Allelopathy—Chemical Warfare Between Aquatic Plants

By Dr. Ole Pedersen

Think about your first reaction if you saw a poster at your local pet shop announcing **"New Ornamental Plant Kills All Algae in Your Tank Within 24 Hours—Money Back Guarantee!"** *How much would you be willing to spend on such a plant? Unfortunately, no such plant has yet been identified. But it is a scientific fact that some plants secrete chemicals that are toxic to other plants. Can we use such plants in algae control in our aquaria or does it explain why some plants do poorly in our aquaria?*

In 1999, Diana Walstad published perhaps the best book ever written on planted aquaria. In her book *Ecology of the Planted Aquarium,* she devoted an entire chapter to the phenomenon of allelopathy and this has inspired me to go deeper into this fascinating subject (Walstad, 1999). I must also say that my search through the scientific literature has made me more skeptical about the importance of this phenomenon in planted aquaria. I am sure that Diana Walstad in her book exaggerates the prevalence of true allelopathy in planted aquaria.

By definition, allelopathy is the negative influence on other organisms—including higher plants and algae—by excretion of toxic chemicals (Rice, 1984). The ecological benefits of allelopathic behavior are evident. It provides the plant with great competitive advantage with a limited investment in toxic chemicals that are harmless to the plant itself. Allelopathy is rather well documented for a variety of terrestrial plants, but the information on how widespread this phenomenon is among aquatic plants is scanty (Gopal & Goel, 1993).

Allelo-chemicals

Let us first take a closer look at the groups of chemicals are known to play a role in allelopathy. The most important group considered as toxic chemicals produced by plants is the huge group of phenolics including the subgroups of flavonoids and tannins. Flavonoids are phenolic compounds that may be employed by plants as visual and olfactory attractants. Anthocyanins are flavonoids that are the source of most red, pink, purple and blue colors in plant parts, including the many red varieties of *Echinodorus* and *Cryptocorynes.* The epidermis of the leaves of all plants contains flavonoids that protect against UV-B radiation (280–320 nm). These compounds absorb light in the UV-B range but allow visible light to pass through uninterrupted for photosynthesis. Flavonoids are also toxic but they are usually not excreted to any significant extent from living plants. On the other hand, the flavonoids may be released to the surroundings when dead plant litter is decomposed. Once released into the environment, the flavonoids may be toxic to other plants and animals but the release of toxic substances from dead material does *not* follow the strict definition of allelopathy.

Tannins are polymerized flavonoids. Tannins are general toxins that reduce the growth and survival of herbivores. They are feeding repellents that bind salivary proteins, and plant parts high in tannins are usually avoided by herbivorous insects. Tannins are therefore considered as a major anti-grazing chemical. However, apples, blackberries, tea and red wine contain tannins, which provide a desirable level of astringency (a dry or puckery sensation). Tannins are used to preserve animal skins because they bind to proteins susceptible to microbial attack, preserving the skins. There is clear evidence that Egyptians used tanned leather to make sandals more than 3,000 years ago. Unfortunately, there is lack of scientific evidence that tannins are released into the environment by living plants to any great extent.

In terrestrial plant communities perhaps the most important allelo-chemical is the group of terpenoids, which is a subgroup of lipids. Camphor belongs to this group and is produced, for example, by *Eucalyptus*. One of the best illustrated cases of allelopathy in terrestrial ecosystems is the production of terpenes (pinene, camphene, camphor, cineole and dipentene) by *Salvia leucophylla.* The terpenes evaporate from the leaves and are subsequently deposited in dew on the nearby vegetation, creating a bare sandy band separating the *Salvia* vegetation from the surrounding vegetation. A puzzling example of the use of allelo-chemicals is the production of terpenes by Milkweed *(Asclepias tuberosa).* The larvae of Monarch butterflies feed on milkweed and accumulate the toxin, which is later found stored in the wings of the butterflies. The butterflies are therefore toxic to predators such as birds.

Finally, the groups of alkaloids (cocaine and quinine), cinnamic acids (cafeic acid in for example potatoes and species of seagrasses, Zapata & McMillan, 1979; Cuny et al., 1995; Vergeer & Develi, 1996) and simple lactones (penicillic acid in fungi) have been shown to act as allelo-chemicals in various organisms.

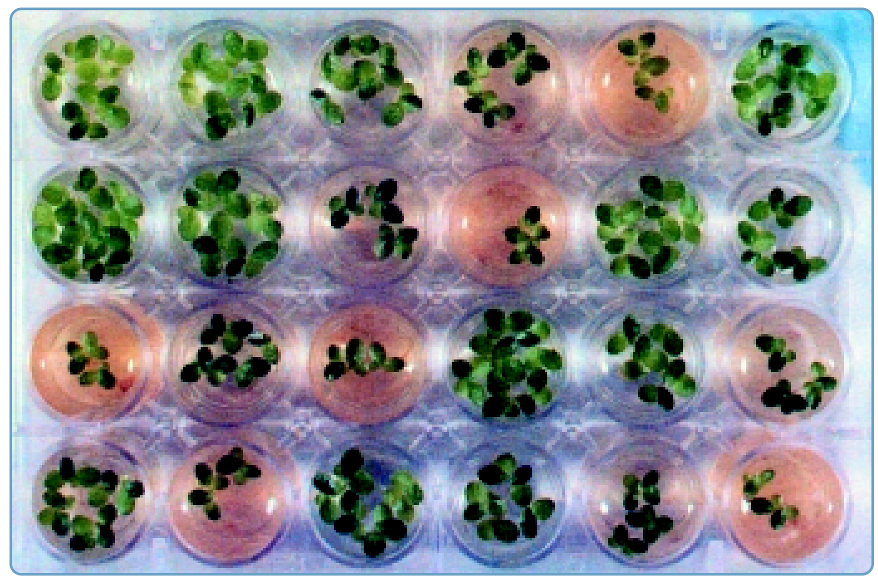
Allelopathy in Aquatic Plants

Experiments designed to demonstrate allelopathy in aquatic plants can be divided into two principally different categories: 1) experiments that include intact plants where the allelo-chemicals are naturally excreted by the tested plants, and 2) experiments where various sorts of plant cell juices are produced, which are subsequently tested for toxicity on living plants or animals.

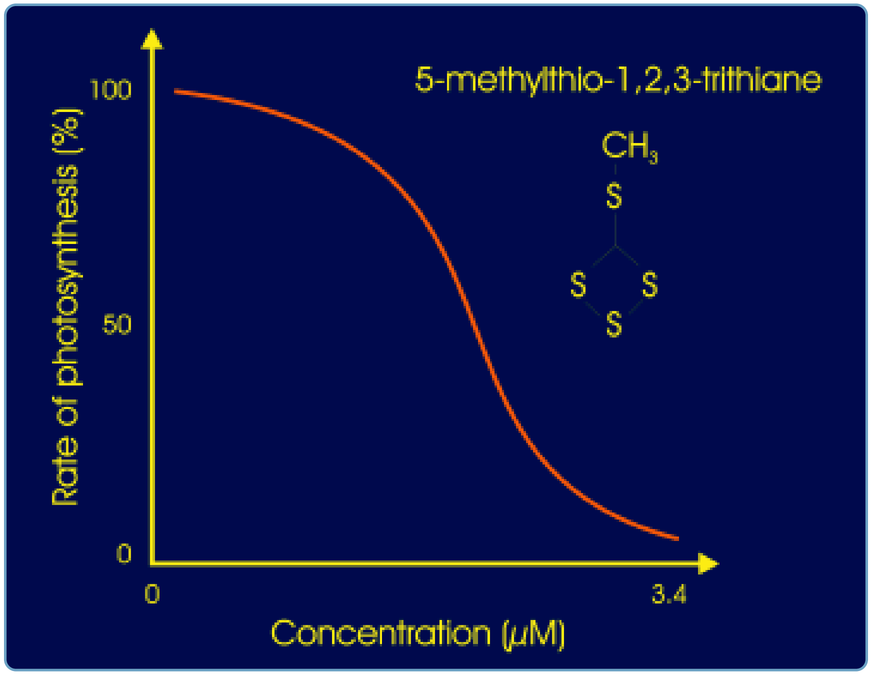
Dr. Stella Elakovich, former professor at the University of Southern Mississippi, has beyond comparison contributed the most to the latter category of experiments.

As a chemist, she has probably been more interested in the detection and identification of the individual chemical compound rather than the ecological relevance of the experiments. A report produced for the US Army Corps of Engineers is found among her comprehensive work (Elakovich & Wooten, 1986). Here, 16 aquatic plant species were tested on two bioassays—one where cell extracts were tested on lettuce seedlings and one on the growth of Duckweed *(Lemna minor).* Six out of the 16 tested species exerted a significant inhibitory effect on the organisms used in the test assay and, in particular, the *Nymphaea odorata* and *Brasenia schreberi* showed high toxicity. In other studies, Dr. Elakovich has used similar approaches and demonstrated that all seven species of Spikerush *(Eleocharis)* inhibited the growth of lettuce seedlings when cell extracts were added to the growth medium (Wooten & Elakovich, 1991). Another aquatic species that always comes out as potentially toxic in such experiments is the Yellow Waterlily *(Nuphar lutea).* Here, the toxins have been isolated and they all belong to the group of alkaloids (Elakovich & Yang, 1996).

Similar studies have been carried out by Wium-Andersen and co-workers and they have shown that the sulfur containing extracts of



A bioassay with *Lemna minor* as test plant. Various aliquots of plants extracts are added to the different cells. One or two fronds are used as inoculums and the total leaf area, the total amount of chlorophyll or the plant dry weight is then measured after a certain incubation time (photo from Elakovich & Wooten, 1986).

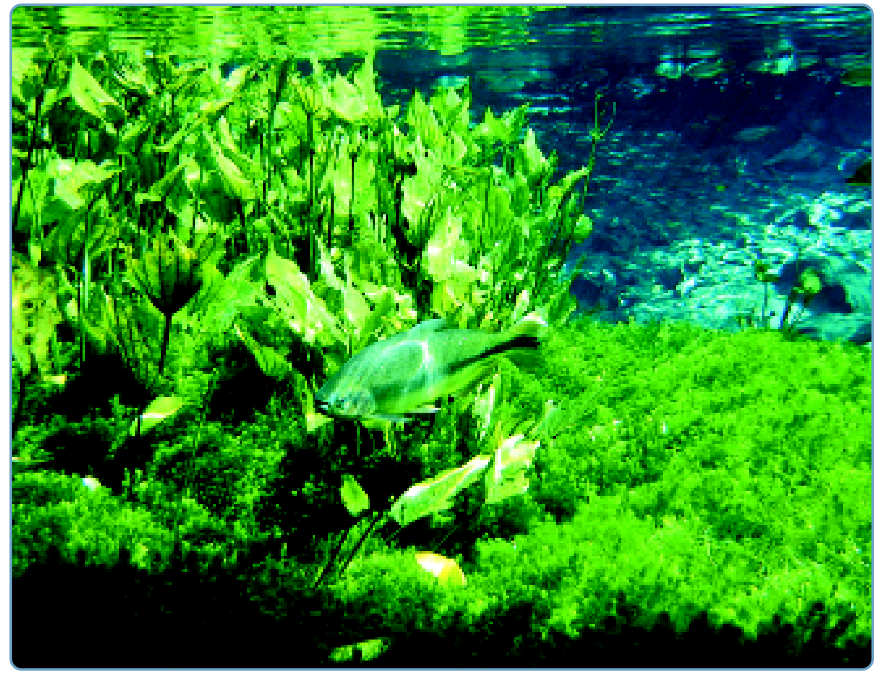


Toxicity curve of a sulfur compound produced by *Chara*. Most *Chara* species synthesize 5-methylthio-1,2,3-trithiane and if it is released to the surroundings, it has a strong negative effect upon microalgae photosynthesis. It may explain why *Chara* in many natural stands avoids epiphytic growth (data from Wium-Andersen et al., 1982).

Nitella, Chara and *Ceratophyllum* inhibit the photosynthesis of natural phytoplankton communities (Wium-Andersen et al., 1982; Wium-Andersen et al., 1983; Wium-Andersen, 1987; Wium-Andersen et al., 1987).

The studies mentioned above are just examples and in Table 1 (pg. 14) most of the tested plants are compiled from the scientific literature. Personally, I do not see much ecological relevance in these kinds of experiments. At best, they may be used to look for potential candidates of true allelopathic behavior because the studies, after all, demonstrate that the plants contain toxic compounds. However, many of these studies take the conclusion much too far and recommend using the plants for aquatic weed management or algae control without the necessary documentation for allelopathic behavior in nature.

A much more interesting and relevant type of allelopathic experiment is the kind where intact plants are used. Unfortunately, these studies are quite cumbersome to perform and they are therefore fairly sparse in the literature.

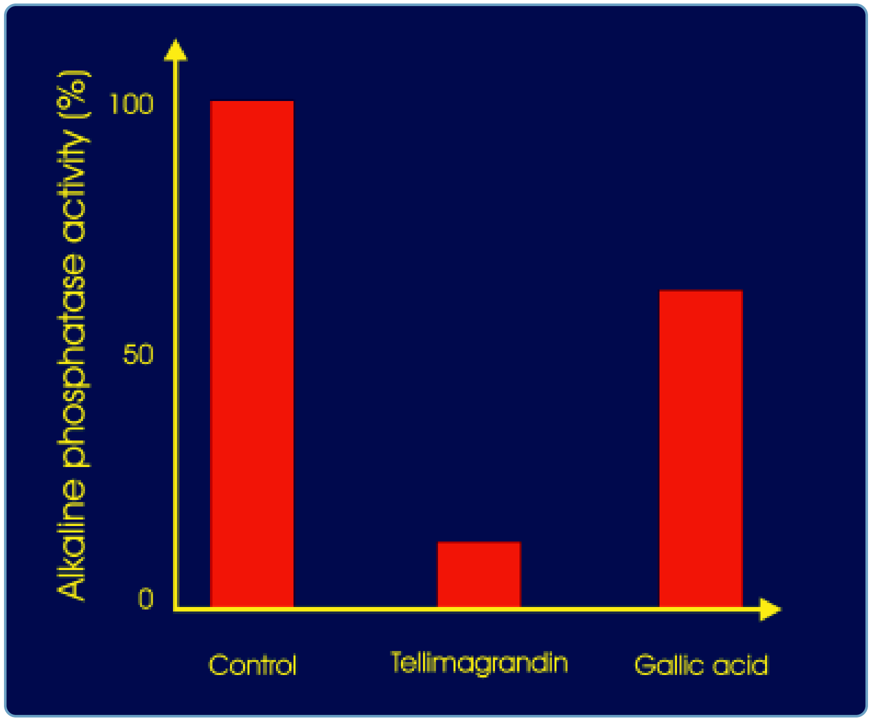


Claus Christensen, Tropica Aquarium Plants

***Echinodorus* standing in a carpet of *Chara*. Species of Characeae is well known to produce toxic substances that may prevent epiphytes from colonizing the thallus surface.**

Dr. Elisabeth Gross from the Limnological Station at University of Konstanz is well known for her outstanding experimental approach to allelopathy among aquatic plants. She has worked with axenic (sterile in the way that the root and leaf surfaces are free of any bacteria, fungi and algae) cultures of *Myriophyllum spicatum* and has succeeded in demonstrating that this fairly common plant excretes phenolic substances under natural circumstances (Gross, et al., 1996). In this particular case, the phenolic compound was tellimagrandin, which has an extraordinarily strong algicidal effect—i.e. a concentration of only 0.2 μ moles per liter inhibited the enzymatic activity in blue-green algae (cyanobacteria) by more than 10%. Her study showed that *Myriophyllum* released up to 0.4 mg toxin per mg dry weight per day and this may be sufficient to reduce the cover of epiphytes on the leaves of *Myriophyllum* under natural circumstances—a conclusion that is also supported by the work of Planas et al. (1981) and Agami and Waisel (1985).

Negative interactions between two species of higher plants have also been shown to take place under standardized conditions. In a meticulous setup, Frank &



Toxicity of *Myriophyllum*-produced phenolic compound. Tellimagrandin is a phenolic compound that is synthesized in *Myriophyllum spicatum*. It has a strong algicidal effect (stronger than the well-known gallic acid) and in this case it inhibits the important exoenzyme alkaline phosphatase in blue-green algae. *Myriophyllum* slowly releases tellimagrandin under natural circumstances and it may thereby prevent the plant from developing a thick cover of epiphytes (data from Gross et al., 1996).

Dechoretz (1980) showed that the negative effect of *Eleocharis coloradoensis* upon the growth of *Potamogeton pecticantus* was caused by root excretion of allelo-chemicals. They constructed an experimental setup to demonstrate that no negative effect was apparent when the two plants shared the same water around the shoot (the two plants were grown spatially separated while the water around the shoot was circulated between the aquaria). On the contrary, a strong allelopathic effect was observed when they circulated the porewater between the two aquaria leading to the conclusion that the allelo-chemicals were excreted by the root of *Eleocharis coloradoensis*.

Algae may also affect higher plants negatively by excreting toxic chemicals, as shown by Sharma (1986) when the water hyacinth *(Eichhornia crassipes)* was grown in water containing a mixed algae culture. The algae culture contained very common genera of algae—for example, *Aphanothece, Chlorella* and *Euglena*. In the presence of these algae, the growth of the water hyacinth was reduced by more than 80% and the plants were slowly dying.

Allelopathy in the Aquarium

In her book *Ecology of the Planted Aquarium,* Diana Walstad lists a number of observations of fish kills, plants dwindling away for no apparent reason and the like. She attributes all these "unexplainable" events to allelopathy in either higher plants or in algae. Personally, I find it unlikely that the following statement has anything to do with allelopathy: "*For example, tanks with heavy plant growth often seem to have very little algae*" (Walstad, 1999). It is much more likely that this general observation is due to efficient competition for resources (light, nitrogen, phosphorus and CO_2) from the higher aquarium plants and this may prevent the algae from ever getting a hold in the tank. A natural question to pose would be: *Can allelopathy be used to control algae growth in the aquarium?* The answer would be NO! One would have to advocate lowering the water exchange, which would be controversial during an algae plague! Only by a very modest water exchange program would the toxic chemicals be able to build up to a significant concentration level required to pose a toxic effect.

Her statement that: "*Some plant species in my tanks dwindle away with time for no apparent reason*" is unlikely to have anything to do with allelopathy. It could be, however it is more likely a matter of general poor growth because the fundamental requirements of the plants are not met in the aquarium.

In fact, Diana Walstad's book only holds one observation that may be attributed to allelopathy. She once experienced a massive fish kill when cleaning the glass of the aquarium from microalgae. Doing so will necessarily rupture many of the algae cells and if they contain toxic chemicals, these will be released into the water, where they may cause the observed fish kill. However, this should not lead anyone to draw the conclusion that you should not clean the glass of the aquarium! If it was a very widespread phenomenon, we would probably have heard about it more often and I think that she was unlucky that her aquarium accidentally developed a toxic biofilm on the glass surface.

Hopefully, this article has provided you with sufficient knowledge so that you are naturally skeptical next time you meet these allegations on miraculous algae control by means of allelopathy. The best algae control will always be a densely planted aquarium with a limited stock of fish combined with frequent water exchange. In particular the last point probably prevents allelopathy from becoming important in planted aquaria since the toxic chemicals never build up to significant concentration levels and

Species Tested	Toxic to
Brasenia schreberi	*Lemna minor*
Cabomba caroliniana	*Lemna minor*
Ceratophyllum demersum	*Lemna minor* (tested but no effect)
Eleocharis acicularis	*Hydrilla verticillata*
Eleocharis geniculata	*Lemna minor*
Eleocharis obtusa	*Lemna minor* (tested but no effect)
Eleocharis parvula	*Lemna minor*
Equisetum fluviatile	*Phragmites australis*
Equisetum limosum	*Phragmites australis*
Equisetum palustris	*Thypa latifolia*
Hydrilla verticillata	*Ceratophyllum demersum*
Ipomoea aquatica	*Pennisetum typhoideum*
Juncus repens	*Lemna minor*
Limnobium spongia	*Lemna minor*
Ludwigia adscendens	*Pennisetum typhoideum*
Myriophyllum aquaticum	*Lemna minor*
Myriophyllum spicatum	*Najas marina*
Najas guadalupensis	*Lemna minor* (tested but no effect)
Nymphaea ordonata	*Lemna minor*
Nymphoides cordata	*Lemna minor*
Nyphar lutea	*Lemna minor*
Peltandra virginica	*lettuce seedlings*
Phragmites australis	*Carex elata*
Potamogeton amplifolius	*Vallisneria americana*
Potamogeton foliosus	*Lemna minor*
Sagittaria graminea	*Hydrilla verticillata*
Sagittaria pygmaea	*rice*
Sagittaria subulata	*Potamogeton sp.*
Schoenoplectus lacustris	*Potamogeton australis*
Sparganium americanum	*Lemna minor* (tested but no effect)
Thypa latifolia	*Acorus calamus*
Vallisneria americana	*Lemna minor* (tested but no effect)

Table 1. Many aquatic plants have been tested in order to demonstrate the content of toxic chemicals. The experiments are based on crude extracts from the species tested and these extracts are typically added to test species in standardized bioassays. Lettuce seedlings and *Lemna minor* are commonly used as test species because they are easily grown and hence the potential effects are easily recognized.

therefore the effect, if any, will never materialize.

The Author

Ole Pedersen is associate professor at the Freshwater Biological Laboratory, University of Copenhagen. He is working with the ecology and physiology of aquatic plants with particular emphasis on plant-sediment interactions. Read more at www.bio-web.dk/op/.

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