US Army Corps of Engineers

ENVIRONMENTAL LABORATORY

AQUATIC PLANT CONTROL
RESEARCH PROGRAM

TECHNICAL REPORT A-89-2

ALLELOPATHIC AQUATIC PLANTS FOR AQUATIC PLANT MANAGEMENT; A FEASIBILITY STUDY

by

Stella D. Elakovich, Jean W. Wooten

University of Southern Mississippi
Hattiesburg, Mississippi 39406

October 1989
Final Report

Prepared for DEPARTMENT OF THE ARMY
US Army Corps of Engineers
Washington, DC 20314-1000

Monitored by Environmental Laboratory
US Army Engineer Waterways Experiment Station
3909 Halls Ferry Road, Vicksburg, Mississippi 39180-6199

Unclassified
SECURITY CLASSIFICATION OF THIS PAGE

REPORT DOCUMENTATION PAGE

Form Approved OMB No. 0704-0188

1a. REPORT SECURITY CLASSIFICATION Unclassified	1b. RESTRICTIVE MARKINGS
2a. SECURITY CLASSIFICATION AUTHORITY	3. DISTRIBUTION/AVAILABILITY OF REPORT Approved for public release; distribution unlimited.
2b. DECLASSIFICATION/DOWNGRADING SCHEDULE	
4. PERFORMING ORGANIZATION REPORT NUMBER(S)	5. MONITORING ORGANIZATION REPORT NUMBER(S) Technical Report A-89-2
6a. NAME OF PERFORMING ORGANIZATION University of Southern Mississippi 6b. OFFICE SYMBOL (If applicable)	7a. NAME OF MONITORING ORGANIZATION USAEWES Environmental Laboratory
6c. ADDRESS (City, State, and ZIP Code) Hattiesburg, MS 39406	7b. ADDRESS (City, State, and ZIP Code) 3909 Halls Ferry Road Vicksburg, MS 39180-6199
8a. NAME OF FUNDING/SPONSORING ORGANIZATION US Army Corps of Engineers 8b. OFFICE SYMBOL (If applicable)	9. PROCUREMENT INSTRUMENT IDENTIFICATION NUMBER
8c. ADDRESS (City, State, and ZIP Code) Washington, DC 20314-1000	10. SOURCE OF FUNDING NUMBERS PROGRAM ELEMENT NO. / PROJECT NO. / TASK NO. / WORK UNIT ACCESSION NO.

11. TITLE (Include Security Classification)

Allelopathic Aquatic Plants for Aquatic Plant Management; A Feasibility Study

12. PERSONAL AUTHOR(S)
Elakovich, Stella D.; Wooten, Jean W.

13a. TYPE OF REPORT	13b. TIME COVERED	14. DATE OF REPORT (Year, Month, Day)	15. PAGE COUNT
Final report	FROM _____ TO _____	October 1989	40

16. SUPPLEMENTARY NOTATION
Available from National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22161.

17. COSATI CODES		
FIELD	GROUP	SUB-GROUP

18. SUBJECT TERMS (Continue on reverse if necessary and identify by block number)

Allelopathy; Bioassay; Growth inhibition; Aquatic macrophytes; Biocontrol; *Lemna minor*

19. ABSTRACT (Continue on reverse if necessary and identify by block number)

This report presents results of a literature search and feasibility study of the use of allelopathic aquatic plants for aquatic plant management. To establish a list of potential allelopathic plants, 16 aquatic macrophytes native to the southeastern United States were subjected to two bioassays--one involving lettuce seedlings and one involving the aquatic plant *Lemna minor* as the target species. The results suggest that *Nymphaea odorata* and *Brasenia schreberi* are both highly inhibitory and are therefore candidates for aquatic weed management. The results also indicate that the simple lettuce seedling assay may be a reasonable first "easy" assay for determining the allelopathic potential of aquatic plants.

20. DISTRIBUTION/AVAILABILITY OF ABSTRACT ☒ UNCLASSIFIED/UNLIMITED ☐ SAME AS RPT. ☐ DTIC USERS	21. ABSTRACT SECURITY CLASSIFICATION Unclassified
22a. NAME OF RESPONSIBLE INDIVIDUAL	22b. TELEPHONE (Include Area Code) / 22c. OFFICE SYMBOL

DD Form 1473, JUN 86 *Previous editions are obsolete.*

SECURITY CLASSIFICATION OF THIS PAGE
Unclassified

Preface

This study was conducted for the US Army Corps of Engineers (USACE) Aquatic Plant Control Research Program (APCRP). Funds for the study were provided by the Headquarters, USACE, under Department of the Army Appropriation No. 96X3122, Construction General. The USACE Technical Monitor for the APCRP was Mr. E. Carl Brown.

The principal investigators for the work and authors of this report were Dr. Stella D. Elakovich, Professor of Chemistry, and Dr. Jean W. Wooten, Professor of Biological Sciences, both of the University of Southern Mississippi (USM), Hattiesburg, MS. The report was edited by Ms. Jessica S. Ruff of the WES Information Technology Laboratory.

Mses. Amanda Letchworth, Laschinski Tillis, and Bonnie Sanders, USM, provided technical assistance. Dr. Gerald R. Leather, US Department of Agriculture, Agricultural Research Service, Frederick, MD, supplied an axenic culture of *Lemna minor*.

The research was monitored at WES by Mr. Edwin A. Theriot and Dr. Alfred F. Cofrancesco, Jr., of the Environmental Laboratory (EL), Environmental Resources Division (ERD), Aquatic Habitat Group (AHG). The study was conducted under the general supervision of Dr. John Harrison, Chief, EL, and Dr. Conrad J. Kirby, Chief, ERD, and under the direct supervision of Mr. Theriot, Chief, AHG. Mr. J. Lewis Decell was Manager of the APCRP.

Commander and Director of the WES was COL Larry B. Fulton, EN. Technical Director was Dr. Robert W. Whalin.

This report should be cited as follows:

Elakovich, Stella D., and Wooten, Jean W. 1989. "Allelopathic Aquatic Plants for Aquatic Plant Management; A Feasibility Study," Technical Report A-89-2, US Army Engineer Waterways Experiment Station, Vicksburg, MS.

Contents

ALLELOPATHIC AQUATIC PLANTS FOR AQUATIC PLANT MANAGEMENT; A FEASIBILITY STUDY

Introduction

Background

1. Use of allelopathic terrestrial plants has received attention in agriculture as a weed management strategy. Putnam (1983) has achieved success with annual rotation of allelopathic crops or companion plantings of allelopathic and perennial crops. He has been able to suppress up to 95 percent of several important weeds. Allelopathic aquatic plants may provide a management system for undesirable aquatic vegetation. The replacement of an undesirable species by a desirable one as a long-term, site-specific method of aquatic plant management was suggested over 30 years ago by Oborn et al. (1954). They observed that *Sagittaria subulata* (dwarf arrowhead) and *Eleocharis acicularis* (spikerush) crowded out pondweed over a 2-year period and suggested the desirability of planting one or both plants to prevent "growth of the ranker growing pondweeds." This method of aquatic plant management is not likely to replace other control methods, either biological or chemical, but certainly it should be complementary to them. This report presents results of a feasibility study of the use of allelopathic aquatic plants for aquatic plant management.

2. The plan for assessing the feasibility of using allelopathic aquatic plants as replacement species for aquatic plant management involved the following steps:

a. A thorough search of the literature to compile a list of "known" allelopathic aquatic plants.

b. Selection of a list of "most likely candidates" from the list of allelopathic aquatic plants.

c. Bioassay of the selected plants to compare the relative activities of each. (Two bioassay systems are included.)

Interactions among plants

3. By definition, competition occurs when two or more organisms, or other organismic units such as populations, interfere with or inhibit one another. Plants typically use some common resources that are often in short supply. Also, the presence of each plant reduces the fitness and/or

equilibrium population size of the other. Competition may be direct, as in the case of interspecific territoriality, and is called "interference competition." Indirect competition can occur, such as that arising through joint use of the same limited resource; this is termed "exploitation competition." Because it is always advantageous for either unit in competitive interaction to avoid the other whenever possible, competition presumably promotes the use of different resources and generates ecological diversity. The way in which a community of plants partition resources among themselves and reduce interspecific competition affects community structure and may influence species diversity.

4. Ecologists are divided in their opinion regarding the importance of competition in structuring natural populations of plants. A solution to this division may be not to view competition as an all-or-nothing phenomenon. Perhaps it is best to think of competition as gradients of intensity varying from no competition to a situation in which demand equals the supply of all environmental parameters.

5. One school of ecological thought has maintained that populations of plants are in some way regulated by "density-dependent factors," i.e., processes that either increase mortality or decrease fecundity as the density of the population increases. Thus, there would be a density-dependent feedback that holds the population within certain limits. A second school of thought has maintained that density-independent factors such as weather conditions or disturbance are more important in determining population size. These density-dependent factors may operate at any time of year when populations may be at any size. They may be sporadic and may interact with density-independent factors. The controversy over the existence, importance, and results of these two factors seems to exist because of a lack of adequate information about density-dependent regulation. There are technical problems in censusing populations and studying the results of these factors. The great variability of most natural communities demands very rigorous approaches to the investigation of competitive interactions.

6. Density-dependent regulation in natural plant populations is not well understood. This type of regulation is usually divided into intraspecific and interspecific competition. Intraspecific competition is defined as competition among individuals of the same species and has been documented in natural populations. The results appear to be plants of different sizes and

distances apart, and are positively correlated. Also, mortality exhibited by fewer individuals than expected by chance in the immediate proximity of other individuals is often a result of this type of competition. Density effects can be established by comparisons of plant size and population dynamics in plots of different plant density. The problems with these comparisons is the necessity for rigidly controlling environmental conditions.

7. Competitive effects can be measured by perturbation experiments in which rates of population growth of competitors are monitored as they approach equilibrium and by addition and/or removal experiments, in which the population density of a species is measured both in the presence and absence of its competitor. Removal experiments under field conditions are difficult to perform. The substitute approach to field studies of competition relies upon experiments in which aspects of the population are compared between areas where the plants occur alone (allopatry) with other areas where the plants occur with another competing species (sympatry). If the areas are similar, shifts observed in sympatry should reflect the response to interspecific competition.

8. Some very good possibilities exist for manipulation of densities in the field and introduction or removal of species. Monitoring of changes in population densities and/or niche shifts before, during, and after the experimental manipulation appears to be a good way to study competition in the field. It has become apparent that precise demonstration and quantification of density-dependent effects require manipulation or perturbation of the density of natural populations.

9. Plant responses to allelochemicals may be similar to species' responses to competition. Chemical inhibition may have a role in eliminating competitors in field situations. However, other factors such as effects of competition for light, nutrients, water, and other biotic effects could have overriding effects that appear as competition or allelopathy. These biotic factors must be eliminated before allelopathy or competition can be considered to account for observed differences in field communities of plants.

10. It can be argued that the fact that many plants appear tolerant of secondary chemicals does not preclude their importance; most plants are adapted to the prevailing chemical and physical environment, which ecologists consider important. These secondary chemicals may be essential regulators in the growth and development of ecosystems. Allelopathy is effective, and

documented first evidence came from arid vegetation, chaparral. The production of toxins to inhibit neighboring plants seems to be a desirable evolutionary strategy for plants. The constraints to production of an allelochemical by plants are that there must be strong biochemical limitations on the amounts produced. A plant will not benefit from allelochemical production if it is sensitive to its own toxins or if its seed germination is inhibited. The allelochemical must be produced by the plant within the leaves or roots without damaging its own physiological processes. And, at this time, too little evidence exists to state how much plant distribution is controlled by allelochemicals. It appears logical to assume that the benefit of production of allelochemicals by a plant species is a reduction of competition in the immediate environment where the plants are growing. Reduced competition can result in faster growth and reproduction. This could mean that allelochemical interactions could arise from competition.

11. Perhaps it would be of value to consider other plant parameters, excepting those commonly used, such as size and mortality, as indicators of allelopathy. If effects of competition can be validly viewed along a continuum, then it would appear logical to so view effects of allelopathy. For example, plants need not die to have reduced productivity. Effects of allelopathy could reasonably be expected to reduce plant productivity by partial death of photosynthetic cells, reduced root uptake of nutrients and water, reduced rates of biochemical processes within cells, reduced fecundity or propagule production, and a lessening of the ability of the plants to compete in a stressed situation. Legitimate experiments could determine if this idea is valid.

Literature Review

12. The University of Southern Mississippi's computer-assisted retrieval system was used to search Chemical Abstracts, Biological Abstracts, and Agricola from 1970 to date. Search strategy included the terms allelopathy, competition, and toxic and aquatic plants (or weeds or vegetation). In addition, 20 specific plant names were searched.

13. Of the approximately 100 papers located in the literature search, only 19 reported experimental evidence or field observations in support of allelopathic aquatic plants. Of these, five reported on *Eleocharis*

coloradoensis (dwarf spikerush) as the allelopathic plant; another four reported on *Typha latifolia* (cattail). Other plants identified are listed in Table 1. Complete bibliographic citations for the documents listed in Table 1 are provided in the References at the conclusion of the main text. Also, an annotated bibliography of the Table 1 citations is provided as Appendix A.

14. A problem with much of this literature is that definitive testing methods for allelopathy have not been developed; consequently, inconsistencies exist in the literature. For example, Yeo (1976) reported that *Eleocharis acicularis* and *E. coloradoensis* can encroach upon the area previously occupied by pondweeds *Potamogeton crispus* and *P. pectinatus* and prevent their growth. Yeo (1980a) reported that *P. crispus* was not replaced by *E. coloradoensis*. Grace (1983) refuted McNaughton's (1968) much quoted report of the autotoxicity of *T. latifolia*. Some of these publications report field observations alone (Nichols and Shaw 1983), some report activities of plant extracts (Frank and Dechoretz 1980; Ashton, DiTomaso, and Anderson 1985), and others report carefully constructed competitive studies of whole plants. It is difficult to draw conclusions as to the most promising allelopathic aquatic plants from the literature available.

Bioassay Procedures

Selection of study plants

15. Many of the 24 plants identified in Table 1 as allelopathic aquatic plants are not deep-water plants. Many are shoreline plants that would not be effective in control of the worst aquatic weeds, *Hydrilla verticillata* (hydrilla) and *Myriophyllum spicatum* (Eurasian watermilfoil). Some are not native to the southeastern United States and so were not available for this feasibility study. Sixteen plants (listed on the following page) were selected as potentially useful allelopathic aquatic plants. These plants were selected for a variety of reasons. *Brasenia schreberi* (watershield) and *Eleocharis acicularis* (spikerush) were selected because they had been reported as allelopathic (Table 1). *Eleocharis obtusa* was included because of the importance of *Eleocharis* in allelopathy. No sample of *E. coloradoensis* was included because it does not occur in the southeastern United States. Hydrilla and Eurasian watermilfoil were included for the purpose of evaluating their activity in the assay system. *Myriophyllum aquaticum* (parrotfeather)

Code No.	Scientific Name	Common Name
1	*Brasenia schreberi*	Watershield
2	*Cabomba caroliniana*	Fanwort
3	*Ceratophyllum demersum*	Coontail
4	*Eleocharis acicularis*	Spikerush
5	*Eleocharis obtusa*	Spikerush
6	*Hydrilla verticillata*	Hydrilla
7	*Juncus repens*	Rush
8	*Limnobium spongia*	Frog's bit
9	*Myriophyllum aquaticum*	Parrotfeather
10	*Myriophyllum spicatum*	Eurasian watermilfoil
11	*Najas guadalupensis*	Common water nymph
12	*Nymphaea odorata* (leaves and stems)	Fragrant white waterlily
13	*Nymphaea odorata* (roots)	
14	*Nymphoides cordata*	Floating-hearts
15	*Potamogeton foliosus*	Pondweed
16	*Sparganium americanum*	Bur-reed
17	*Vallisneria americana*	Tapegrass

was selected because it is a desirable plant of the same genus as the nuisance Eurasian watermilfoil. The remaining plants were selected either because of their observed potential allelopathic activity as determined by their growth patterns, or because they are desirable replacement species.

Plant collection and processing

16. Sufficient quantities of each selected plant were collected by hand and transported to the laboratory in plastic bags. In those cases where the plants were kept longer than 0.5 hr after collection, they were kept on ice. The plants were washed free of debris and were spread on newspaper to dry to the "drip-dry" stage. Voucher specimens were deposited in the University of Southern Mississippi herbarium. A 200-g aliquot of the drip-dry plants was thoroughly blended with 200 ml of distilled, deionized water, and the resulting pulpy mixture was refrigerated for 24 to 72 hr to enhance the extraction of organic materials. The mixture was filtered through cheesecloth to remove the majority of the cellulosic material, through filter paper to remove

smaller particulate matter, and finally through a 0.45-μ millipore filter to render the solution sterile. This sterile solution was either assayed immediately or stored frozen.

17. In all cases except one, the entire plant, including roots, was extracted. The exception was *Nymphaea odorata* (fragrant white waterlily), which was divided into two portions, leaves/stems and roots. The two portions were treated as separate samples in all subsequent assays.

Lettuce seedling bioassay

18. Aqueous extracts of the 16 selected plants were subjected to lettuce seedling bioassay as a first "easy" assay for allelopathic potential. Advantages of this assay method are experimental simplicity, short duration, and sensitivity. The major disadvantage is that aquatic plants are being tested against a terrestrial plant target species (Ashton, DiTomaso, and Anderson 1985). Factors influencing the growth of aquatic plants may be very different from those factors influencing terrestrial plant growth. Therefore, the aqueous extracts were also subjected to a bioassay involving the aquatic plant *Lemna minor* (duckweed) as the target species. A third (proposed) assay will involve *H. verticillata* as the target species. This will allow the evaluation of activity toward another aquatic plant, but more importantly, toward hydrilla, one of the most noxious of aquatic plants. It is of particular interest to determine whether good correlation exists between results from terrestrial plant bioassay and aquatic plant bioassay.

19. Experimental methods. The effect of the aqueous plant extracts on lettuce seedling radical growth was measured at three extract concentration levels (1, 5, and 10 ml) of extract per test plate, each diluted to 40 ml by the addition of 30 ml of 0.5-percent agar and the appropriate amount of distilled water. The control contained 30 ml of 0.5-percent agar and 10 ml of distilled water. Tests were run in 9-cm disposable sterile petri dishes. Lettuce seeds were first germinated on 0.5-percent agar in a growth chamber set at 22° C, 16-hr days and 18° C, 8-hr nights. Twenty germinated seedlings were transferred to the petri dishes containing extract and agar and were incubated under the same light and temperature conditions for 3 to 4 days or until a control plate (no extract) showed good growth. Length of the lettuce seedling roots was measured to the nearest millimeter.

20. The results of the seedling growth bioassays were analyzed separately using a Honeywell DPS-8 mainframe computer and a statistical package

for the social sciences, version 9.* The data were tested for homogeneity of variances of all treatments, and the Duncan multiple-range test was applied to detect differences among all treatment means.

21. Results and discussion. Results from the lettuce seedling bioassay at three extract concentrations are presented in Table 2 and illustrated in Figure 1. Extracts of six plants inhibited greater than 77 percent of lettuce seedling radical growth. From most to least inhibitory, these are: *Nymphaea odorata* (roots), *Juncus repens*, *Vallisneria americana*, *Brasenia schreberi*, *Ceratophyllum demersum*, *Eleocharis acicularis*, and *Nymphaea odorata* (leaves and stems). Of these, *N. odorata* root extract was the most active, with 95-percent inhibition of lettuce radical growth by 10 ml of aqueous extract. *Ceratophyllum demersum* extracts brought about the greatest inhibition (66 percent) at the 1-ml concentration. Both *B. schreberi* and *V. americana* are strongly inhibitory at 10-ml levels, but are stimulatory at 1-ml levels. Rice (1984) has suggested that many, perhaps most, plant growth inhibitors may be growth stimulators at some much lower concentrations.

Lemna minor bioassay

22. The bioassay method using *L. minor* offers advantages in that *L. minor* is an aquatic plant and therefore potentially more appropriate than terrestrial plants as the target species in an assay for allelopathy. Also, the method is sensitive and reproducible. However, the *L. minor* bioassay is more complex than the lettuce seedling bioassay and requires 7 to 10 days, a distinct disadvantage. An additional disadvantage is that axenic cultures of *L. minor* must be continuously maintained. The limits of the method have been examined by other workers (Leather and Einhellig 1985).

23. Experimental methods. Intensive efforts to produce an axenic culture of *L. minor* from field-gathered plants were unsuccessful, thus delaying completion of the assay. However, an axenic culture of *L. minor* (strain 5) was obtained from Dr. Gerald R. Leather, Plant Physiologist, US Department of Agriculture, Agricultural Research Service, Frederick, MD. This *Lemna* was maintained in both liquid culture (E medium) and agar slants (E medium/ 1-percent agar to which 600 mg/ℓ of bactotryphone and 100 mg/ℓ of yeast extract were added). *Lemna* from the liquid culture was used for bioassay.

---

* C. H. Hull, and N. H. Nie. 1981. SPSS Update 7-9, McGraw-Hill, New York.

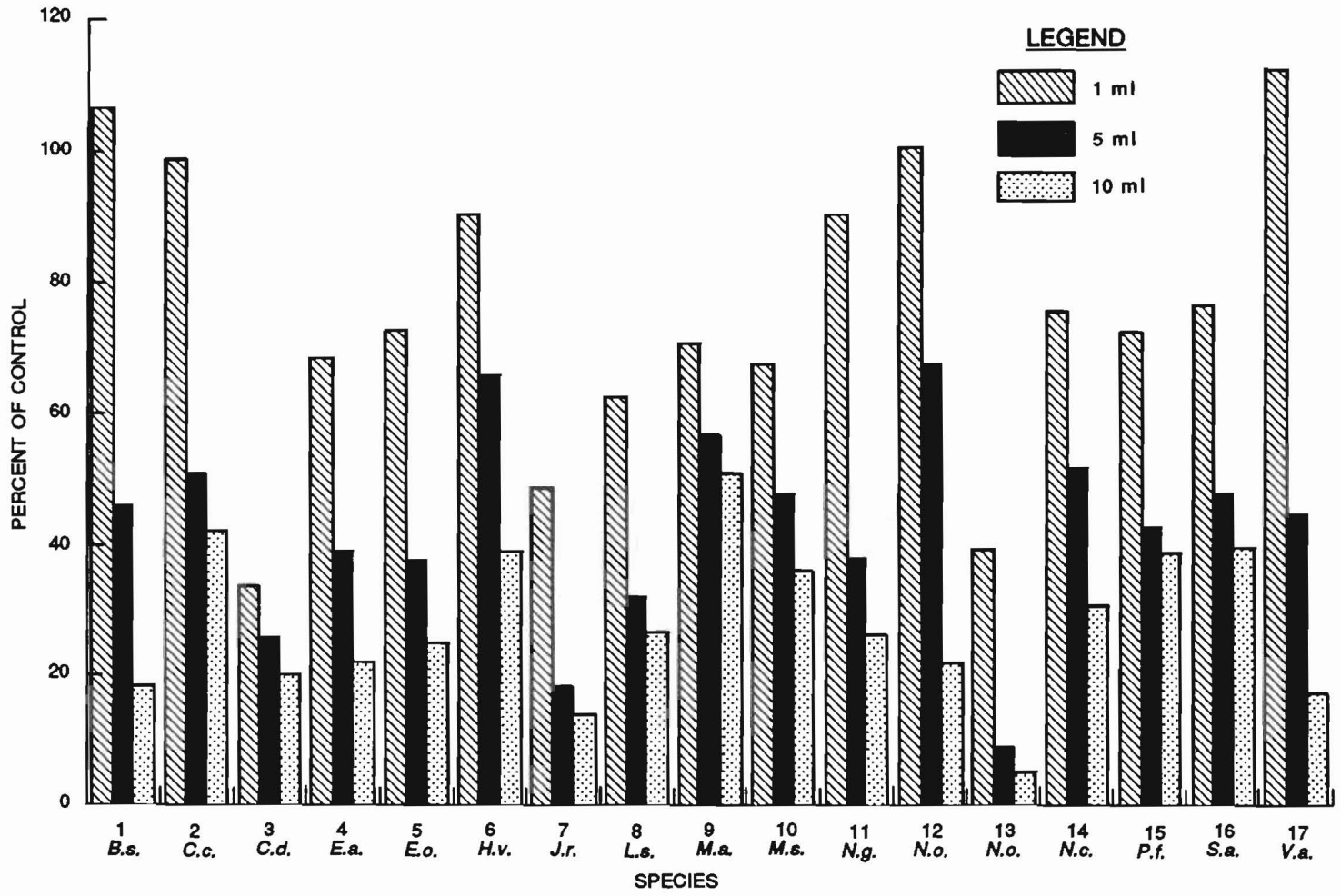


Figure 1. Results of lettuce seedling bioassay of aquatic plant species (code numbers are identified in paragraph 15 of the text)

24. Preparation of E medium involved preparation of the following six stock solutions using glass-distilled water (personal communication, G. R. Leather):

a. 50 × major elements (g/500 ml)

$Ca(NO_3)_2 \cdot 4H_2O$	29.50
KNO_3	37.88
KH_2PO_4	17.00

b. 100 × trace elements (mg/500 ml)

H_3BO_3	143
$ZnSO_4 \cdot 7H_2O$	11
$Na_2MoO_4 \cdot 2H_2O$	6
$CaSO_4 \cdot 5H_2O$	4
$MnCl_2 \cdot 4H_2O$	181

c. 1,000 × tartaric acid
300 mg/100 ml

d. 1,000 × iron
540 mg of $FeCl_3 \cdot 6H_2O$ per 100 ml

e. 1,000 × EDTA (ethylenediaminetetraacetic acid)
900 mg of EDTA per 100 ml
(must add about 4 ml of 6N KOH to dissolve EDTA)

f. 100 × magnesium
25 g of $MgSO_4 \cdot 7H_2O$ per 500 ml

25. The E medium was prepared from the following amounts of the above stock solutions:

a. Major elements, 20 ml.

b. Minor elements, 10 ml.

c. Tartaric acid, 1 ml.

d. Iron, 1 ml.

e. EDTA, 1 ml.

f. Magnesium, 10 ml.

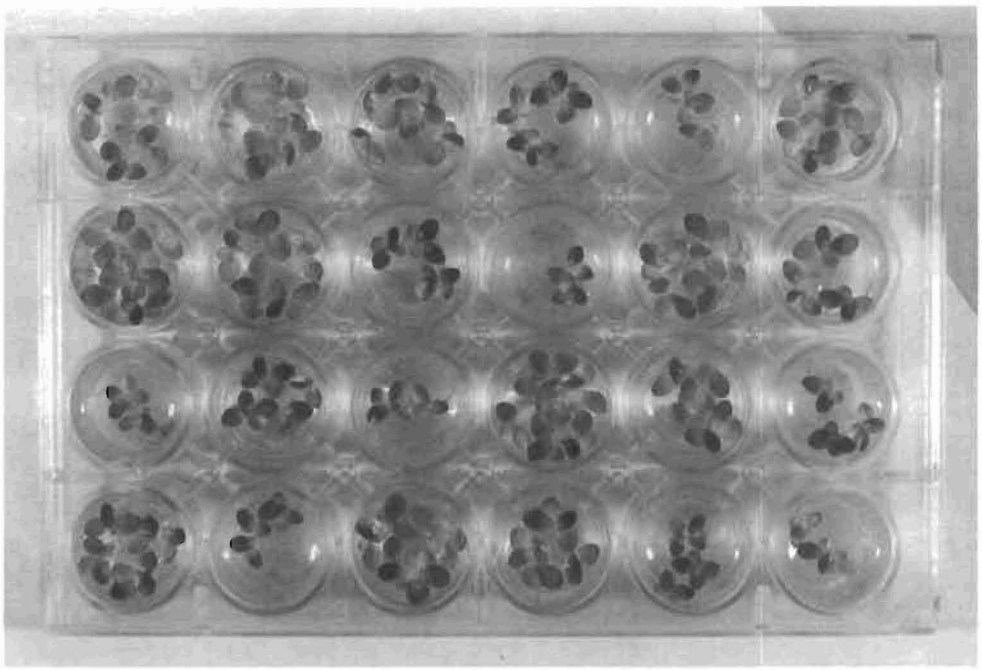
To these six solutions was added 10 g of sucrose and glass-distilled water to make 1 ℓ. The pH was adjusted to 4.6 with KOH and HCl. The medium was autoclaved for 15 to 20 min at 15 psi (103 kPa).

26. For assays, Lemna was cultured in 1.5 ml of E medium in 24-well, sterile, disposable tissue culture dishes (Figure 2). Three test levels and a control were included in each plate in a design that ensures that each treatment occupies one corner and three edge wells. Sterile aqueous plant extracts were added (see tabulation below); the total volume was adjusted with sterile, glass-distilled water; and three fronds of axenic *L. minor* were added to each well. The covered culture dishes were placed in a growth chamber set at 28° C, 24 hr light. High humidity (~60 percent) was maintained by placing a large pan of water in the chamber. Test plates were monitored daily. Evaporated water was replaced as needed. Assays were scored when the control wells contained at least 20 fronds (7 to 11 days).

Test Well	E Medium ml	H_2O, ml	Plant Extract	
			ml	Final Concentration, ppm*
Control	1.5	0.375	0	0
Concentration 1	1.5	0.337	0.038	20,000
Concentration 2	1.5	0.187	0.188	100,000
Concentration 3	1.5	0	0.375	200,000

* These three concentration levels can be compared with the three levels used in the lettuce seedling assay. In that assay, 1, 5, and 10 ml of plant extract represent concentrations of 25,000, 125,000, and 250,000 ppm, respectively.

27. Reproduction was scored by frond number. Counted fronds were placed in a small test tube, and 1.5 ml of 95-percent ethanol was added to extract chlorophyll. The tubes were allowed to stand at room temperature for 24 hr or were refrigerated for 48 to 72 hr, at which time 1.5 ml of water was added to each tube. The fronds were removed, air-dried, stored in a desiccator for at least 2 days, and then weighed on a five-place analytical balance to determine dry weight (growth). The absorbance (A) of the chlorophyll



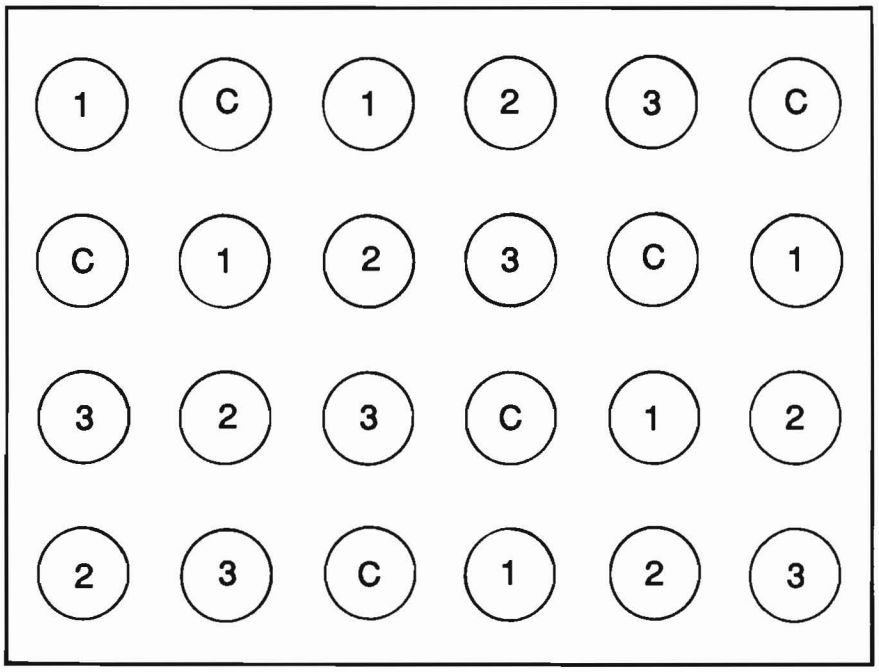


Figure 2. *Lemna minor* bioassay test plate. Results are shown for *C. caroliniana* where C = control, 1 = 0.038-ml extract, 2 = 0.188-ml extract, and 3 = 0.375-ml extract

extracts was read at 649 and 665 nm. Chlorophyll-a concentration was calculated from the following formula (personal communication, G. R. Leather):

$$\frac{\mu g \text{ chlorophyll-a}}{ml \text{ solution}} = (13.7)(A665 \text{ nm}) - (5.76)(A649 \text{ nm})$$

Statistical analyses were performed in the same manner as for the lettuce seedling bioassay.

28. Results and discussion. Compared to the lettuce seedling assay, the *L. minor* assay is very complex, both experimentally and interpretively. Each 24-well test plate allows six replications of each of three test concentrations and a control. The lettuce seedling assay easily allows 20 test plants for each concentration. Given the immense variability of plant growth, 20 replications is certainly far superior to six. The reproducibility of the *L. minor* assay is variable. For this study, all assays were run in duplicate. Some duplicate assays corresponded well; some did not. It is likely that the small replication number (six) contributes significantly to the lack of correspondence.

29. In the *L. minor* assay, three measurements were taken: frond number, a measure of reproduction; dry weight, a measure of biomass; and chlorophyll-a, a measure related to biomass. Problems are associated with each of these. In many cases, high test extract concentrations produced fronds one half to one third the normal size. Thus, frond number is often not a good indication of growth inhibition. Often these stunted fronds were also chlorotic, which would negatively affect the chlorophyll-a measurement. Some of the stunted fronds apparently had thicker than normal cuticles, which retarded chlorophyll extraction, also negatively affecting the chlorophyll-a measurements. Also, it is difficult to hand-count fronds accurately. How large should a frond be to be counted as "one frond"? It was decided to count new fronds as 0.5 frond. A better method would be to instrumentally measure surface area occupied by the fronds. Such an area measurement would negate the frond size problem. Unfortunately, the necessary instrumentation for such area measurements was not available.

30. Results from the *L. minor* bioassay are presented in Tables 3-5. Extract concentrations were selected to compare with the concentrations used in the lettuce seedling assay (see tabulation, paragraph 26). Extracts of

five plants inhibited 60 percent or greater of *L. minor* frond reproduction (Table 3 and Figure 3). These are, with the most inhibitory first, *N. odorata* leaves and stems, *M. aquaticum*, *B. schreberi*, *N. odorata* roots, and *C. caroliniana*. The chlorophyll-a results (Table 5) are largely confirmatory--the same five plants reduced chlorophyll-a content by 60 percent or more as compared with the control. The activity order is different, and five additional plants also exhibit 60-percent or greater inhibition. However, the five plants listed above as most inhibitory toward frond reproduction are also the five showing the greatest chlorophyll-a reduction. Thus, correspondence between these two measurements is good.

31. Measurement of plant dry weight should give an accurate measure of biomass, comparable to the frond area measurement. With this assay, only milligram and submilligram amounts of *L. minor* dry weight are produced. Thus, weights must be determined using a five-place analytical balance. The work is tedious, and small errors in transfer of material are critical. Results of *L. minor* biomass reduction as measured by plant dry weight are presented in Table 4. Measurements were not made for all plants, but overall comparison of frond number inhibition and biomass reduction suggests that plant dry weight is not as sensitive a measurement of growth inhibition as frond number. Comparison of the values in Tables 3 and 4 shows roughly 15 to 30 percent greater inhibition of frond growth for a given plant, although the results for a few plants show good agreement.

Comparison of lettuce seedling and *Lemna minor* bioassay results

32. It is important to reiterate why two bioassays were conducted for this study. The lettuce seedling assay is a widely used, experimentally simple assay to determine allelopathic (growth inhibition or stimulation) activity. However, it uses lettuce, a terrestrial plant, as the target species and thus may be less appropriate for use with aquatic plants. The *L. minor* assay involves an aquatic plant as the target species and was more appropriate for the study. However, it is experimentally much more complex and time consuming. Lettuce seedling assays with 20 replications per concentration can be run in 4 days; *L. minor* assays with only six replications per concentration require 8 to 11 days. Scoring the *L. minor* assay requires a minimum of 3.5 hr of a technician's time for each assay, excluding setup time

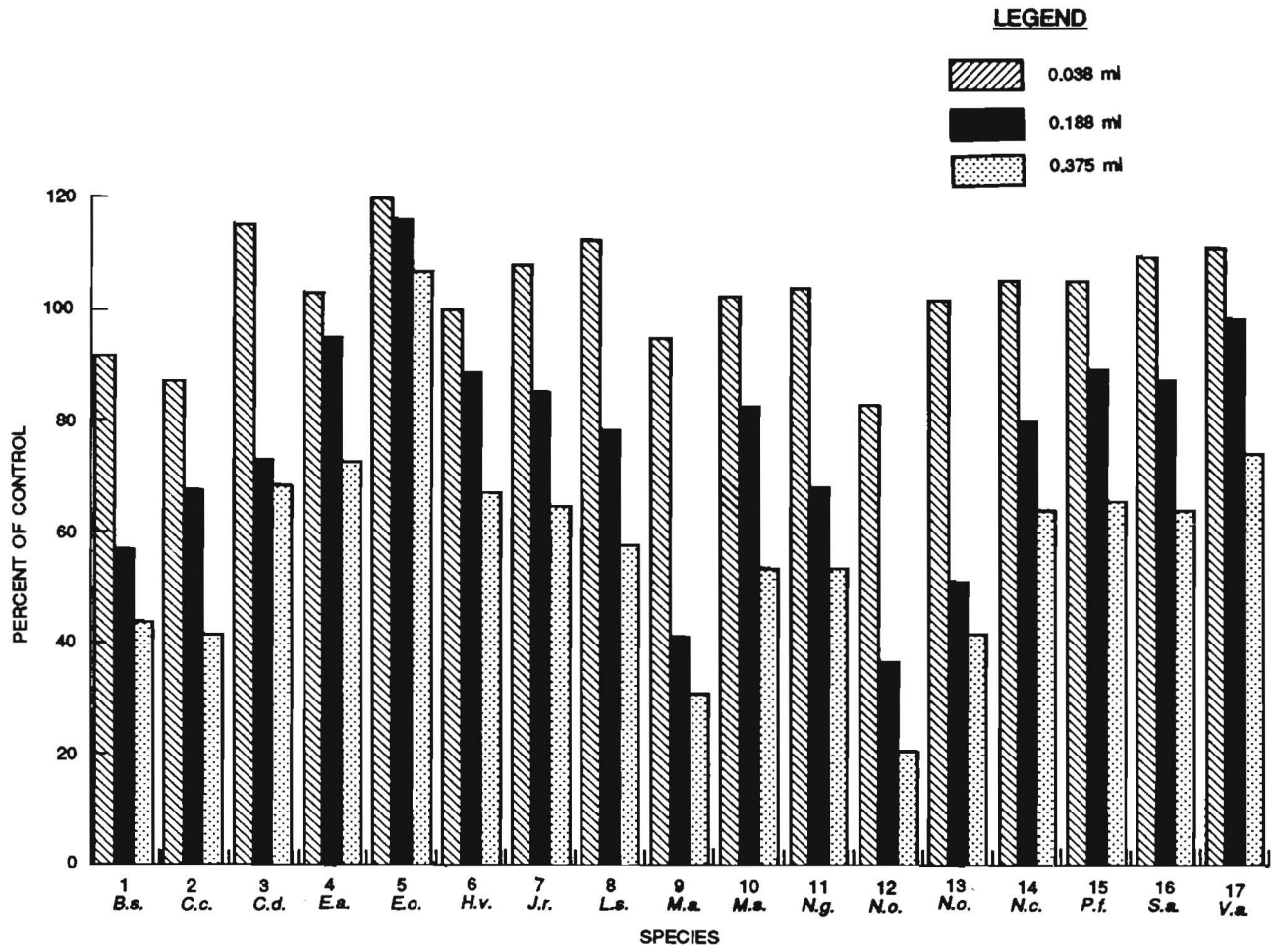


Figure 3. Results of *L. minor* bioassay of aquatic plant species - frond reproduction inhibition. (Species codes are defined in paragraph 15 of the text)

and statistical analysis of the results. The question then becomes: Is it worth it?

33. *Nymphaea odorata* (roots) was the most inhibitory plant tested by lettuce seedling assay, inhibiting 95 percent of seedling radical growth (Table 2) at the highest (10-ml) extract concentration. *Nymphaea odorata* (roots) also inhibited *L. minor* frond reproduction (Table 3) and chlorophyll-a production (Table 5) by greater than 60 percent. This percentage would have been greater if the assay were scored by subtracting the number of fronds originally placed in each well from the number present on the day the assay was scored.

34. *Nymphaea odorata* (leaves and stems) was the most inhibitory plant tested by *L. minor* assay, inhibiting 90 percent of frond reproduction, 60 percent of plant biomass, and >60 percent of chlorophyll-a. *Nymphaea odorata* (leaves and stems) also inhibited 78 percent of lettuce seedling radical growth.

35. *Brasenia schreberi* inhibited 82 percent of lettuce seedling radical growth and also inhibited 64 percent of frond reproduction in one *L. minor* assay. Less activity was exhibited in the second *L. minor* assay.

36. These results would suggest that both *N. odorata* and *B. schreberi* are excellent candidates for aquatic plant management. On the other hand, *Juncus repens*, the second most active plant by lettuce seedling assay, does not appear highly allelopathic by *L. minor* assay. The original question, "Are additional assays worth the effort?" must be answered with a resounding "yes." Where the assay results are confirmatory, field studies can begin. Where conflicting results occur, additional assays are needed. Ideally, the bioassay should have as its target species the plant that is to be eliminated. However, these results have shown that the experimentally simple, widely used lettuce seedling assay is a useful first assay system.

Conclusions and Recommendations

37. Aquatic weed management by use of allelopathic aquatic plants or plants with some competitive edge has great practical potential. These initial studies indicate that such a management system is feasible, but more information is needed before field studies can be initiated. Some reasonable approaches include the following:

a. The list of potential allelopathic plants must be expanded. The 16 plants selected in the initial study represent readily available species in Mississippi and Louisiana. Many plants with allelopathic potential can be found in other areas of the southeastern United States. Since both hydrilla and Eurasian watermilfoil are also found in areas such as Florida, where different and more numerous aquatic species exist, it is important to examine additional native species.

b. The plants selected in step a should be collected and subjected to lettuce seedling bioassay and *L. minor* bioassay so that their growth inhibitory activity can be compared with the initial 16 plants examined and an activity ranking can be made.

c. An assay involving *H. verticillata* as the target species should be developed. All selected plants should be subjected to this hydrilla explant assay. This third bioassay would allow the evaluation of activity toward a submersed aquatic plant, but more importantly, toward hydrilla, one of the most noxious of aquatic weeds.

38. While collecting some of the 16 species that were tested for allelopathic activity, the authors were reminded of the lack of information on why certain species of plants are extant in some locations and not in others (given that propagules are equally available in all areas). Definitive explanations for aquatic plant distribution are never comprehensive, for, in an ever-changing environment, it is probably impossible to examine enough parameters to fully explain the presence or absence of a given species in a given area.

39. Observations of hydrilla and Eurasian watermilfoil in a number of habitats could afford some ideas about what types of plants do or do not grow with these nuisance plants. Although this does not indicate that chemically antagonistic effects are involved, it does provide a starting point for seeking the most likely plants to examine for allelopathy. Further, it gives some idea of the plants to use in future competition studies.

40. After completion of the proposed laboratory work, the next logical step would be glasshouse testing of the replacement species. Such studies could be made recognizing that competition may produce results difficult to differentiate from effects due to allelopathy. However, since the final aim of this work is to find plant species to replace noxious species, the differentiation of cause, whether competition or allelopathy, is less important initially.

41. The laboratory studies will provide information sufficient to develop experimental designs for glasshouse testing of desirable candidate species against hydrilla and Eurasian watermilfoil. It is anticipated that large-scale glasshouse competitive studies would be the next stage of this project prior to field testing.

References*

Agami, M., and Y. Waisel. 1984. "Germination of *Najas marina* L.," Aquat. Bot., 19, 37-44. [Germination, *Najas*]

_____. 1985. "Interrelationships between *Najas marina* and three other species of aquatic macrophytes," Hydrobiologia, 126(2), 169-174. [Allelopathy, Aquatic macrophytes, Competition, *Myriophyllum*, *Potamogeton*, *Scirpus*]

Anderson, L. W. J. 1985. "Use of bioassays for allelochemicals in aquatic plants," The Chemistry of Allelopathy, ACS Symposium Series 268, A. C. Thompson, ed., American Chemical Society, Washington, DC, pp 351-370. [Allelopathy, Aquatic plants, Bioassay, Explants, *Hydrilla*, *Potamogeton*]

Anderson, R. C., and O. L. Loucks. 1966. "Osmotic pressure influence in germination tests for antibiosis," Science, 152, 771-773. [Antibiotic, Germination, Osmotic pressure]

Antonelli, P. L. 1983. "Competition and productivity in aquatic plant communities; experiments and theories," Rev. Bio-Math., (84), 1-26. [Allelopathy, Aquatic plants, Competition, Mathematics, Productivity]

Ashton, F. M., J. M. DiTomaso, and L. W. J. Anderson. 1985. "Spikerush (*Eleocharis* spp.): A source of allelopathics for the control of undesirable aquatic plants," ACS Symposium Series 268, 401-414. [Allelopathy, Aquatic plants, *Eleocharis*, Management, Spikerush]

Barko, J. W. 1982. "Influence of potassium source (sediment vs. open water) and sediment composition on the growth and nutrition of a submersed freshwater macrophyte," Aquat. Bot., 12, 157-172. [Allelopathy, Aquatic plants, Hydrilla, Potassium, Sediment]

_____. 1983. "The growth of *Myriophyllum spicatum* L. in relation to selected characteristics of sediment and solution," Aquat. Bot., 15, 91-103. [Growth, *Myriophyllum*, Sediment]

Barko, J. W., and R. M. Smart. 1983. "Effects of organic matter additions to sediment on the growth of aquatic plants," J. Ecol., 71, 161-175. [Allelopathy, *Elodea*, *Hydrilla*, *Myriophyllum*, *Potamogeton*, *Sagittaria*, Sediment]

Barko, J. W., M. S. Adams, and N. L. Clesceri. 1986. "Environmental factors and their consideration in the management of submersed aquatic vegetation: A review," J. Aquat. Plant Manage., 24, 1-10. [Ecology, Inorganic carbon, Light, Nutrients, Sediment chemistry, Temperature, Water chemistry]

* Key words are given at the conclusion of each citation (shown in brackets).

Barltrop, J., and D. F. Martin. 1983. "Evidence for photodynamic action by a naturally occurring Hydrilla growth inhibitor," J. Environ. Sci. Health; Part A, Environ. Sci. Eng., 18(1), 29-36. [Growth inhibitor, Hydrilla, Soil extract]

Bell, David J. 1974. "The influence of osmotic pressure in tests for allelopathy," Trans. Ill. State Acad. Sci., 67, 312-317. [Allelopathy, Assay, Osmotic pressure]

Blotnick, J. R., J. Rho, and H. B. Gunner. 1980. "Ecological characteristics of rhizosphere microflora of *Myriophyllum heterophyllum*," J. Environ. Qual., 9, 209-210. [Microbial populations, *Myriophyllum*, Rhizoplane]

Bonasera, J., J. Lynch, and M. A. Leck. 1978. "An allelopathy study of marsh plants and soils," Bull N. J. Acad Sci., 23(2), 3. [Allelopathy, Marsh plants, Soil]

_____. 1979. "Comparison of the allelopathic potential of four marsh species. Bull Torrey Bot. Club, 106, 217-222. [Allelopathy, *Ambrosia*, *Bidens*, Marsh plants, *Peltandra*, *Typha*]

Breck, J. F., R. T. Prentki, and O. L. Loucks, eds. 1979. "Aquatic plants, lake management, and ecosystem consequences of lake harvesting," Proc. Conf. Madison, WI, Institute for Environmental Studies, Univ. Wisconsin-Madison. [Harvesting, *Myriophyllum spicatum*, Sediment]

Buchanan, B. A., K. T. Harper, and N. C. Frischknecht. 1978. "Allelopathic effects of bur buttercup tissue on germination and growth of various grasses and forbs in-vitro and in soil," Great Basin Nat., 38(1), 90-96. [Allelopathy, Forbs, Grasses]

Cameron, H. J., and G. R. Julion. 1980. "Inhibition of protein synthesis in lettuce (*Latuca sativa* L.) by allelopathic compounds," J. Chem. Ecol., 6(6), 989-995. [Allelopathy, Assay, Lettuce]

Dawson, F. H. 1978. "Aquatic plant management in semi-natural streams: The role of marginal vegetation," J. Envir. Manage., 6, 213-221. [Aquatic plant, Management]

Dawson, F. H., and U. Kern-Hansen. 1977. "Aquatic weed management in natural streams: The effect of shade by marginal vegetation," Proc. 10th Congr. Int. Ver. Theor. Angew. Limnol., Copenhagen, pp 1451-1456. [Aquatic weed, Littoral, Management]

del Moral, R., and Rex G. Cates. 1971. "Allelopathic potential of the dominant vegetation of western Washington," Ecology, 52, 1030-1037. [Allelopathy, Conifers, Dicots, Ferns]

Dooris, P. M., and D. F. Martin. 1981. "Growth inhibition of *Hydrilla verticillata* by selected lake sediment extracts," Wat. Res. Bull., 16, 112-117. [Growth inhibition, Hydrilla, Sediment]

Dooris, P. M., W. S. Silver, and D. F. Martin. 1982. "Effect of *Hydrilla verticillata* growth inhibiting extracts upon the growth of *Scenedesmus obliquns* (an alga)," J. Environ. Sci. Health; Part A. Environ Sci. Eng., 17(5), 639-646. [Algal inhibition, Hydrilla, Sediment]

Dunst, R. C., S. M. Born, P. D. Uttormark, S. A. Smith, S. A. Nichols, J. O. Peterson, and R. D. Knauer. 1974. "Survey of lake rehabilitation techniques and experiences," Technical Bulletin No. 75, Wisconsin Department of Natural Resources, Madison. [Algae, Biological control, Snails, White amur]

Einhellig, F. A., G. R. Leather, and L. L. Hobbs. 1985. "Use of *Lemna minor* L. as a bioassay in allelopathy," J. Chem. Ecol., ii(i), 65-72. [Bioassay, *Lemna*]

Elakovich, Stella D., and Jean W. Wooten. 1987. "An examination of the phytotoxicity of the water shield, *Brasenia schreberi*," J. Chem. Ecol., 13, 1935-1940. [Allelopathy, Aquatic macrophyte, *Brasenia*, Water shield]

Elser, H. J. 1969. "Observations on the decline of the water milfoil and other aquatic plants, Maryland, 1962-1967," Hyacinth Control J., 8, 52-60. [*Myriophyllum spicatum*, Pathological diseases]

Fitzgerald, G. P. 1969. "Some factors in competition or antagonism among bacteria, algae, and aquatic weeds," J. Phycol., 5, 351-359. [Algae, *Ceratophyllum*, *Cladophora*, *Lemna minor*, *Myriophyllum*, Nitrogen, *Pithophora oldogonium*]

Frank, P. A., and N. Dechoretz. 1980. "Allelopathy in dwarf spikerush *Eleocharis coloradoensis*," Weed Sci., 28(5), 499-505. [Allelopathy, *Eleocharis*, Spikerush]

Fuerst, E. P., and A. R. Putnam. 1983. "Separating the competitive and allelopathic components of interference," J. Chem. Ecol., 9(8), 937-944. [Allelopathy, Competition]

Grace, James B. 1983. "Autotoxic inhibition of seed germination by *Typha latifolia*: An evaluation," Decologia (Berlin), 59, 366-369. [Allelopathy, Germination, *Typha*]

Grace, J. B., and R. G. Wetzel. 1978. "The production biology of Eurasian watermilfoil (*Myriophyllum spicatum* L.); a review," J. Aquat. Plant Manage., 16, 1-11. [Mineral nutrients, Photosynthesis, Respiration]

_____. 1981. "Habitat partitioning and competitive displacement in cattails (*Typha*): Experimental field studies," Am. Nat., 118, 463-474. [Competition, Field studies, *Typha*]

Gururaja, Rao G., Rao K. Naravana, and Rao G. Rajeswara. 1980. "Biochemical studies of *Hydrilla verticillata* and its leachates," Indian J. Exp. Biol., 18(7), 771-772. [Hydrilla, Leachate, Phenolics]

Haller, W. T., J. L. Miller, and L. A. Garrard. 1976. "Seasonal production and germination of Hydrilla vegetative propagules," J. Aquat. Plant Manage., 14, 26-29. [Growth characteristics, Hydrilla, Management]

Haller, W. T., and D. L. Sutton. 1975. "Community structure and competition between the aquatic weed *Hydrilla verticillata* and *Vallisneria neotropicalis*," Hyacinth Control J., 13, 48-50. [Biomass, Competition, Hydrilla, Light, *Vallisneria neotropicalis*]

Hao, Q. N., and H. A. M. Khuda. 1973. "Polysaccharide constituents of the aquatic plant *Hydrilla verticillata*," Bangladesh J. Sci. Ind. Res., 8(1-4), 32-36. [Hydrilla, Polysaccharide structure]

Hunding, C., and R. Lange. 1978. "Ecotoxicology of aquatic plant communities," Principles of Ecotoxicology, SCOPE Report 12, Chapter 11, pp 239-255. [Heavy metals, Pollutants, Toxicity]

Hutchinson, G. E. 1970. "The chemical ecology of three species of *Myriophyllum* (Angiospermae, Haloragaceae)," [Limnol. Oceanogr., 15, 1-5 [Ecology, *Myriophyllum*, pH limitation, Water hardness]

Johnston, D. L., D. L. Sutton, V. V. Vandiver, Jr., and K. A. Langeland. 1983. "Replacement of *Hydrilla verticillata* by other aquatic plants in a pond with emphasis on growth of American lotus (*Nelumbo lutea*)," J. Aquat. Plant Manage., 21(0), 41-43. [Grass carp, Hydrilla, *Nelumbo lutea*]

Jones, R. C., K. Walti, and M. S. Adams. 1983. "Phytoplankton as a factor in decline of the submersed macrophyte *Myriophyllum spicatum* L. in Lake Wingra, Wisconsin," Hydrobiologia, 107, 213-219. [Allelopathy, *Myriophyllum*, Phytoplankton]

Kirpenko, N. I. 1986. "Phytopathic properties of the toxin of blue-green algae," Gidrobiol. Zh., 22(1), 48-50. [*Aphanizomenon flos-aqua*, Duckweed, *Elodea*, Germination, Inhibition, *Microcystis*, Poppy, Radish]

Klaine, S. J., and C. H. Ward. 1984. "Environmental and chemical control of vegetative dormant bud production in *Hydrilla verticillata*," Ann. Bot. (Hond.), 53(4), 503-514. [Bud production, Hydrilla]

Kulshreshtha, M., and B. Gopol. 1983. "Allelopathic influences of *Hydrilla verticillata* (L.f.) Royle on the distribution of *Ceratophyllum* species," Aquat. Bot., 16, 207-209, [Allelopathy, *Ceratophyllum*, Distribution, *Hydrilla*]

Latheef, M. A., and R. D. Irwin. 1980. "Effects of companionate planting on snap bean insects *Epilachna varivestia* and *Heliothis zea*," Environ. Entomol., 9(2), 195-198. [Allelopathy, Companion planting, Insect control]

Leather, G. R., and F. A. Einhellig. 1985. "Mechanisms of allelopathic action in bioassay," The Chemistry of Allelopathy, A. C. Thompson, ed., American Chemical Society, Washington, DC, pp 197-205. [Allelopathy, Bioassay]

Lee, H. K., and J. O. Guh. 1982. "Study on competition ability and chemical control of *Sagittaria pygmaea* Miquel, a perennial weed in paddy field," Nongsa Sihom Yongu Pogo, 24, 16-23. [Chemical control, Competition, *Sagittaria pygmaea*]

Maestrini, S. Y., and D. J. Bonin. 1981. "Allelopathic relationships between phytoplankton species; Algae, ecology, toxicity," Can. Bull. Fish Aquat. Sci., Ottawa Govt. of Canada, Fisheries and Oceans, pp 323-338. [Algae, Allelopathy, Ecology, Succession, Toxicity]

Martin, D. F. 1983. "Structural studies of a naturally occurring hydrilla inhibitor," Miscellaneous Paper A-83-2, US Army Engineer Waterways Experiment Station, Vicksburg, MS (NTIS No. AD A129 105). [Allelopathy, Hydrilla, Structural studies]

McClintock, W. L., J. W. Frye, and W. D. Hogan. 1974. "Development of the bottom placement technique for *Hydrilla verticillata* and eelgrass control," Hyacinth Control J., 12, 46-47. [Eelgrass, Hydrilla, Mechanical control, Tapegrass, *Vallisneria americana*]

McCreary, N. J., and S. R. Carpenter. 1983. "Competition among submersed perennial plants: Use of reciprocal replacement series in situ," Proc. Int. Symp. Aquat. Macrophytes, Nijmegen, 18-23 September, pp 134-138. [Experimental methods]

McCreary, N. J., S. R. Carpenter, and J. E. Chaney. 1983. "Coexistence and interference in two submersed freshwater perennial plants," Oecologia, 59, 393-396. [*Eleocharis*, Interference, *Juncus pelocarpus*]

McIntosh, R. P. 1970. "Community, competition and adaption," Quart. Rev. Biol., 45, 259-280. [Competition, Plant community]

McNaughton, S. J. 1968. "Autotoxic feedback in relation to germination and seedling growth in *Typha latifolia*," Ecology, 49, 367-369. [Germination, Seedling growth, *Typha*]

Meteiko, T. Ya. 1981. "Metabolites of higher aquatic plants and their role in hydro bio cenoses; Review" (in Russian), Gidro Biol ZH, 27(4), 3-14. [Allelopathy, Aquatic plants, Metabolites]

Mitchell, D. S. 1979. "Formulating aquatic weed management programs," J. Aquat. Plant Manage., 17, 22-24. [Allelopathy, Weed management]

Nichols, S. A., and B. H. Shaw. 1983. "Physical, chemical and biological control of aquatic macrophytes," Lake Restoration, Protection and Management, US Environmental Protection Agency, pp 181-192. [Allelopathy, Aquatic plants, Spikerush]

Oborn, E. T., W. T. Moran, K. T. Greene, and T. R. Bartley. 1954. Weed control investigations on some important plants which impede flow of western irrigation waters," Joint Lab. Rpt. SI-2, USDA, Bur. Reclam. Eng. Lab., and USDA, ARS Field Crops Branch, pp 16-17. [Dwarf arrowhead, Growth inhibition, Needle spikerush, Pondweeds]

Perkins, B. David. 1978. "Approaches in biological control of aquatic weeds," Proc. EWRS 5th Symposium on Aquatic Weeds, pp 9-15. [Aquatic weeds, Biological control]

Perkins, M. A. 1980. "Managing aquatic plants with fiberglass screen," Proc. Int. Symp., Restoration of Lakes and Inland Waters, US Environmental Protection Agency, Washington, DC, pp 245-248. [Aquatic plants, Management]

Pip, E. 1972. "Survey of the ecology of submerged aquatic macrophytes in central Canada," Aquat. Bot., 7, 339-357. [Plant correlations, Water chemistry]

Pip, E., and J. M. Stewart. 1974. "The dynamics of two plant snail interactions in certain aquatic systems in Manitoba," Am. J. Bot., 61(5), 6. [Competition, Gastropod, *Potamogeton*]

Ponnamperuma, F. N. 1972. "The chemistry of submerged soils," Adv. Agron., 24, 29-96. [Soil chemistry]

Putnam, A. R. 1983. "Allelopathic chemicals," Chem. Eng. News, 24-25. [Allelopathy, Review]

Rice, E. L. 1984. Allelopathy, 2d ed., Academic Press, New York. [Allelopathy, Review]

Robson, T. O. 1977. "Perspectives of biological control of aquatic weeds in temperate climatic zones," Aquat. Bot., 3(2), 125-132. [Biological control, Overview]

Sailer, R. I. 1972. "Biological control of aquatic weeds; Recent progress," Proc. Northeast Weed Sci. Soc., 26, 180-182. [*Althernanthera philoxeroides*, Flea beetle, Waterhyacinth]

Sanders, Dana R., and Millard O. Mangrum. 1973. "Competition between *Cabomba* and *Anacharis* in Black Lake, Louisiana," Proc., S. Weed Sci. Soc., 26, 361-366. [*Anacharis, Cabomba caroliniana*]

Sastroutoma, S. S. 1981. "Turion formation, dormancy and germination of curly pondweed (*Potamogeton crispus* L.)," Aquat. Bot., 1, 161-173. [Germination, Growth, *Potamogeton*]

Seidel, K. 1975. "Allelopathy and succession in *Typha augustifolia*," Naturwissenchaften, 62(7), 35. [Allelopathy, *Typha*]

Singhvi, N. R., and K. D. Sharma. 1984. "Allelopathic effects of *Ludwigia adscendens* Linn. and *Ipomoea aquatica* Forsk on seedling growth of pearlmillet (*Pennisetum typhoideum* Rich.)," Trans. Isdt. and Ucds., 9(2), 95-100. [Allelochemicals, Growth inhibition, Growth stimulation]

Sircar, S. M., and M. Kundu. 1959. "Effect of root extract of water hyacinth on the growth and flowering of rice," Sci. and Cul., 24, 332-333. [Growth inhibition/stimulation, Rice, Waterhyacinth]

_____. 1960. "Growth regulation properties of the root extract of water hyacinth," Physiol. Plants, 13, 56-63. [Growth inhibition/stimulation, Waterhyacinth]

Smart, R. M., and J. W. Barko. 1985. "Laboratory culture of submersed freshwater macrophytes on natural sediments," Aquat. Bot., 21, 251-263. [Culture conditions, Macrophyte cultures, Sediment nutrients]

Spencer, N. R., and M. Lekic. 1974. "Prospects for biological control of Eurasian watermilfoil," Weed Sci., 22, 401-404. [Biocontrol, Insects, *Myriophyllum spicatum*]

Steward, K. K., and T. D. Center. 1979. "Evaluation of methan for control of hydrilla regrowth from tubers," J. Aquat. Plant Manage., 17, 76-77. [Hydrilla, Methan, Soil fumigant]

Stom, D. I., and R. Roth. 1981. "Some effects of polyphenols on aquatic plants; I, Toxicity of phenols in aquatic plants," Bull. Environ. Contam. Toxicol., 27, 332-337. [*Elodea canadensis, Lemna minor, Vallisneria spiralis*]

Sutton, David L. 1986. "Growth of hydrilla in established stands of spikerush and slender arrowhead," J. Aquat. Plant Manage., 24, 16-20. [Allelopathy, Hydrilla, *Sagittaria*, Spikerush]

Sutton, D. L., R. C. Littell, and K. A. Langeland. 1980. "Intraspecific competition of *Hydrilla verticillata*," Weed Sci., 28, 425-428. [Growth, Hydrilla]

Swindale, D. N., and J. T. Curtis. 1957. "Phyto-sociology of the larger submerged plants in Wisconsin lakes," Ecology, 38, 397-407. [Community, Ecology]

Szczepanska, W. 1971. "Allelopathy among the aquatic plants," Pol. Arch. Hydrobiol., 18, 17-30. [Allelopathy, Aquatic plants]

_____. 1977. "Interactions of *Phragmites communis* Trin. and *Carex hudsonii* Bennet," Ekol. Pol, 25(3), 431-436. [Allelopathy, Reed, Sedge]

Szczepanska, W., and A. Szczepanski. 1973. "Emergent macrophytes and their role in wetland ecosystems, Pol. Arch. Hydrobiol., 20, 41-50. [Competition, *Phragmites australis*, Production, *Typha latifolia*]

_____. 1976. "Growth of *Phragmites communis* Trin. and *Typha latifolia* in relation to the fertility of soils," Pol. Arch. Hydrobiol., 23, 233-248. [Growth, *Phragmites communis*, Soils, *Typha latifolia*]

Szczepanski, A. J. 1977. "Allelopathy as a means of biological control of water weeds," Aquat. Bot., 3, 193-197. [Allelopathy, Aquatic plants, Biological control]

Timmons, F. L. 1970. "Control of aquatic weeds," Tech. Papers of the FAO Internat. Conf. on Weed Control, June 22-July 1, Davis, CA, Weed Science Soc. of America, pp 357-373. [Aquatic weeds, Control]

Titus, J. E., and M. S. Adams. 1979. "Coexistence and the comparative light relations of the submersed macrophytes *Myriophyllum spicatum* L. and *Vallisneria americana* Michx.," Oecologia, 40, 273-286. [Competition, *Myriophyllum*, *Vallisneria*]

Titus, J. E., and M. D. Stephens. 1983. "Neighbor influence and seasonal growth patterns for *Vallisneria americana* in a mesotrophic lake," Oecologia, 56, 23-29. [Allelopathy, *Chara vulgaris*, *Potamogeton amplifolius*, *Vallisneria americana*]

Van, T. K., W. T. Haller, and G. Bowes. 1976. "Comparison of the photosynthetic characteristics of three submersed aquatic plants," Plant Physiol., 58, 761-768. [C_3, CO_2 photosynthetic rate, Coontail, Hydrilla, Light, Milfoil]

Vanzon, J. C. J. 1973. "Studies on the biological control of aquatic weeds in the Netherlands," Third Internat. Symp. Biol. Cont. Weeds. [Aquatic weeds, Biocontrol, *Eleocharia acicularis*]

Waisel, Y. 1971. "Seasonal activity and reproductive behavior of some submerged hydrophytes in Israel," Hydrobiologia (Bucharest), 12, 219-227. [Germination, *Potamogeton crispus*, *Potamogeton pectinatus*, Vegetative reproduction]

Watch, M. J. 1979. "Phytotoxicity of leachates from terraria containing dwarf spikerush (*Eleocharis coloradoensis*) and slender spikerush (*Eleocharis*)," M.S. thesis, Botany Dept., Univ. Calif. [Alleopathy, *Eleocharis*, Phytotoxicity]

Westlake, D. F. 1982. "Ecology-community metabolism and production: The primary productivity of water plants," Studies on Aquatic Vascular Plants, J. J. Symoens, S. S. Hooper, and P. Compere, eds., Royal Botanical Society of Belgium, Brussels. [Aquatic plants, Production]

Wetzel, R. G., and J. B. Grace. 1983. "Aquatic plant communities," CO_2 and Plants," E. R. Lemon, ed., AAAS Selected Symp. Series, Westview Press, Inc., Boulder, CO, pp 223-280. [Aquatic plants, CO_2]

Whitehead, D. C., H. Dibb, and R. D. Hartley. 1982. "Phenolic compounds in soil as influenced by the growth of different plant species," [J. Appl. Ecol., 19(2), 579-588. [Phenolics, Soil]

Whittaker, R. H., and P. P. Feeny. 1971. "Allelochemics: Chemical interactions between species," Science, 171, 757-770. [Chemical interactions]

Wolek, J. 1974. "A preliminary investigation in interactions (competition, allelopathy) between some species of *Lemna, Spirodella* and *Wolffia*," Ber. Geobot. ETH Stiftung Rubel., 42, 140-162. [Allelopathy, Competition, *Lemna, Spirodella, Wolffia*]

Wolfe, James M., and Elroy L. Rice. 1979. "Allelopathic interactions among algae," J. Chem. Ecol., 5, 533-542. [Algal succession, Allelopathy, *Botrydium, Chlorella*, Cosmarium, Pandorina, Pediastrum]

Yeo, R. R. 1972. "Control of rooted submersed aquatic weeds with competitive plants," WSSA Meeting Abstracts, St. Louis, MO. [Allelopathy, Aquatic plant management]

Yeo, R. R. 1976. "Naturally occurring antagonistic relationships among aquatic plants that may be useful in their management," Proc., IC Internat. Symp. Biol. Cont. Weeds, Gainesville, FL, pp 290-293. [Algae, Allelopathy, Aquatic plants, Competition]

_____. 1980a. "Spikerush may help control water weeds," Calif. Agric., 34, 13-14. [Spikerush]

_____. 1980b. "Life history and ecology of dwarf spikerush (*Eleocharis coloradoensis*)," Weed Science, 28(3), 263-272. [Dwarf spikerush, *Eleocharis*, Hydrosoils, Light, Plant interactions, Production, Tolerance]

Yeo, R. R., and T. W. Fisher. 1970. "Progress and potential for biological weed control with fish, pathogens, competititve plants, and snails," Tech. Papers of FAO Internat. Conf. on Weed Control, June 22-July 1, Davis, CA, Weed Sci. Soc. of America, pp 450-463. [Biological control, Waterweeds]

Yeo, R. R., and J. R. Thurston. 1984. "The effect of dwarf spikerush (*Eleocharis coloradoensis*) on several submersed aquatic weeds," J. Aquatic Plant Manage., 22, 52-56. [Allelopathy, Competition, Displacement, *Eleocharis*, Turion]

Table 1

Allelopathic Aquatic Plants

Allelopathic Plant	Affected Plant(s)	Reference
Ambrosia trifida	Lettuce, radish, tomato, cucumber	Bonasera, Lynch, and Leck 1979
Bidens laevis	Lettuce, radish, tomato, cucumber	Bonasera, Lynch, and Leck 1979
Brasenia schreberi	Lettuce	Elakovich and Wooten 1987
Carex hudsonii	*Phragmites communis*	Szczepanska 1977
Chara vulgaris	*Vallisneria americana*	Titus and Stephens 1983
Eleocharis acicularis	*Potamogeton* (pondweeds)	Oborn et al. 1954
	Waterweeds	Nichols and Shaw 1983
	Elodea canadensis *Potamogeton pectinatus* *Potamogeton crispus*	Yeo and Fisher 1970
Eleocharis coloradoensis	*Potamogeton pectinatus* *Potamogeton nodosus* *Potamogeton pusillus* *Potamogeton foliosus* *Najas guadalupensis* *Elodea canadensis* *Elodea nuttallii*	Yeo 1980a
	Potamogeton nodosus *Potamogeton pectinatus*	Frank and Dechoretz 1980
	Zannichellia palustris *Elodea nuttallii* *Elodea canadensis* *Hydrilla verticillata* *Potamogeton nodosus* *Potamogeton pectinatus* *Myriophyllum spicatum*	Yeo and Thurston 1984
	Hydrilla verticillata *Potamogeton pectinatus* Tomato cell culture Lettuce seedling roots	Ashton, DiTomaso, and Anderson 1985
	Waterweeds	Nichols and Shaw 1983

(Continued)

Note: Complete bibliographic citations are provided in the References at the conclusion of the main text. A summary of each of the references cited in Table 1 is given in Appendix A.

Table 1 (Concluded)

Allelopathic Plant	Affected Plant(s)	Reference
Eleocharis geniculata	*Hydrilla verticillata*	Sutton 1986
Eleocharis parvula	Waterweeds	Nichols and Shaw 1983
Equisetum fluviatile	*Phragmites australis*	Szczepanski 1977
Equisetum limosum	*Phragmites communis*	Szczepanska 1971
Equisetum palustris	*Phragmites australis* *Typha latifolia*	Szczepanski 1977
Hydrilla verticillata	*Ceratophyllum demersum* *Ceratophyllum muricatum*	Kulshreshtha and Gopol 1983
Ipomoea aquatica	*Pennisetum typhoideum*	Singhvi and Sharma 1984
Ludwigia adscendens	*Pennisetum typhoideum*	Singhvi and Sharma 1984
Myriophyllum spicatum	*Najas marina*	Agami and Waisel 1985
Peltandra virginica	Lettuce, radish, tomato, cucumber	Bonasera, Lynch, and Leck 1979
Phragmites australis	*Carex elata*	Szczepanski 1977
Potamogeton amplifolius	*Vallisneria americana*	Titus and Stephens 1983
Sagittaria graminea	*Hydrilla verticillata*	Sutton 1986
Sagittaria pygmaea	Rice	Lee and Guh 1982
Sagittaria subulata	*Potamogeton* (pondweeds)	Oborn et al. 1954
Schoenoplectus lacustris	*Potamogeton australis*	Szczepanski 1977
	Equisetum limosum *Phragmites communis*	Szczepanska 1971
Typha latifolia	*Acorus calamus* *Glyceria maxima* *Phragmites australis* *Equisetum fluviatile* *Typha angustifolia*	Szczepanski 1977
	Lettuce, radish, tomato, cucumber	Bonasera, Lynch, and Leck 1979
	Typha latifolia	McNaughton 1968
	Phragmites communis	Szczepanska 1971

Table 2

Results of Lettuce Seedling Radical Inhibition by Aqueous Extracts of Selected Aquatic Plants

Plant	Control	Percent Control		
		1 ml	5 ml	10 ml
Brasenia schreberi Gmel.	100a* (60)**	107b (40)	46c (40)	18d (40)
Cabomba caroliniana Gray	100a (30)	99a (30)	51b (30)	42b (30)
Ceratophyllum demersum L.	100a (45)	34b (40)	26c (40)	20d (40)
Eleocharis acicularis (L.) R. and S.†	100a (45)	69b (30)	39c (30)	22d (30)
Eleocharis obtusa (Willd.) Schultes†	100a (45)	73b (36)	38c (36)	25d (36)
Hydrilla verticillata (L.f.) Royle	100a (30)	91a (30)	66b (30)	39c (30)
Juncus repens Michx.	100a (60)	49b (40)	18c (40)	14c (40)
Limnobium spongia (Bosc.) Steud.	100a (30)	63b (30)	32c (30)	27c (30)
Myriophyllum aquaticum (Vell.) Verdc.	100a (40)	71b (40)	57c (40)	51c (40)
Myriophyllum spicatum L.	100a (45)	68b (40)	48c (40)	36d (40)
Najas guadalupensis (Spreng.) Magus	100a (30)	91a (30)	38b (30)	26c (30)
Nymphaea odorata Ait. (leaves and stems)	100a (60)	101a (40)	68b (40)	22c (40)
Nymphaea odorata Ait. (roots)	100a (60)	40b (40)	9.3c (40)	5c (35)
Nymphoides cordata (Ell.) Fern.	100a (60)	76b (40)	52c (40)	31d (40)
Potamogeton foliosus Raf.	100a (40)	73b (40)	43c (40)	39c (40)
Sparganium americanum Nutt.††	100a (60)	77b (45)	48c (45)	40d (45)
Vallisneria americana Michx.	100a (60)	113b (40)	45c (40)	17d (38)

* Values followed by the same letters are not significantly different according to the Duncan's Multiple Range Test at $P \leq 0.05$.

** Values in parentheses are numbers of cases.

† 200 g fresh plants was blended with 350 ml of water.

†† 200 g fresh plants was blended with 225 ml of water.

Table 3

Results of *Lemna minor* Frond Growth Inhibition By Aqueous Extracts of Selected Aquatic Plants

Plant	Control	Percent Control		
		0.038 ml	0.188 ml	0.375 ml
Brasenia schreberi Gmel.	100a*,**	90a	47b	36b
		94a	67b	52b
Cabomba caroliniana Gray	100a	78b	73b	43c
		97a	62b	40c
Ceratophyllum demersum L.	100a	104a	65b	66b
		127b	81c	71c
Eleocharis acicularis (L.) R. and S.†	100a	113a	103a	82b
		94a	87a,b	64b
Eleocharis obtusa (Willd.) Schultes†	100a	133a	128a	129a
		108a	105a	85b
Hydrilla verticillata (L.f.) Royle	100a	98a	88a	69b
		103a	90a	66b
Juncus repens Michx.	100a	106a	90a	61b
		111a	81a,b	69b
Limnobium spongia (Bosc.) Steud.	100a	101a	79b	60c
		125b	79c	56d
Myriophyllum aquaticum (Vell.) Verdc.	100a	102a	43b	25c
		89a	40b	38b
Myriophyllum spicatum L.	100a	109a	88a,b	56c
		97a	78b	52c
Najas guadalupensis (Spreng.) Magus	100a	103a	79b	67b
		106a	58b	41b
Nymphaea odorata Ait. (leaves and stems)	100a	70b	40c	19d
		97a	34b	23c
Nymphaea odorata Ait. (roots)	100a	94a	50b	39b
		111b	53c	46c
Nymphoides cordata (Ell.) Fern.	100a	113a	80b	70b
		104a	81b	59c
Potamogeton foliosus Raf.	100a	108a	89a	56b
Sparganium americanum Nutt.††	100a	116a,b	94a	78a
		105a	82a,b	51c
Vallisneria americana Michx.	100a	114a,b	114a,b	80a
		110a	84a,b	70b
		109a	91a,b	76b

* Values followed by the same letters in the same line are not significantly different according to the Duncan's Multiple Range Test at $P \leq 0.05$.

** Values across a line represent a single assay. Each assay included a control against which other values were compared. Each plant was assayed twice.

† 200 g fresh plants was blended with 350 ml of water.

†† 200 g fresh plants was blended with 225 ml of water.

Table 4

Results of *Lemna minor* Dry Weight Reduction by Aqueous Extracts of Selected Aquatic Plants

Plant	Percent Control*		
	0.038 ml	0.188 ml	0.375 ml
Brasenia schreberi Gmel.			
Cabomba caroliniana Gray			
Ceratophyllum demersum L.	103	84	84
Eleocharis acicularis (L.) R. and S.**	112	89	81
Eleocharis obtusa (Willd.) Schultes**	133	132	128
Hydrilla verticillata (L.f.) Royle			
Juncus repens Michx.	111	96	81
Limnobium spongia	102	93	84
(Bosc.) Steud.	115	94	81
Myriophyllum aquaticum (Vell.) Verdc.			
Myriophyllum spicatum L.	97	89	72
Najas guadalupensis	89	71	89
(Spreng.) Magus	99	80	71
Nymphaea odorata Ait. (leaves and stems)	75	59	37
Nymphaea odorata Ait. (roots)	100	94	73
Nymphoides cordata (Ell.) Fern.			
Potamogeton foliosus Raf.	101	88	83
	93	77	86
Sparganium americanum	99	91	92
Nutt.†	112	86	74
Vallisneria americana Michx.	107	81	67

* Data for duplicate assays are given. Each data set was compared with its own control. Data presented have not been statistically analyzed.

** 200 g fresh plants was blended with 350 ml of water.

† 200 g fresh plants was blended with 225 ml of water.

Table 5

Results of *Lemna minor* Chlorophyll-a Reduction By Aqueous Extracts of Selected Aquatic Plants

Plant	Control	Percent Control* 0.038 ml	0.188 ml	0.375 ml
Brasenia schreberi Gmel.	100a**,†	94	30	22
		91	55	38
Cabomba caroliniana Gray	100a	96a	63b	27c
		84	69	28
Ceratophyllum demersum L.	100a	70a	74a	76a
		101	64	54
Eleocharis acicularis (L.) R. and S.††	100a	108a	89a,b	71c
		91	80	54
Eleocharis obtusa (Willd.) Schultes ††	100a	135a	134a	103a
		113	92	86
Hydrilla verticillata (L.f.) Royle	100a	98a	90a	53b
		106a	78a,b	63b
Juncus repens Michx.	100a	93a	72b	52c
		107a	74b	64b
Limnobium spongia (Bosc.) Steud.	100a	117a	85a	145a
		100a	66b	33b
Myriophyllum aquaticum (Vell.) Verdc.	100a	61	60	37
		77	31	27
Myriophyllum spicatum L.	100a	103a	75b	32c
		82a	70a	33b
Najas guadalupensis (Spreng.) Magus	100a	107a	42b	55a,b
		120a,b	110a	62a,c
Nymphaea odorata Ait. (leaves and stems)	100a	97a	29b	9b
		105	71	46
Nymphaea odorata Ait. (roots)	100a	85a	63a	39a
		118	37	28
Nymphoides cordata (Ell.) Fern.	100a	73	53	39
		100	63	38
Potamogeton foliosus Raf.	100a	100a	89a	35b
		104a	84b	58c
Sparganium americanum Nutt.‡	100a	79a	72a	56a
		114a,b	83a,c	39d
Vallisneria americana Michx.	100a	113a	108a	62b
		110a	82a	53b

* Data for duplicate assays are given. Each data set was compared with its own control. All data have not been statistically analyzed.

** Values followed by the same letters in the same line are not significantly different according to the Duncan's Multiple Range Test at $P \leq 0.05$.

† Values across a line represent a single assay. Each assay included a control against which other values were compared. Each plant was assayed twice.

†† 200 g fresh plants was blended with 350 ml of water.

‡ 200 g fresh plants was blended with 225 ml of water.

Appendix A: Annotated Bibliography of Aquatic Plant Allelopathy

1. Table 1 lists in alphabetical order those aquatic plants that have been described as allelopathic. The table summarizes the plant(s) affected in each case and gives the literature reference. Presented below is an annotated list, alphabetical by author, of all references given in Table 1. Bibliographic information for each of the references is given in the References at the conclusion of the main text.

Agami and Waisel (1985) conducted outdoor competitive experiments in 200-ℓ containers. The effect on growth of *Najas marina* L. was observed when co-planted with *Myriophyllum spicatum* L., *Potamogeton lucens* L., and *Scirpus litoralis* Schard. Only *M. spicatum* reduced the growth of *Najas*. Submerging *Najas* in water in which *M. spicatum* had been grown also reduced *Najas* growth. The authors suggest there exists a bilateral negative relationship between *Najas* and *Myriophyllum* that is allelopathic in nature.

Ashton, DiTomaso, and Anderson (1985) axenicly cultured *Eleocharis coloradoensis*, periodically removed the culture media, and separated the leached organics into several fractions. The fractions were separately bioassayed and found to be inhibitory toward *Hydrilla verticillata* and *Potamogeton pectinatus* as well as toward tomato cell cultures and lettuce seedling roots.

Bonasera, Lynch, and Leck (1979) tested various leaf, stem, root, rhizome, and soil extracts of *Ambrosia trifida*, *Bidens laevis*, *peltandra virginica*, and *Typha latifolia* against root growth of lettuce, radish, tomato, and cucumber. Some extracts of all four marsh species were inhibitory toward at least some of the test plants. Of the bioassay species, lettuce was the most sensitive, radish and tomato somewhat less sensitive, and cucumber the least sensitive.

Elakovich and Wooten (1987) found that extracts of *Brasenia schreberi* inhibited lateral growth of the eukaryotic alga *Chlorella pyrenoidosa*, the prokaryotic alga *Anabena flosagua*, nine different bacteria, and lettuce. The authors suggest that these phytotoxic properties contribute to the observed dominance of *B. schreberi* in aquatic environments.

Frank and Dechoretz (1980) planted *Potamogeton nodosus* Poir and *P. pectinatus* L. in *Eleocharis coloradoensis* (Britt.) Gilly sod and also in aquaria to which was daily added 500 ml of leachate from *E. coloradoensis* sod. New shoots of *Potamogeton* were significantly reduced in each case. There was also a reduction in biomass. *Potamogeton pectinatus* was more sensitive to the influence of *E. coloradoensis* than was *P. nodosus*.

Kulshreshtha and Gopol (1983) planted *Hydrilla verticillata* with *Ceratophyllum demersum*, and in a separate concrete tank, with *C. muricatum*. The two species in each tank were separated by a wire netting so that the plants were not competing for space. Control tanks contained single species. After 70 days, both *Ceratophyllum* species

grown with hydrilla had died completely, whereas the controls were healthy. Aqueous extracts of hydrilla and of *Hygroihiza* sp. were also detrimental to *Ceratophyllum* growth.

Lee and Guh (1982) found rice plants were most damaged by *Sagittaria pygmaea* 31 to 37 days after transplanting. *Sagittaria pygmaea* could be controlled by application of herbicides. (This publication is in Korean. Only the abstract is available in English--Chem. Abstr., 98:102600m, 1983.)

McNaughton (1968) reported the autotoxic nature of *Typha latifolia*. He found *T. latifolia* seed germination was inhibited completely by an aqueous extract of cattail leaves, but only partially by the same extract from which phenolic compounds had been removed. Seedling growth was inhibited by water from cattail marshes and by water squeezed from soil in which cattails were growing.

Nichols and Shaw (1982) review management tactics for integrated aquatic weed management. They devote two short paragraphs to "small spikerush" in which they note that *Eleocharis coloradoensis*, *E. acicularis*, and *E. parvula* displace other aquatic plants. They imply that *Potamogeton crispus* is prominent among the displaced plants, but the reference they provide does not confirm this. They report field observations, not experimental data.

Oborn et al. (1954) in a frequently quoted early publication, states that "laboratory evidence over a 2-year period indicated that either or both of these plants [dwarf arrowhead and needle spikerush] growing in association with the taller more obnoxious pond weed growth would, over a period of time, crowd out the pond weed growth." He gives no experimental details or references.

Singhvi and Sharma (1984) examined the effects of the extract of different plant parts of *Ludwigia adscendens* Linn. and *Ipomoea aquatica* Forsk on the growth and biomass of *Pennisetum typhoideum* Rich. *Ludwigia adscendens* seems to be growth stimulatory while *I. aquatica* is growth inhibitory. They suggest that the growth-promoting effect may be due to terpenoids and that the growth-inhibiting effect may be due to phenols.

Sutton (1986) established *Eleocharis genticulata* (L.) R. and S. and *Sagittaria graminea* Michx. separately in 7,790-ℓ circular, plastic-lined outdoor pools. Sprouted *Hydrilla verticillata* tubers were introduced into these pools. Shoot weight of hydrilla was not reduced by *E. genticulata* in one experiment, but in two replicate experiments, shoot weight, root weight, and number of tubers produced in an 8-week growth period were all reduced. Hydrilla shoot weight, root weight, and tuber number were all reduced to a greater extent when co-planted with *S. graminea*. Sutton suggests *S. graminea* has the greatest potential for use in reducing hydrilla growth.

Szczepanska (1971) established experimental cultures in 5-ℓ buckets, 10-ℓ pots, or 0.8-ℓ plastic boxes. Soil was varied, ranging from sand to peat to garden soil to sediment from a eutrophic lake. Monospecific cultures as well as the combinations of *Phragmites communis* and *Typha latifolia*, *Phragmites communis* and *Schoenoplectus lacustris*, and *Phragmites communis* and *Equisetum limosum* were cultivated. They found plant-plant influences depend on soil type. *Typha latifolia*, *S.*

lacustris, and *E. limosum* all caused a decrease in *P. communis* growth. *Schoenoplectus lacustris* also caused a decrease in *E. limosum* growth.

Later work by Szczepanska (1977) examined interactions between *Phragmites communis* Trin. and *Carex hudsonii* Bennet grown on garden soil in 10-ℓ pots over 4 years. *Carex* (a sedge) growth steadily increased as *Phragmites* (a reed) growth decreased, each as compared with monoculture controls. These results suggest that the frequently observed field succession of sedge pushing out rushes is at least partly allelopathic in nature.

Szczepanski (1977) reviews work of his own and others on allelopathy as a means of biological control of water weeds. He reports results of competition studies of *Typha latifolia* and *Phragmites australis* (= *P. communis*) with six other aquatic plants.

Titus and Stephens (1983) carried out field studies with *Vallisneria americana*, *Potamogeton amplifolius*, and *Chara vulgaris*. They selected random 0.25-m^2 quadrats within monospecific *V. americana* stands for biomass studies. Neighbor removal experiments involved individuals of *V. americana* growing naturally within relatively dense stands of *P. amplifolius* and *C. vulgaris*. Neighbors of some individuals were carefully removed, and eight variables were examined at the end of the growing season. Neighbors had a significant influence on the growth pattern of *V. americana*.

Yeo (1980a) observed *Eleocharis coloradoensis* over a 12-year period in several water systems in California. He found that *Potamogeton pectinatus*, *P. nodosus*, *P. prisillus*, and *Najas guadalupensis* were displaced by *E. coloradoensis* within 2 years. *Elodea canadensis* and *E. nuttallii* were displaced, but required longer than 2 years. Five additional plants were not displaced by *E. coloradoensis*, including *E. acicularis* and *E. parvula*.

Yeo and Fisher (1970) observed that *Eleocharis acicularis* in natural stands crowded out *Elodea canadensis* and *Potamogeton crispus*. When *E. acicularis* was planted in an irrigation canal where *Potamogeton pectinatus* existed, the *P. pectinatus* had disappeared by the time (3 years later) the *Eleocharis* was established.

Yeo and Thurston (1984) conducted outdoor competitive experiments in 75-ℓ plastic tubs with a surface area of 0.21 m^2. Planting schemes included the seven individual aquatic plants, each aquatic plant co-planted with *Eleocharis coloradoensis*, and *E. coloradoensis* alone. Each planting scheme was replicated six times (90 tubs). They present a detailed discussion of their results. Dry weight of all seven of the aquatic weeds was reduced when the plants were grown with *E. coloradoensis*; for six of the seven, dry weight was ≤35 percent of the dry weight of aquatic weeds in monoculture.