelon (= of each other) and pathos (=to suffer), was introduced by Molisch (1937) to describe the biochemical interactions between all types of plants and microorganisms. Rice (1984) modified the definition to refer to any direct or indirect harmful or beneficial effect of one plant or microorganism on another through chemicals that are released into the environment. Most recently, allelopathy was formulated as 'any process involving secondary metabolites produced by plants, algae, bacteria, and fungi that influence the growth and development of agricultural and biological systems.

Competition for resources can occur as exploitation and / or interference. Exploitation means the direct use of a resource, reducing its availability to a competing individual or species. In interference, access to a resource is denied to competitors by the dominant individual or species, due to release of antibiotics, territorial behavior and social hierarchies. Allelopathy is an example of

interference competition with a passive character (Reigosa *et al.*, 1999), compared with e.g. territorial behavior. The Allelopathic organisms release chemicals that inhibit the growth of a competing organism and thus indirectly prevent it from using common resources.

Due to the economic importance of agricultural and forest ecosystems, terrestrial allelopathy has been widely studied (Rice, 1984). In aquatic environments, studies are complicated e.g. by the high diffusive potential of compounds, as well as difficulties in collecting and culturing the organisms. Definitive evidence for allelopathy in the field is almost impossible to obtain due to the complexity of natural interactions. However, allelopathy is considered as important process that occurs among all groups of marine and freshwater primary producers (Gross, 2003; Legrand *et al.*, 2003). Most of the studies on aquatic allelopathy have focused on freshwater Macrophytes, but the interest in Allelopathic interactions within the phytoplankton has recently been kindled.

EVOLUTION OF CONCEPT

Early observations and experimentations in allelopathy were based on the concept that Allelopathic donor plants release allelochemicals (from root exudates, volatiles from above ground components or decaying plant litter) in the environment that interferes with the growth of nearby plants. From this, the donor plants would gain competitive advantage, out-compete their neighbours and bring about individual and population level changes. Molisch (1937) demonstrated, with simple laboratory experiments, that toxic volatile (ethylene) from plant (apple) can affect the growth (wilting, bud and root inhibition of stem cutting) of other plants. From this he cautiously speculated that chemicals of plant origin (allelochemicals) have potential for bringing about population level change by affecting the growth of neighboring plants. He named this phenomenon as allelopathy and became the father of allelopathy.

ALLELOCHEMICALS AS WEED CONTROL AGENTS

There are several approaches to weed control, most popular being total elimination of weeds by chemical herbicides widely practiced in industrial agriculture. There are potent allelochemicals in plants (Nimbal *et al.*, 1996) but the chance of finding allelochemicals that can be used as industrial bioherbicides for successful weed control is not good (Duke *et al.*, 2001). However, microbially synthesized herbicides such as bialophos has been in the market for several years showing success in weed control in agriculture and forestry (Jobidon, 1991). The second approach is using Allelopathic plants as mulch, cover crop, row crop etc

that take advantage of not just the chemicals inhibiting seed germination and growth of crops but its biomass which physically suppress weed growth. This method does not aim for complete eradication of weeds by chemicals but rather allows coexistence of competing plants with much reduced vigor. The biomass added to the soil in this practice incorporates organic matter to the rhizosphere which influences the soil microbial ecology and nutrient conditions. Traditional agriculture has been making use of this approach of weed control and there is room for further improvement through research.

TERRESTRIAL AND AQUATIC ALLELOCHEMICALS

Generally allelopathic interactions in aquatic habitats resemble those in terrestrial systems, although some fundamental differences exist. One major difference is that most aquatic photoautotroph's are surrounded by water instead of air. Allelochemicals released by donor organisms into the water need to be sufficiently hydrophilic and reach their target organism in effective concentrations despite considerable dilution. Algae, cyanobacteria, and fully aquatic angiosperms are leaky may be even more than terrestrial plants. Submerged leaves of aquatic angiosperms have no stomata, a reduced cuticle, 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 cuticle. However, leakage through open stomata or from epidermal cells may occur. Allelopathic interactions of aquatic photoautotroph's may also occur via root exudation. Commonly, simplified model systems are used to evaluate allelopathic root exudates (Gallardo *et al.*, 1998). Physico-chemical processes in root compartments (or terrestrial plants) are diverse and may be complex. Aerobic microzones around roots of aquatic angiosperms are small (approx. 1mm), but may significantly alter the redox potential of the soil (Flessa, 1994). Certainly, these microzones have an impact on the transfer of allelopathically active bioactive metabolites in the rhizosphere and around roots were discussed by Neerí *et al.* (2000). Two different types of Allelopathic interactions occur in the 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) 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 a major problem in

this type of allelopathic interaction . Secondly, in aquatic environment we are dealing with aquatic 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, epiphytes, and /or phytoplankton. 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 other wise associated with the surface of the plant. Wetland plants are at the interface of terrestrial and aquatic systems. Some of them have allelopathic properties (Elakovich and Wooten, 1989).

AQUATIC ALLELOPATHY

Allelopathy has been observed in a number of aquatic autotrophs. Allelopathy in marine ecosystems may occur between phytoplankton species or in benthic areas where macroalgae, corals, and a few species of angiosperms are present. Angiosperms, macroalgae, and corals produce inhibitory compounds interfering with epiphytes and other epibionts, competing for light and / or space. Only few aquatic angiosperms live in marine littoral areas. *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 like that phenolic allelochemicals were responsible for the observed effect (Quackenbush *et al.*, 1986). *Ruppia maritima* (Potamogetonaceae) growing in brackish or salt water produces antialgal diterpenes (Della Greca *et al.*, 2000).

Allelochemicals interference of macroalgae with microalgae has long been known (Shapiro, 1957; Sieburth, 1968). Prevention of epiphyte growth on macroalgal tissue by Allelopathic mechanisms occurs frequently. Extracts of various macroalgae inhibited the settlement and growth of chlorophyte *Enteromorpha porifera* (Young Cho *et al.*, 2001) a common epiphyte on other macroalgae. Crustose algae are prone to standing 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 substance of low molecular weight that destroys zoospores of the phaeophyte *Laminaria religiosa* (Suzuki *et al.*, 1998).

As far as microalgae are concerned most of the 60 to 80 harmful marine phytoplankton species are flagellates, particularly dinoflagellates. 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). 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 *Prorocentrum lima*.

Many dominant species of cyanobacteria for example, *Lyngbya majuscula*, produce bioactive compounds, but no allelopathically active compounds were isolated so far. It was shown that *Nodularia harveyana*, a nitrogen - fixing cyanobacteria 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 especially benthic forms produce allelopathically active compounds, similar activities can be expected in marine benthic cyanobacteria.

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 . The competition for space among some scleractinian corals seems to depend on allelopathy. Corals are sometimes susceptible to the allelochemicals released by neighboring sponges.

In freshwater systems we find allelopathic interactions among photoautotroph's both in pelagic and in benthic or littoral zones. In contrasts to marine benthic areas, freshwater littoral zones are generally dominated by diverse aquatic angiosperms of different growth form, but only few macroalgae occur. Among freshwater angiosperms allelopathic interactions were reviewed by Szczepanska (1987), focussing on interspecific effects of emergent Macrophytes such as *Phragmites australis* and *Typha latifolia*, both growing frequently in the same littoral area. Submerged macrophyte *Ceratophyllum demersum*, a non-rooting, canopy forming angiosperm, showed allelopathic activity towards phytoplankton (Kogan and Chinnova, 1972). Allelopathy has been considered frequently as an adaptive trait of macroalgae *Chara* to prevent dense phytoplankton and epiphyte development. Only a few recent studies reveal allelopathic interactions of freshwater microalgae. Cyanobacteria are toxic to a variety of higher plants when applied as spray on the leaves but not via root intake. The floating macrophyte *Lemna gibba* was severely inhibited when cyanobacteria (Gleason *et al.*, 1986). Exudates of the filamentous cyanobacterium *Trichormus doliolus* inhibited other cyanobacterium and some chlorophytes (Von Elert and Juttner, 1996).

MODE OF ACTION OF ALLELOCHEMICALS

Allelochemicals can interfere with many processes of target organisms. Many aquatic organisms produce extracellular enzymes that enable them to use complex substrates or are involved in colonization of surfaces. (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. The inhibition of photosynthesis, the central physiological process of competing primary producers, is an effective defense strategy of many aquatic angiosperms, algae, and cyanobacteria. Many studies have shown 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. Extracts from *Myriophyllum spicatum* inhibit photosynthesis of various cyanobacteria, chlorophytes, and diatoms (Korner and Nicklisch, 2000). 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.

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