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Algal Allelopathy

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I. Abstract

The comprehensive review on allelopathy (Rice, 1979, 1984) has been largely responsible for the evolution of allelopathy as an independent branch of chemical/physiological ecology. The allelopathic research during the last four decades drew attention to different facets of the interactions among the constituents of habitat, calling for an understanding of the role of allelopathy under different habitat conditions. In view of this, we have reviewed the existing information on allelopathic interactions in aquatic habitats with special reference to algal allelopathy. This review has been mainly confined, therefore, to different aspects of algal allelopathy such as allelopathic interactions in algae, algal toxins, bioassays, and implications of algal allelopathy.

In spite of the large number of reviews on allelopathy (see section III), no independent review appears on algal allelopathy. Although there were reports of toxins from cyanobacteria and other algae, no appreciable attempt was made to implicate algal toxins in allelopathy under field conditions. Knowledge of chemistry and biology of allelochemical can help in their potential use in controlling plant diseases and weeds. Therefore, it is urgent to study algal toxins for their involvement in ecological phenomena such as succession, for their uses as herbicides, weedicides, and pesticides, for their uses in solving some of the problems of algal ecology, and for their involvement in applied aspects.

Algal allelopathy is a manifold ecological/physiological phenomenon. Chemicals contributed by the alga can affect (1) other algae in its vicinity, (2) its own growth (i.e., autotoxicity), (3) microbes associated with it, (4) higher plants in its vicinity, and (5) accumulation and availability of nutrient ions which can influence the distribution, growth and establishment of other algae, microorganisms, and plants. However, to establish algal allelopathy of ecological relevance, it is essential to demonstrate the involvement of allelopathy under field conditions. Further, comments should be made on residence time, biological active concentration, mode of renewability, static and dynamic availability of allelochemical, and its variation, if any, with season, site, habitat, and environmental factors.

Further, many algae, especially blue-green, influence the zooplankton population. Is it just a toxic effect of blue-green algae (BGA), or can it be included under allelopathy? This point has been debated and is discussed in the present article.

II. Introduction

Rice (1984) defined allelopathy as any direct or indirect harmful or beneficial effects of one plant, including microbes, on other plants in its vicinity through chemicals that escape into the environment. Allelopathic interactions involve chemical-mediated influences (detrimental/beneficial) among all classes of plants, and are inextricably interwoven into all ecological phenomena. Extensive research has been carried out with terrestrial plants (Inderjit & Dakshini, 1990, 1991a, 1992b; Putnam & Tang, 1986; Rice, 1984). However, chemical interactions among different species of algae have not yet received much attention, in spite of reports on the presence of such phenomena in cyanobacteria and other classes of algae (Keating, 1977, 1978; Patterson et al., 1979; Pratt, 1942; Rice, 1984; Wium-Anderson et al., 1982; Wolf & Rice, 1979).

Harder (1917) first noted algal allelopathy, and, according to Rice (1984), Akehurst (1931) was the first to postulate algal allelopathy as a factor in algal succession. In comparison to terrestrial plants, the progress of algal allelopathy research is slow, in spite of our understanding of the presence of algal toxins (Rice, 1984; Carmichael, 1981, 1982, 1986, 1988, 1989, 1992; Carmichael et al., 1990; Carmichael & Falconer, 1993). Therefore, it is necessary that algal allelopathy research should be looked into more comprehensively. Although algae are considered comparatively less advanced than higher organisms, their great diversity in morphology, biochemistry (Evans & Trewavas, 1991), and production of novel compounds requires an in-depth study of allelopathy. In this article, we review the present status and future prospects of algal allelopathy.

III. Literature on Allelopathy

During the last four decades, there has been a potential contribution to the understanding and advancement of allelopathy by scientists working in different disciplines. Rice (1979) listed various reviews of allelopathy since 1937. Grodzinsky (1965) and Rice (1984) published comprehensive books on allelopathy. There are several edited volumes on different aspects of allelopathy (Chou & Waller, 1983; Putnam & Tang, 1986; Rizvi & Rizvi, 1992; Thompson, 1985; Waller, 1987). The two international journals *Journal of Chemical Ecology* (vol. 9, no. 8) and *Plant and Soil* (vol. 98) published special volumes on allelopathy in 1973 and 1987, respectively. The other relevant review articles are published by Fisher (1979), Harborne (1987), Horsley (1991), and Lovett (1991). However, in spite of the large number of research papers, books, and other literature, less attention was given to algal allelopathy. Rice (1984) discussed algal allelopathy in the second edition of his book. The number of published research papers on algal allelopathy is very small in comparison to the number of papers on other aspects of allelopathy. Further, no review on algal allelopathy has yet appeared; therefore, we endeavour to review algal allelopathy with special emphasis on its present status and future prospects.

IV. Algae with Allelopathic Potential

Algal allelopathy could be operative in four ways: (1) chemicals from one alga affecting the growth of another alga, (2) chemicals secreted by algae inhibiting their own growth (i.e., algal autotoxicity), (3) algal toxins influencing the growth of other microorganisms, and (4) algal toxins affecting the growth of higher plants.

A. ALLELOPATHIC INTERACTIONS AMONG ALGAE

Allelopathy has been exploited to explain the primary production of phytoplankton in brackish water areas having extensive growths of *Chara* (Wium-Anderson et al., 1982). Crawford (1979) observed inhibition of phytoplankton blooms by introduction of *Chara*. In mixed cultures of *Nitzschia frustulum* and *Chlorella vulgaris*, the former grows well, while *Chlorella vulgaris* suffers a 40% reduction in population size to that when grown alone (see Rice, 1984). It is also reported that the planktonic alga *Asterinoella formosa* in the presence of *Chlorella vulgaris* had a reduction in its cell-division rate. According to Rice (1984), Lefevere et al. (1950) reported that filtered water from a canal infested with *Aphanizomenon gracile* killed *Pediastrum boryanum, P. clathratum* var. *punctulatum, Cosmarium lundellii,* and *Phormidium uncinatum* and inhibited the growth of *Micrasterias papillifera*. Further, they reported that water from a canal infested with *Oscillatoria planctonica* killed *Chlorella pyrenoidosa, Cosmarium lundellii, C. obtusatum, Pediastrum boryanum, Phormidium uncinatum, P. autumnale*, and *Scenedesmus quadricauda,* while *Micrasterias papillifera* was less affected. According to Rice (1984), Lefevere and Nisbet (1948) reported the allelopathic influences of *Scenedesmus quadricauda* on *Pediastrum boryanum* while both of these green algae inhibited *Cosmarium botrytis*. Jorgensen (1956) reported that *Chlorella* filtrate inhibited the growth of *Nitzschia*, while it stimulated the growth of *Scenedesmus*. Procter (1957) found that the green alga *Haematococcus pluvialis* died when grown with *Chlamydomonas reinhardii* and was severly inhibited in the presence of *Scenedesmus quadricauda*. Pratt (1966) studied blooms of *Skeletonema*

costatum and *Olithodiscus luteus*. Growth of *Skeletonema* was reduced by high concentrations of *Olithodiscus*-conditioned medium, while the growth was stimulated at low concentrations. Monahan & Trainor (1970) found that the green alga *Hormotila blennista* had pH-dependent stimulatory (pH = 6.3) or inhibitory (pH = 7.7) effects on the growth of *Scenedesmus*. Harris (1970) found an autoinhibitory substance from a colonial alga, *Platydorina caudata* (Volvocaceae), which also inhibited the growth of *Pandorina charkowiensis, Volvox globator, V. tertius,* and *Volvulina pringsheimii* (Harris, 1971a). Harris (1971b) found a concentration-dependent reduction in the photosynthetic rate of *Volvox globator* in the presence of *Pandorina morum* filtrate, while respiration was not affected. The mode of action of this photosynthetic inhibitor was investigated by Harris and Caldwell (1974). It was found that the substance inhibits the light reaction of photosynthesis, since it reduced significantly the oxygen evolution of *Gonium pectorale* and *Eudorina cylindrica*. However, it was less effective against *Pandorina morum* (see also Harris & Parekh, 1974). Keating (1977, 1978) reported that cell-free filtrates of water from a fresh-water lake dominated by cyanobacteria inhibited the growth of diatoms. She offered evidence for probable involvement of allelopathy in algal succession in the eutrophic lake. Kustenko (1975) found that the marine algae, *Thalassionema nitzschioides* and *Skeletonema costatum*, depending on growth stage, influenced each other's growth. Wolf and Rice (1979) studied allelopathic interactions among certain species of algae such as *Pandorina morum, Scenedesmus incrassatulus* var. *mononae, Cosmarium vexatum,* and *Botrydium becherianum*. The brown alga *Fucus vesiculosus* inhibited the growth of *Monochrysis lutheri* and *Porphyridium* sp. through phenolic compounds (McLachlan & Craigie, 1964). Jorgensen (1956) found that when *Nitzschia palea* was cultured in filtrates from *Scenedesmus quadricauda* and *Chlorella pyrenoidosa, Scenedesmus* formed a substance that inhibited *Nitzschia* growth. Martin et al. (1974) found that the cyanobacterium *Gomphospaeria aponina* had allelopathic influences on growth of the red alga, *Gymnodinium breve*. Antibiotic from *Oscillatoria late-virens* affected growth, photosynthesis, and toxicity of BGA *Microcystis aeruginosa* (Bagchi et al., 1993).

B. AUTOTOXICITY AMONG ALGAE

Pratt & Fong (1940) isolated autotoxins from *Chlorella vulgaris*. Jorgensen (1956) found that *Nitzschia palea* formed an autotoxic substance while *Asterionella formosa* formed a substance that accelerated its growth. Monahan and Trainor (1970) found that filtrate of the green alga *Hormotila blennista* was autostimulatory. *Platydorina caudata* (Volvocaceae) first attained high growth and then reduction in the number of colonies, followed by death in its axenic culture (Harris, 1970). This autoinhibitory fraction had properties of protein and was relatively stable at high temperature.

C. TOXIC EFFECTS OF ALGAE ON MICROBES AND HIGHER PLANTS

The allelopathic activity of algae on growth of certain bacteria was demonstrated by Pratt et al. (1944), Jorgensen (1962), and Jorgensen and Nielsen (1961). According to Rice (1984), Mautner et al. (1953) found that the red alga *Rhodomela larix* had allelopathic interference to several gram-positive and gram-negative bacteria, which was due to the production of bromonated phenols. Cell-free extracts of the BGA *Scytonema hofmanni* inhibited the bacterium *Bacillus brevis*, while growth of actino-

mycetes was promoted (Mason & Gleason, 1981). It was reported that the diatom *Asterionella japonica* produced a toxin which was effective against bacteria (see Rice, 1984). Jorgensen (1962) found that ether and ethanolic extracts of *Chlorella vulgaris, Scenedesmus quadricauda,* and *Chlamydomonas reinhardii* had inhibitory effects on the bacterium *Bacillus subtilis.* Jorgensen & Nielsen (1961) found that *Chlorella vulgaris* filtrate affected growth of bacterium *Staphylococcus aureus.* The chrysophyte *Ochromonas malhamensis* inhibited the growth of the bacteria *Staphylococcus aureus, Bacillus megaterium,* and *B. subtilis* (Hanson, 1973). The antibacterial activity of the sea water was probably due to production of toxins by phytoplankton (Moebus, 1972).

Further, there are reports that algal toxins influence the growth of higher plants. Cyanobacterin, a secondary metabolite from the BGA *Scytonema hofmanni,* inhibited growth of the aquatic weed *Lemna gibba* and the terrestrial angiosperm species such as *Setaria viridis, Avena fatua, Rumex crispus,* and *Polygonum convolvulus* while killing seedlings of *Zea mays* and *Pisum sativum* (Gleason & Case, 1986). Antibiotic from *Oscillatoria* sp. inhibited the growth of an aquatic angiosperm *Spirodela polyrhiza* and terrestrial angiosperms such as wheat, pigeon pea, black gram, coriander and mustard, and inhibited photosynthetic reactions in spinach chloroplasts (Chauhan et al., 1992).

D. EFFECT OF ALGAL TOXINS ON ZOOPLANKTON

Francis (1878) reported the toxic effects of cyanobacteria on animals. Lampert (1982) studied the inhibitory effect of the toxins produced by *Microcystis aeruginosa* on filtering rate of zooplankton community structure. DeMott and Moxter (1991) studied the influence of cyanobacteria of varying toxicity, size, and morphology on copepods, and recommended the detailed study of ecological and evolutionary interactions among zooplanktons and BGA. DeMott et al. (1991) found that the cyclic hepatotoxins, microcystin-LR from *Microcystis aeruginosa,* and nodularin from *Nodularia spumigena* affect the survival and feeding of copepod *Diaptomus birgei* and three species of *Daphnia,* i.e., *D. pulex, D. pulicaria,* and *D. hyalina.* However, according to Haney (1987), there was no proof for influence of BGA toxicity on zooplankton under field conditions. Kirk and Gilbert (1992) found that toxins from *Anabaena affinis* had detrimental effects on various zooplankton taxa. They suggested that detrimental influences of toxic BGA affect the species and size structure of zooplankton communities. Furthermore, evidence was presented to prove that cyanobacteria located in and around crevices may be responsible for recognition of carabid beetle habitat (Evans, 1986; Chou & Su, 1989). It was found that the intertidal carabid *Thalassotrechus barbarae* is confined mainly to zones occupied by the cyanobacteria. This chemo-orientation of the beetle, leading to habitat recognition, may be due to chemicals produced by cyanobacteria and other microalgae which grow in and around crevices. However, such studies need more experimental evidences and attention.

Many algae secrete polymers that render water so viscous that fish have difficulty pumping water through their gills (Wyatt & Pazos, 1992). These authors also reported that *Chrysochromulina polylepis* produced a toxin that was harmful to fish, invertebrates, and other algae.

However, since allelopathy deals mainly with the harmful or beneficial effects of

chemical contributed by the plant, directly or indirectly on other plants or microbes in its vicinity, it is worthwhile to debate the inclusion of "toxic effect of cyanobacteria on zooplankton" under allelopathy. Further, it is highly desirable to study and assess these aspects under field conditions as suggested by Haney (1987).

V. Algal Toxins

There have been extensive studies on cyanotoxins (Carmichael, 1981, 1988, 1989, 1992; Carmichael et al., 1990; Codd & Bell, 1985; Gorham & Carmichael, 1988), red algae toxins (Fenical, 1975), and toxins from other algae (Rice, 1984). However, not much work has been done to study the allelopathic nature of these toxins in the field. Therefore, an important area for research would be to study and establish the allelopathic nature of various algal toxins.

Carmichael (1992) suggested that cyanotoxins are biologically active against algae, bacteria, fungi, and mammalian cell tissue. Most cyanobacteria reported to possess toxicity belong to order Nostocales and Stigonematales, which are mainly fresh-water and terrestrial in distribution. Carmichael (1992) mainly classified cyanotoxins into (1) biotoxins, (2) neurotoxins, and (3) hepatotoxins. Biotoxins are produced mainly by *Anabaena, Nostoc, Aphanizomenon,* and *Oscillatoria,* while hepatotoxins are produced by *Microcystis, Anabaena, Nodularia, Oscillatoria,* and *Nostoc,* and unidentified hepatotoxins are produced by *Cylindrospermum, Aphanizomenon, Gloeotrichia,* and *Coelosphaerium.* Hepatotoxins include the widely studied toxin microcystin produced by BGA, *Microcystis,* and *Oscillatoria* (DeMott et al., 1991). Watanabe et al. (1992) detected microcystins in *Microcystis,* and a correlation of season and spatial variation was found in toxin quantity. However, we cannot designate these toxins as allelochemicals until we establish that (1) toxins are contributed to the environment under natural conditions in biologically active concentrations, and have enough persistence to influence the associated plants, microbes, or environment; and (2) availability and renewability of these toxins is maintained under field conditions.

Pratt (1942, 1944, 1948) isolated and characterized a toxin, chlorellin, from *Chlorella vulgaris.* Armstrong and Boalch (1961) reported the ultraviolet absorption by sea water. However, these authors did not carry out detailed investigations. Craigie and McLachlan (1964) found the excretion of ultraviolet-absorbing substances by marine alga *Fucus vesiculosus.* Fogg et al. (1965) established through radioactive studies that there was extensive liberation of extracellular products by phytoplankton, which interfered with the growth of other microorganisms. Sieburth (1960) found that phytoplankton dominated by *Phaeocystis* had antimicrobial activity against *Staphylococcus aureus* and *Mycobacterium smegmatis* and toxins identified as acrylic acid. Replacement of diatoms with *Phaeocystis* was also attributed to the antifungal properties of acrylic acids. Maksimova and Pimenova (1969) found that formic, acetic, glycolic, lactic, pyruvic, α-ketogluteric, and acetoacetic acids during autotrophic growth of *Chlorella vulgaris* and *C. pyrenoidosa.* Four ether-soluble yellow compounds were detected in the culture medium of *Ectocarpus confervoides* (Fogg & Boalch, 1958), and the compounds were tentatively identified as flavonols or catechin-type tannins (Craigie & McLachlan, 1964). Murphy et al. (1976) reported the unavailability of iron to other algae because of excretion of hydroxomate chelaters by BGA such as *Anabaena flos-aquae, Microcystis aeruginosa,* and *Phormidium autumnale.* This was a case of chemical interference and not of nutrient deficiency, as the primary

cause of iron deficiency was chemical (Rice, 1984). The inhibitory factors were found to be free fatty acid in *Chlamydomonas reinhardii,* and the toxicity was enhanced by the presence of a double bond (McCraken et al., 1980). Halogenated toxins produced by rhodophyta was reviewed by Fenical (1975). Katayama (1962) categorized the volatile constituents of several green, brown, and red algae into sulfur, acids, aldehydes, phenols, terpenes, alcohols, and hydrocarbons. Berglund (1969) found growth stimulation of two marine algae by ether-extracted organic substance from *Enteromorpha linza* in both unialgal and axenic cultures. Patterson et al. (1979) isolated an unidentified toxin having low molecular weight (1000–1500) from the green alga *Pandorina morum,* and found that it interfered with the net photosynthetic and mitochondrial electron transport.

According to Wium-Andersen et al. (1982), Steemann-Nielsen (1973) suggested that low primary production of phytoplankton in brackish water areas was due to the allelopathic influence of *Chara.* Biologically active sulfur compounds, lithiolane and trithiane, were isolated from *Chara globuloris* (Anthoni et al., 1980). Later, Wium-Andersen et al. (1982) isolated these two allelochemicals from fresh-water and brackish water areas infested with *Chara baltica, C. hispida,* and also *Nitella transluencs* and *Tolypella nidifica.* Further, it was found that trithiane inhibited photosynthesis of *Nitzschia palea* while dithiolane was less toxic.

Mason et al. (1982) found that growth of intact cells or filaments of Cyanophyceae *(Synechococcus* sp., *Anacystis nidulans, Microcystis aeruginosa, Aphanocapsa* sp. 6308, *Gloeocapsa alpicola, Agmenellum quadruplicatum, Anabaena cylindrica, A. flos-aquae, Nostoc muscorum, N. commune, Cylindrospermum maius, Tolypothrix tenuis, Fremyella diplosiphon, Plectonema boryanum, P. calothricoides, Oscillatoria prolifera, Phormidium autumnale, Lyngbya kuetzingii),* Chlorophyceae (*Ankistrodesmus angustus, Characium californicum, Coelastrum proboscideum* var. *gracile, Cosmarium botrytis, Golenkinia mintissima, Pediastrum biradiatum, Selenastrum capricornnutum, Staurastrum* sp., *Stigeoclonium pascheri, Ulothrix acuminata),* Rhodophyceae (*Porphyridium aerugineum),* and Euglenophyceae (*Euglena gracillis)* was inhibited by the secondary metabolite, cyanobacterin from fresh-water BGA *Scytonema hofmanni.* The structure of cyanobacterin was determined by Pignatello et al. (1983). Cyanobacterin inhibits electron transport in all plants tested, and the most probable site of action is in photosystem II (Gleason & Case, 1986). Cyanobacterin was toxic to the aquatic weed *Lemna gibba,* probably because it was taken up by the *Lemna* roots from the aqueous medium (Gleason & Case, 1986). Further, they found that cyanobacterin inhibited the growth of terrestrial plants such as *Setaria viridis, Avena fatua, Rumex crispus,* and *Polygonium convolvulus,* and completely killed the seedlings of *Zea mays* and *Pisum sativum.*

Moore et al. (1987a) found that the indole alkaloids called haplinodoles from the terrestrial BGA *Hapalosiphon fontinalis* possessed antibacterial and antimycotic properties. Later, two alkaloids, fontonamide and anhydrohapaloxindole, were isolated from *Hapalosiphon fontinalis,* and both these alkaloids appear to be oxidation products of the main alkaloid of this cyanophyte, i.e., hapaloindole, a chlorine-containing isonitrile (Moore et al. 1987b). Moore et al. (1989) further isolated minor indole alkaloids, dechlorofontonamide, anhydrohapaloxindoles B and M, and hapalonamide G, H, and V from *Hapalosiphon fontinalis.* Schwartz et al. (1987) isolated cyclopropane containing hapalindolinones from BGA *Fischerella* (ATCC 53558), during their search for arginine vasopressin-binding inhibitors.

An allelochemical, fischerellin, was isolated from the fresh-water cyanobacterium *Fischerella muscicola* UTEX 1829, which inhibited other cyanobacteria (*Anabaena variabilis, Phormidium* sp., *Synechococcus* sp. PCC 6911 and Synechocystis CB–3) and Chlorophyceae (*Ankistrodesmus obliquus),* although the degree of inhibition varied (Gross et al., 1991). An attempt was made by Flores and Wolk (1986) to screen filamentous nitrogen-fixing bacteria for the production of bacteriocin and other toxins. However, *Fischerella muscicola* was the only strain that produced a toxin that killed all the indicator strains. Gross et al. (1991) found that fischerellin inhibited photosynthesis of BGA and chlorophyceae, while its mode of action is on photosystem II.

Various phenolic compounds were reported from Phaeophyceae, Rhodophyceae, Chlorophyceae, Cyanophyceae, Bacillariophyceae, Xanthophyceae, and Chrysophyceae (Ragan and Craigie, 1978). Polyphloroglucinols were reported from the red algae (Weinstein et al., 1975). Bromophenols were reported from different families such as Ceramiaceae, Delesseriaceae, Bonnemaisoniaceae, Rhodophyllaceae, Corallinaceae, and Rhodomelaceae (Pedersen et al., 1974). Two simple phenols, 2,3-dibromo–4, 5-dihydroxybenzyl alcohol (lanosol), and 3,5'-dibromo-p-hydroxybenzyl alcohol were reported from axenic cultures of BGA *Calothrix brevissima* (Pedersen & DaSilva, 1973). Pryce (1972) reported a natural dihydrostilbene called lunularic acid from Cyanophyceae (*Anabaena* sp.), Bacillariophyceae (*Navicula* sp.), Phaeophyceae (*Ascophyllum nodosum, Fucus ceranoides),* Rhodophyceae (*Chondrus crispus, Polysiphonia urceolata*), Xanthophyceae (*Tribonema* sp.), and Chlorophyceae (*Chlamydomonas* sp., *Chlorella* sp., *Ulva lactuca).*

However, in spite of these reports of the presence of various compounds in different algal classes, the establishment of ecologically relevant algal allelopathy requires that these toxins be present in the environment in biologically active concentrations. Mere presence of the chemical does not establish allelopathy. Further, it is important to collect data on residence time, degradation products (if any), mode of renewability, static and dynamic availability, and mode of action of allelochemicals under natural conditions in order to establish allelopathy of ecological significance. Whether algal toxins are released into the environment in sufficient amount and have enough persistence to influence other plants, microorganisms, and its associated environment remains a critical question in most of the studies of algal allelopathy. To designate algal toxins as allelochemicals, following steps should be taken into consideration:

1. Chemical should be present in the algal associated environment either in its original form or as degraded product, in biologically active concentration.
2. In fresh-water and marine algae, comment should be made on how algae maintain the toxic level of allelochemical.
3. Whether release of chemical in the environment is a natural phenomenon or just a coincidence of environmental factors, and correlation of allelochemical levels with seasons, site, and habitat factors should also be looked into.

VI. Algal Bioassays

Bioassays are the most important part of algal allelopathy, and many bioassays have been proposed (Gross et al., 1991; Rice, 1984). Lukavsky (1992) suggested growth bioassay for the evaluation of algal growth potential and toxicity of water (see also Lukavsky, 1985). Designing algal allelopathic experiments will depend largely upon

algal habitat. Bioassays vary with fresh-water, marine, and terrestrial algae. In aquatic habitats, it is difficult to argue the maintenance of toxic pool, since the toxic factor gets diluted in the environment. Bioassays mainly involve (1) establishing the involvement of chemical in the interference potential of alga, at laboratory and field level, and (2) identification of toxic factor with studies on its residence time, mode of renewability, mechanism of action, and its dynamic and static availability. To establish the involvement of allelopathy in interference potential of algae at laboratory and field level, the following steps should be taken into consideration:

1. Screen algal species associated with the suspected allelopathic alga in different seasons, sites, and habitats, and eliminate the possibilities of other interferences such as light, nutrients, and chemical characteristics of the environment. Various chemical characteristics of the environment such as pH, electrical conductivity, organic matter, and nutrients (PO_4, HCO_3, Cl, Cu, Zn, Na, K, Mg, and Ca) and total phenolics of the various site and habitats in different seasons should be studied to isolate the effect of other environmental factors from that of toxins.
2. Conduct bioassay experiments with algal-associated water (fresh, pond, or marine) in the case of fresh-water and marine algae, and with algal-associated soils in the case of terrestrial algae, using associated algal species or other associated plant species as test species.
3. Study the toxicity of the medium, if any, when suspected allelopathic algae are grown alone in the culture medium.

Harda et al. (1988) proposed the improved methods of purification of toxic peptide produced by BGA. Identification of toxic factor, however, varies with fresh-water and marine algae, since changes in the chemical nature of toxins released by algae cannot be ruled out in marine ecosystem because of the chemical nature (high salt concentration, etc.) of marine water. In fresh-water algae, phytochemical analysis of algae and its associated environment is required in order to know if toxins are direct contributions of algae or are degraded products. However, in marine algae there could be qualitative differences in the algal toxin profile and that of its associated environment. Therefore, in marine algal allelopathy, it is more important to study the phytochemical nature of the associated environment. Phytochemical analysis of marine algae, however, reveals some of the parent compounds which degrade in the marine environment. For terrestrial algae, it is very important to isolate chemicals from the soil associated with the algae, as in the case of other terrestrial allelopathic plants (Inderjit & Dakshini, 1991b, 1992a).

VII. Implications of Algal Allelopathy

Algal allelopathy can be implicated in various ways and even in solving some of the existing problems of algal research. Keating (1977) suggested the implication of algal allelopathy as a controlling factor in bloom sequence determination. She described how in the first winter, cyanobacterial populations dominated when there were no diatoms, while in the third winter, diatom populations dominated and no BGA were found. Algal allelopathy also determines why the algae *Haematococcus pluvialis* is a common ephemeral in rain-water pockets and is never found in permanent water bodies (Procter, 1957). It was concluded that the restricted habitat selection of this

alga was due to toxins synthesized by other algae in the permanent water bodies. Wolf and Rice (1979) found that *Botrydium becherianum* is a terrestrial alga but can grow on liquid culture media. They found that *B. becherianum* was autotoxic and inhibited by *Cosmarium vexatum, Pediastrum boryanum, Scenedesmus incrassatulus, Chlorella ellipsoida* and *Pandorina morum.* Further, *B. becherianum* had stimulatory effects on these five algae, and this may be a significant factor that restricts its distribution mainly to the terrestrial habitat.

Berglund (1969) found that two water-soluble fractions from *Enteromorpha linza* were autostimulatory to its growth. Further, filtrates of chlorophyta *Hormotia bleunista* were autostimulatory (Monahan & Trainor, 1970, 1971). Therefore, growth promoters could affect algal succession in causing stimulated algae to have an advantage in competition/interference. It is highly desirable to identify autostimulatory fractions as well as fractions from those algae which stimulate the growth of other algae. Therefore, under laboratory conditions, poor growth can be improved by the addition of that stimulant. Pratt (1966) found that *Olisthodiscus luteus* achieved dominance by production of ectorine; therefore, ectorine can be used for better growth of *O. luteus* under laboratory conditions.

Many times, algal growth is inhibited after a certain period of time in mass culture. This can be due to the autotoxic nature of some algae, discussed earlier in the text. It is very likely that after a certain period of growth, algae start producing autotoxins. To resolve this problem of autoinhibition in mass culture, we propose a modified technique for mass culturing. A mass-culture tank should have an outlet and an inlet, and fresh water should be periodically replenished. This will serve two purposes: (1) If the alga is autotoxic, most toxins will be removed by the replacement of water; and (2) fresh water, in comparison to drained water, will be nutritionally more beneficial for algal growth. Similarly, in mixed algal mass culturing, it should be ensured that the algal species do not have allelopathic influence on each other.

Water from ponds becomes more toxic during heavy bloom infestations. Allelopathy has been implicated in bloom formation and its control. Supression of phytoplankton blooms in prairie ponds by introduction of *Chara* was exploited by Crawford (1979). According to Rice (1984), Lefevre et al. (1950) reported that filtrate from a canal infested with *Aphanizomenon gracile* inhibited the growth of *Pediastrum boryanum, P. clothratum, Cosmarium lundellii,* and *Phormidium uncinatum.* After five months, bloom of *Oscillatoria planctonica* appeared in the same canal, and its filtrate inhibited *Chlorella pyrenoidosa, Cosmarium lundellii, C. obtusatum, Pediastrum boryanum, Phormidium uncinatum,* and *Scenedesmus quadricauda.* After two months, bloom of *Oscillatoria* completely disappeared, and earlier present algae reappeared. Allelopathy was implicated in such a mechanism. It is likely that *Oscillatoria* secreted a chemical which inhibited the test species. Therefore, if it is possible to identify these chemicals, it would be easy to control blooms of *Pediastrum, Chlorella, Phormidium,* and *Scenedesmus quadricauda.*

VIII. Future Research

The most important question that arises is, Why and at what stage of life cycle of alga are toxins produced? The following are the areas of research which require immediate attention:

1. Study of algal allelopathy under field conditions, with comments on residence time, mode of renewability, and static and dynamic availability of chemicals.
2. At what stage is the release of toxins in biological active concentrations to the environment started?
3. Study of the effect of environmental factors on release, accumulation, and availability of toxins, and of the modification of algal allelopathy by environment, site, season, and habitat.
4. Whether the observed toxic effect of algae is due to chemicals released by the algae or due to their degraded/transformed products.
5. Implication of algal allelopathy in ecological success and evolution of algae.

IX. Acknowledgment

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