J. Aquat. Plant Manage. 27: 57-65

Influence of Iron on *Hydrilla*'s Response to Fluridone[1]

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ABSTRACT

Hydrilla (*Hydrilla verticillata* (L.f.) Royle) was exposed to fluridone (1-methyl-3-phenyl-5-[3-(trifluromethyl)phenyl]-4 (1H)-pyridinone) concentations of 0. 0.05, 0.25, and 0.5 mg/l for 1, 3, or 5 weeks. Plants were exposed to iron concentrations in the water which varied from 0 to 5 mg/l either before, after, or during the fluridone treatments. Recovery from fluridone treatment was directly related to the concentration of active iron (Fe^{2+}) in the plant at the time of treatment. The concentration of iron in the water during treatment did not reduce the phytotoxicity of fluridone. Plants exposed to fluridone for 3 weeks did not recover even though the active iron concentration in the plant was high before treatment. These results may partly explain the variable efficacy which has been reported in the literature, and may offer plant managers a tool for predicting the impact of fluridone applications to field populations of hydrilla.

Key words: Active iron, herbicide efficacy, nutritional status, carotenoids, chlorophyll.

INTRODUCTION

Fluridone inhibits plant growth by disrupting RNA synthesis (Waldrep and Taylor 1976) and the synthesis of photosynthetic pigments (Bartels and Watson 1978; Berard *et al.* 1978). Studies with wheat seedlings (Bartels and Watson 1978) and cell-free carotogenic systems suggest that fluridone interferes with a desaturase enzyme complex which converts phytoene to gamma-carotene (Sandmann and Boger 1986). Limited translocation of fluridone has been observed by aquatic plants (Marquis *et al.* 1981; Anderson 1981). Fluridone effectively controlled the growth of some aquatic plants (Arnold 1979; McCowen *et al.* 1979; Rivera *et al.* 1979). Others have reported that it was less effective, however (Dechoretz and Frank 1978; Hall and Westerdahl 1983; Wells *et al.* 1986). Susceptibility of plants to herbicide treatment depends on the stage of growth (Ross and Lembi 1985) and thus indirectly upon the conditions under which the plants are growing. Information on this subject is limited for aquatic plants. Anderson (1981) reported that germinating American pondweed (*Potamogeton nodosus*) winter buds treated with fluridone and exposed to light did not grow as well as similarly treated winter buds grown in the dark. Westerdahl and Hall (1987) grew hydrilla and water milfoil (*Myriophyllum spicatum*) on nutrient-rich and nutrient-poor substrates and subsequently treated them with fluridone. They reported that hydrilla growing on the nurtient-poor substrate did not respond to fluridone treatment. In contrast, water milfoil growth and pigment production were inhibited for plants grown on both substrates.

Carotenoid synthesis is influenced by environmental conditions including the concentration of iron in the growing medium (Kirk and Tilney-Bassett 1967). The importance of iron may be its presence in the desaturase enzyme complexes such as those involved in carotenoid biosynthesis (Sandmann and Boger 1986; Strittmatter *et al.* 1974). Iron concentrations in lakes are known to vary considerably. For example, the concentration of iron in lake waters and sediments varies geographically among lakes (Linthurst *et al.* 1986) and seasonally within a lake (Wetzel 1983). Therefore, it is reasonable to assume that macrophytes treated with an inhibitor of carotenoid biosynthesis, such as fluridone, may respond differently depending upon their iron nutritional status.

The purpose of this study was to answer the following questions:

1) Does an increase in the iron concentration in the water following a fluridone application influence hydrilla's recovery from fluridone treatment?
2) Does the concentration of iron in the water at the time of a fluridone application reduce fluridone's impact?
3) Does a plant's internal iron concentration at the time of a fluridone application influence its recovery?
4) Does a longer exposure to fluridone overcome internal iron effects?

METHODS

Figure 1 compares the various treatment and sampling regimes used in the experiments reported here.

Experiment One. The purpose of this experiment was to determine if exposure of hydrilla to different concentrations of iron after a 1-week treatment with fluridone influenced recovery from fluridone injury. In this experiment 15-cm apical cuttings from dioecious hydrilla plants (from stock cultures maintained at the USDA Aquatic Weed Lab, Davis, CA) were planted in 125 ml plastic pots containing modified UC mix (Spencer and Anderson 1986), and allowed to grow in the greenhouse with a 14-h photoperiod for 7 days. The plants were transferred to 18-1 glass jars filled with well water. The well water used in these experiments contained low total iron concentrations (0.046 ± 0.027 mg/l; mean ± standard deviation, N = 5). The jars were divided into four groups of 12 jars each. Each jar contained three plants growing in individual pots. The plants in each group were treated with one of the following

[1]Mention of a trade name does not constitute a warranty, guarantee, or an endorsement of the product by the U.S. Department of Agriculture.

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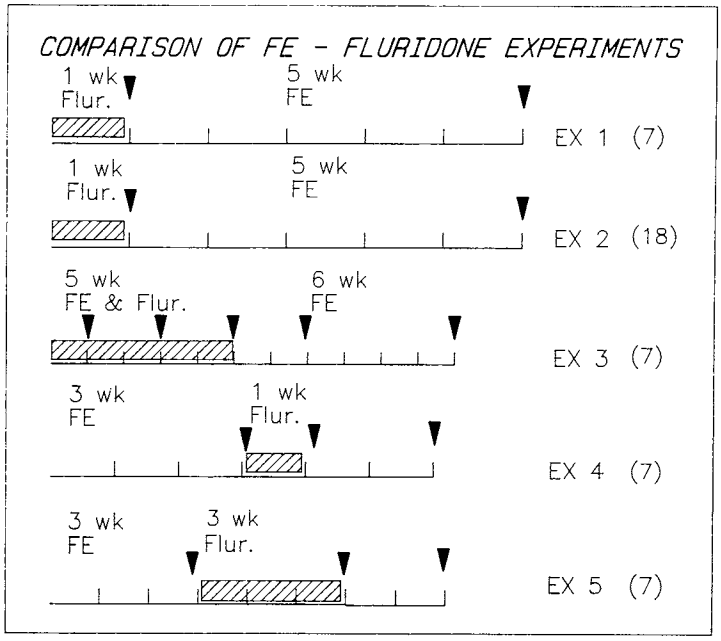

Figure 1. Diagram comparing the timing of iron and fluridone treatments used in the experiments. Solid triangles represent times at which pigment or active iron samples were collected. Dry weights were measured at the end. The number in parenthesis indicates plant age (i.e., days since cuttings were planted) at the start of the experiment.

fluridone concentrations for 1 week: 0, 0.05, 0.25, 0.5 mg/l. Then plants in each group of three jars received one of the following iron treatments: 0, 0.1, 1, or 5 mg iron/l (as Fe-EDTA) added each week for five weeks. One-cm apical cuttings were randomly collected from each jar and pigments extracted using DMSO (Spencer and Ksander 1987) at the end of the fluridone treatment and 5 weeks later (Figure 1). Chlorophyll a is expressed as μg/g fresh weight and carotenoids as μSPU/g fresh weight (one specified plant pigment unit (SPU) is approximately 1 mg (Wetzel and Likens 1979)). At the end of the experiment we measured plant dry weights (105 C for 48 h). We measured internal iron concentrations of shoot tissue using the method described by Pierson and Clark (1984). This technique measures active iron (Fe^{2+}), which is more closely correlated with leaf chlorophyll content than total iron for some terrestrial plants (Katyal and Sharma 1980). Pigment data from both sampling dates were combined and analyzed using a one-way analysis of variance. For this analysis the treatments were: initial (= after initial fluridone treatments); 1 week fluridone + 5 weeks of 0 mg/L iron; 1 week fluridone + 5 weeks of 0.1 mg/L iron; 1 week fluridone + 5 weeks 1.0 mg/l iron; and 1 week fluridone + 5 weeks 5.0 mg/l iron. We used a two-way analysis of variance to analyze the data on active iron and total plant weight for effects due to iron, fluridone, or an iron x fluridone interaction. All statistical analyses were calculated using SAS (SAS Institute 1987).

Experiment Two. This experiment was a repeat of the first. In this experiment hydrilla was grown from 15-cm apical cuttings planted in modified UC mix, but the plants were 18 days old before use. The experimental procedures and treatments were similar to those used in Experiment One.

Experiment Three. We performed a third experiment to determine if high iron concentrations in the water at the time of fluridone treatment would reduce fluridone's phytotoxicity to hydrilla. The experimental details were similar to those described above. In this experiment, fluridone (0 and 0.25 mg/l) was applied weekly to plants which were also receiving weekly iron treatments (0, 0.05, 0.1, and 1 mg/l). Four replicates were used per treatment combination. The simultaneous treatments continued for five weeks. (Note that the fluridone and iron concentrations were maintained by replacing the water in the culture vessel and adding sufficient fluridone and iron to establish the original treatment concentrations each week for 5 weeks.) Plants continued to receive the iron treatments for 6 more weeks following conclusion of the fluridone treatments. Plants were harvested after 11 weeks and dry weights determined (105 C for 48 h). One-cm shoot tips were harvested from each jar at 1, 3, 5, 7, and 11 weeks for pigment determinations (Figure 1). Pigment data were analyzed using an analysis of variance procedure which is appropriate for repeated measures (PROC GLM, SAS Institute 1987).

Experiment Four. The purpose of this experiment was to test the hypothesis that internal concentrations of active iron influence the response of hydrilla to fluridone treatment. In this experiment 15-cm apical cuttings from dioecious hydrilla were planted in small plastic pots containing modified UC mix, and allowed to grow in the greenhouse under a 14-h photoperiod for 7 days. At this point 7 plants were harvested (Figure 1). The remaining plants were transferred to 18-1 glass jars filled with water. The jars were divided into four groups of 13 jars each. Each group received one of the following iron treatments: 0, 0.1, 1, or 5 mg/l of iron (as Fe-EDTA) added each week for three weeks. After 3 weeks, the three plants growing in 1 jar from each iron treatment were harvested. The remaining plants from each iron treatment were treated with fluridone (0, 0.05, 0.25, 0.5 mg/l) for 1 week. The experiment followed a factorial design (four levels of iron pretreatment x four levels of fluridone treatment x three replicates = forty-eight jars; each replicate is a jar with three plants). After the 1-week fluridone treatment, 1-cm apical cuttings were randomly collected from each jar for pigment analysis. The plants were allowed to grow for 2 weeks following the conclusion of the fluridone application and harvested. At each harvest, plants were analyzed for pigment content and active iron. Following the final harvest, we also determined plant dry weights. Pigment data from harvests 3 and 4 were analyzed together using analysis of variance as in Experiment Three. Active iron and total plant weight were analyzed as in Experiment One.

Experiment Five. An additional experiment was similar to Experiment Four except that the exposure to fluridone was 3 weeks instead of 1 week. The plants were harvested 2 weeks after the end of the fluridone exposure (Figure 1).

RESULTS

Experiment One. Total dry weight (Figure 2 B) was significantly reduced by the fluridone treatment, but not influenced by the ensuing iron treatments. Pigment concen-

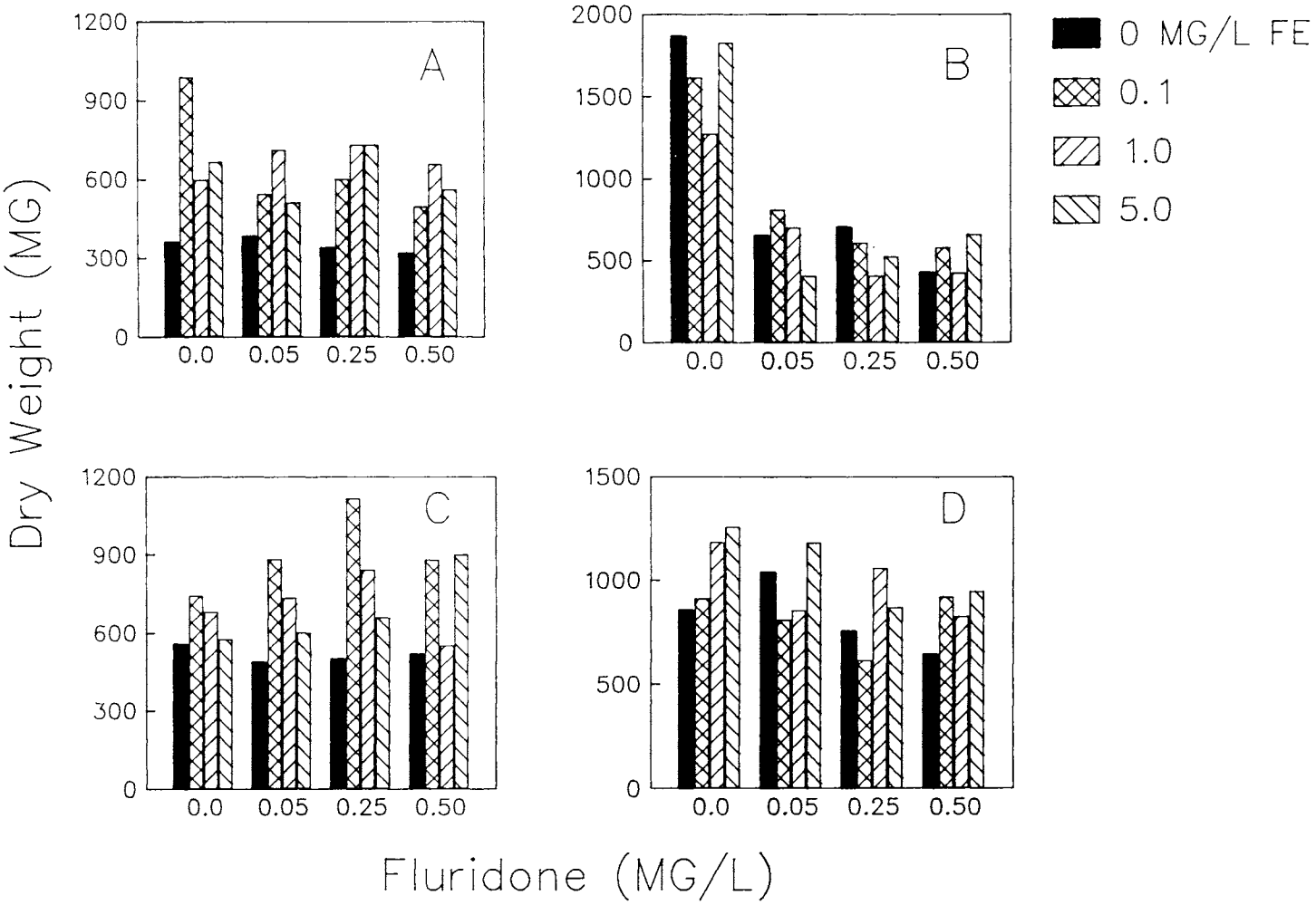

Figure 2. Plant weight for hydrilla. In Experiment Two (A) plants were treated with fluridone for 1 week followed by 5 weeks of iron treatments. In Experiment One (B) plants were treated with fluridone for 1 week followed by 5 weeks of iron treatments. In Experiment Four (C) plants were treated with iron for 3 weeks followed by a 1 week fluridone treatment. Experiment Five is shown in (D). Plants were treated with iron for 3 weeks followed by 3 weeks of fluridone. Plotted values are means of three replicates.

trations (Figure 3 C, D) were greater for iron treated plants. Active iron in the plants varied from 0.007% to 0045% and was related to the iron concentration in the water during the three week period before fluridone treatment (Figure 4B).

Experiment Two. In this experiment, treatment with iron following an initial 1-week fluridone treatment had different consequences for hydrilla. Total dry weight increased significantly for iron-treated plants, but was unaffected by fluridone (Figure 2 A). Concentrations of both chlorophyll a and carotenoids were significantly reduced in plants exposed to fluridone for 1 week (Figure 3 A, B; note the solid bars). Comparison of these pigment concentrations with those measured at the end of the experiment (the hatched bars in Figure 3 A, B) shows that increasing the concentration of iron in the water following fluridone treatment significantly enhanced the recovery of pigment concentrations in hydrilla. Concentrations of active iron in the plants at the end of the experiment were similar to those measured for plants in Experiment One (Figure 4A).

Experiment Three. Iron concentrations in the water did not reduce the effects of 0.25 mg/l fluridone on hydrilla during the five weeks that both were simultaneously applied. Pigment concentrations (Figure 5) declined immediately following the initial fluridone treatment. They increased slightly but remained low during the 5-week fluridone treatment. When the fluridone treatment ended, pigment concentrations began to increase more rapidly. At final harvest, pigment concentrations in plants treated with iron following the fluridone treatment were higher than those in fluridone treated plants which were not subsequently treated with iron. Plant dry weight was significantly reduced by the fluridone treatment, but not affected by either the iron treatment or an interaction between the treatments (Table 1).

Experiment Four. In this experiment plant dry weight was not affected by either treatment or an interaction (Figure 2 C). Pigment concentrations were significantly influenced by both fluridone and iron treatments. The interaction term in the analysis of variance was not significant. Chlorophyll a concentrations were reduced by the fluridone treatment (Figure 6; compare the 3- and 4-week samples in A with those in B, C, D), but plants which had been pre-treated with iron had higher concentrations of

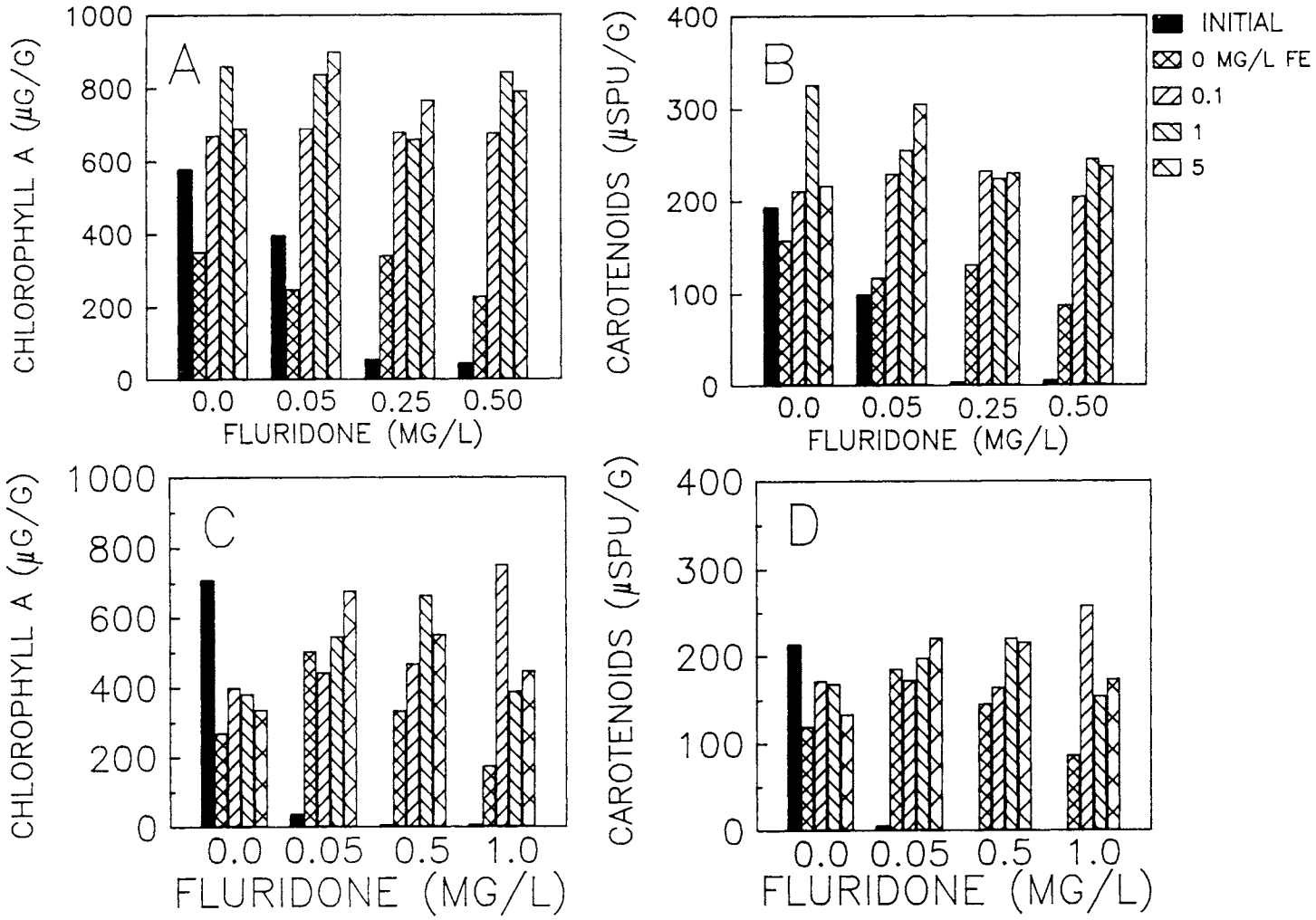

Figure 3. Pigment concentrations for hydrilla from Experiment Two (A, B) and Experiment One (C,D). Plants were treated with fluridone for 1 week followed by 5 weeks of iron treatments. Solid bars represent pigment concentrations in plants immediately after the 1-week fluridone treatment. Cross hatched bars are pigment concentrations 5 weeks later for plants receiving combinations of iron and fluridone.

chlorophyll a. Similar trends were evident 4 weeks after the fluridone treatment (Figure 6; 6-week samples). The response of carotenoids (data not shown) was very similar to that of chlorophyll a. Tissue concentrations of active iron increased following the three week treatment with iron (Figure 4 C; compare the dashed line with the 3-week sample). Although active iron concentrations had declined by the end of the experiment, significant differences in tissue active iron were still apparent three weeks later (Figure 4 C; compare the 3-week sample with those collected at the end of the experiment).

Experiment Five. The iron and fluridone treatments had statistically significant effects on plant dry weight. Treatment with fluridone resulted in lower values (Figure 2 D). Plants grown with iron had higher values. The statistical interaction between iron and fluridone was not significant. The 3-week fluridone treatment caused reduced chlorophyll concentrations (Figure 7; compare the 3-week samples with those collected at 6 and 8 weeks). The 3-week treatment with iron (before the fluridone treatment) did not enhance chlorophyll a concentrations following the fluridone treatment (Figure 7; 6-week sample, A vs. B, C, D) or 2 weeks later (Figure 7; 8-week sample). Carotenoid concentrations displayed a similar response (data not shown). Plant concentrations of active iron increased following the 3-week iron treatment Figure 4 D) and were similar to those in Experiment Four, except that tissue active iron concentrations for plants grown in 1 mg/l iron were lower. In Experiment Five tissue active iron was greater in plants grown at higher iron concentrations except for plants treated with 0.05 mg/l fluridone (Figure 4 D). Tissue active iron was lower at the end of Experiment Five than at the end of Experiment Four (Figure 4 C, D).

DISCUSSION

The persistence of fluridone in natural waters varies (West *et al.* 1979 and 1983; Muir *et al.* 1980). Values for the half life of fluridone in water columns of lakes and ponds ranging from 1 to 60 days have been reported. Fluridone treatments in these experiments were maintained for 1, 3, or 5 weeks to simulate the reported exposures that plants in fluridone treated lakes and ponds experience.

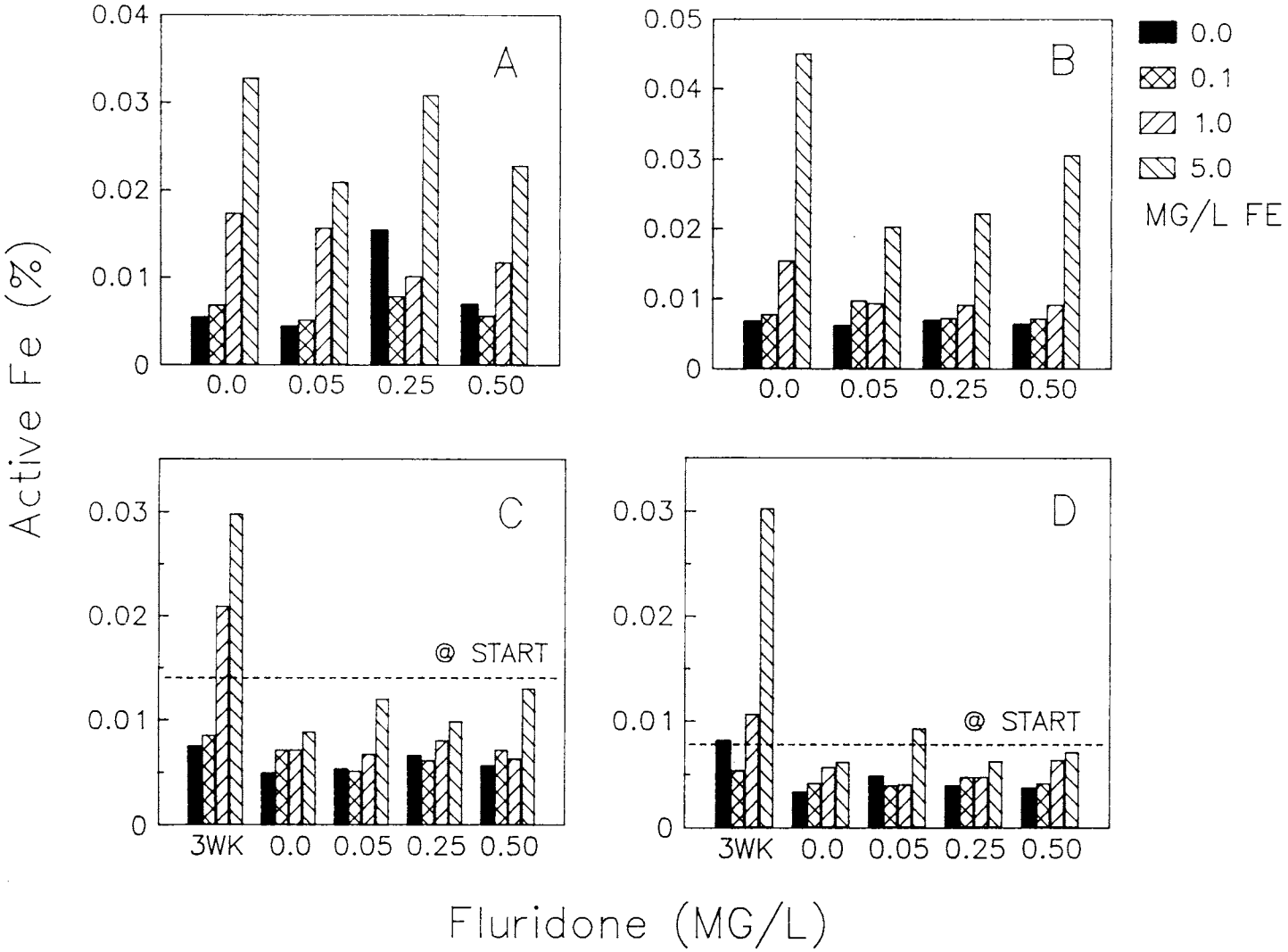

Figure 4. Active iron for hydrilla tissue in Experiment Two (A), Experiment One (B), Experiment Four (C), and Experiment Five (D). The dashed lines in C and D represent the mean (N = 7) concentration in plants before the iron treatment. The group of bars labeled '3WK' represents the mean (N = 4) concentration for plants after the iron treatment and the other groups of bars are the mean (N = 3) concentrations at the end of the experiment.

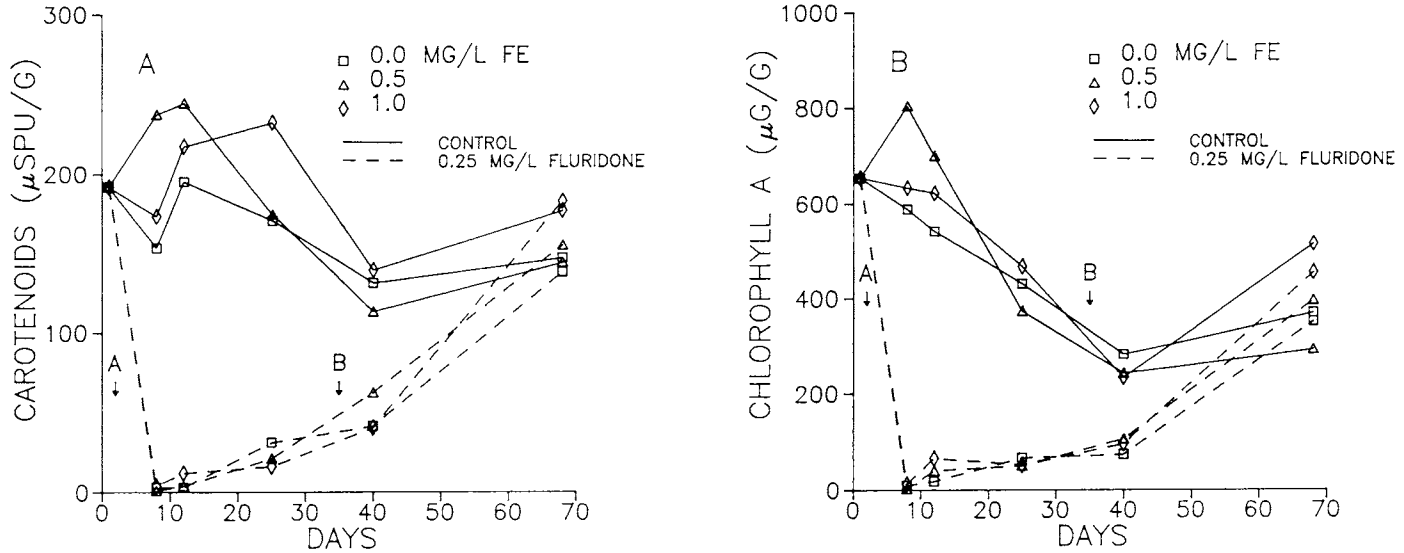

Figure 5. Mean pigment concentrations (N = 4) vs. time for hydrilla in Experiment Three. Plants were treated with fluridone and iron for 5 weeksfollowed by 6 weeks of iron treatments. The arrow marked. A denotes the start of the fluridone treatment, and B denotes the end of fluridone treatment.

TABLE 1. PLANT DRY WEIGHTS FOR EXPERIMENT THEE. VALUES ARE THE MEAN ± STANDARD ERROR (N = 4).

IRON (mg/L)	FLURIDONE (mg/L)	DRY WEIGHT (mg)
0	0	1032 ± 208
0	0.25	339 ± 75
0.5	0	1133 ± 117
0.5	0.25	198 ± 34
1.0	0	1363 ± 241
1.0	0.25	252 ± 40

The somewhat different growth responses observed in Experiments One and Two, may be due to differences in plant status at the time of treatment. In Experiment Two, the plants were 18 days post planting when the fluridone treatments were made, but in Experiment One they were only 7 days post planting when treated. Comparison of the pigment concentrations after the initial fluridone treatment showed that "older" plants were less affected by the initial fluridone treatment. In contrast, shoot tips from the 7-day-old plants were virtually without pigments following similar 1-week treatments. The addition of iron enhanced the recovery of pigment concentrations in fluridone-treated plants in both experiments. This implies that the lag between pigment recovery and plant growth functions that result in biomass accumulation was longer for "younger" plants than for "older" plants. Other workers have also reported that hydrilla recovered from short exposures to fluridone. Van and Steward (1985) treated 21-day-old hydrilla (originally grown from 15-cm apical cuttings) in a flow-through system (i.e., exposure to fluridone was less than 7 days) and reported that pigment concentrations were not distinguishable from un-treated controls after six weeks.

Results of Experiment Three show that the iron concentration in the water at the time of treatment did not reduce fluridone's phytotoxic effects. Pigment concentrations were low and remained low during the entire five week fluridone treatment used in this experiment. Plants treated with iron recovered somewhat quicker than those not treated with iron. In these plants, recovery occurred even though the plants were exposed to fluridone for five weeks.

The results of Experiment Four implicate the internal concentration of active iron as the factor regulating hydrilla's recovery from fluridone treatment. Chlorophyll a and carotenoid concentrations 24 days after treatment were strongly correlated with active iron in the plant before treatment (Figure 8). The correlation disappeared, if data from non-fluridone treated plant were included,

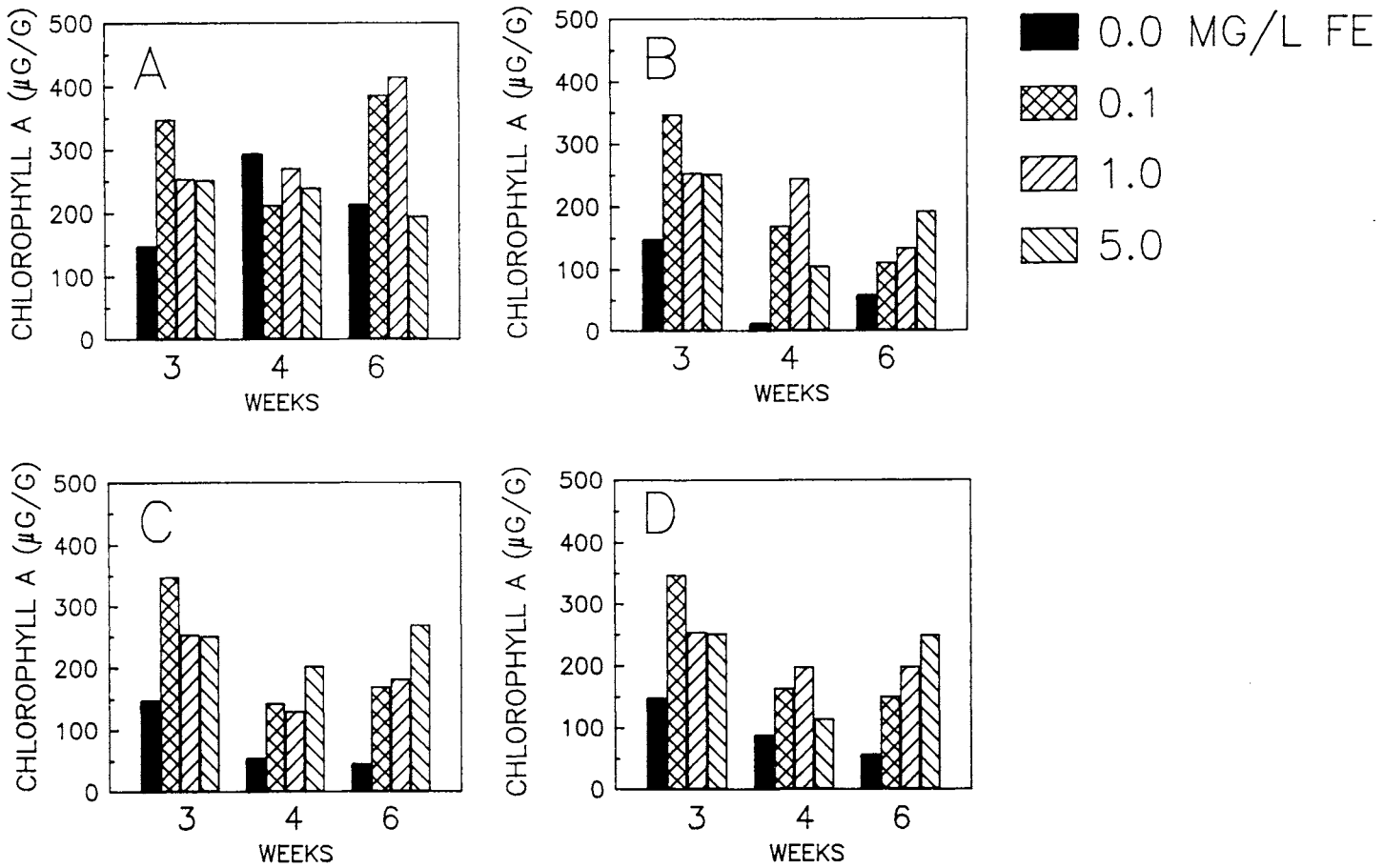

Figure 6. Chlorophyll a concentrations for hydrilla from Experiment Four. Panel A is for plants not treated with fluridone; B is for those treated with 0.05 mg/l fluridone; C is for plants treated with 0.25 mg/l fluridone; and D for plants treated with 0.50 mg/l fluridone. Plotted values are the mean of 3 replicates. The 3-week sample was taken following the iron treatment, just prior to the fluridone treatment. Fluridone effects are evident by comparing the pigment concentrations in panels B, C, and D with those in panel A.

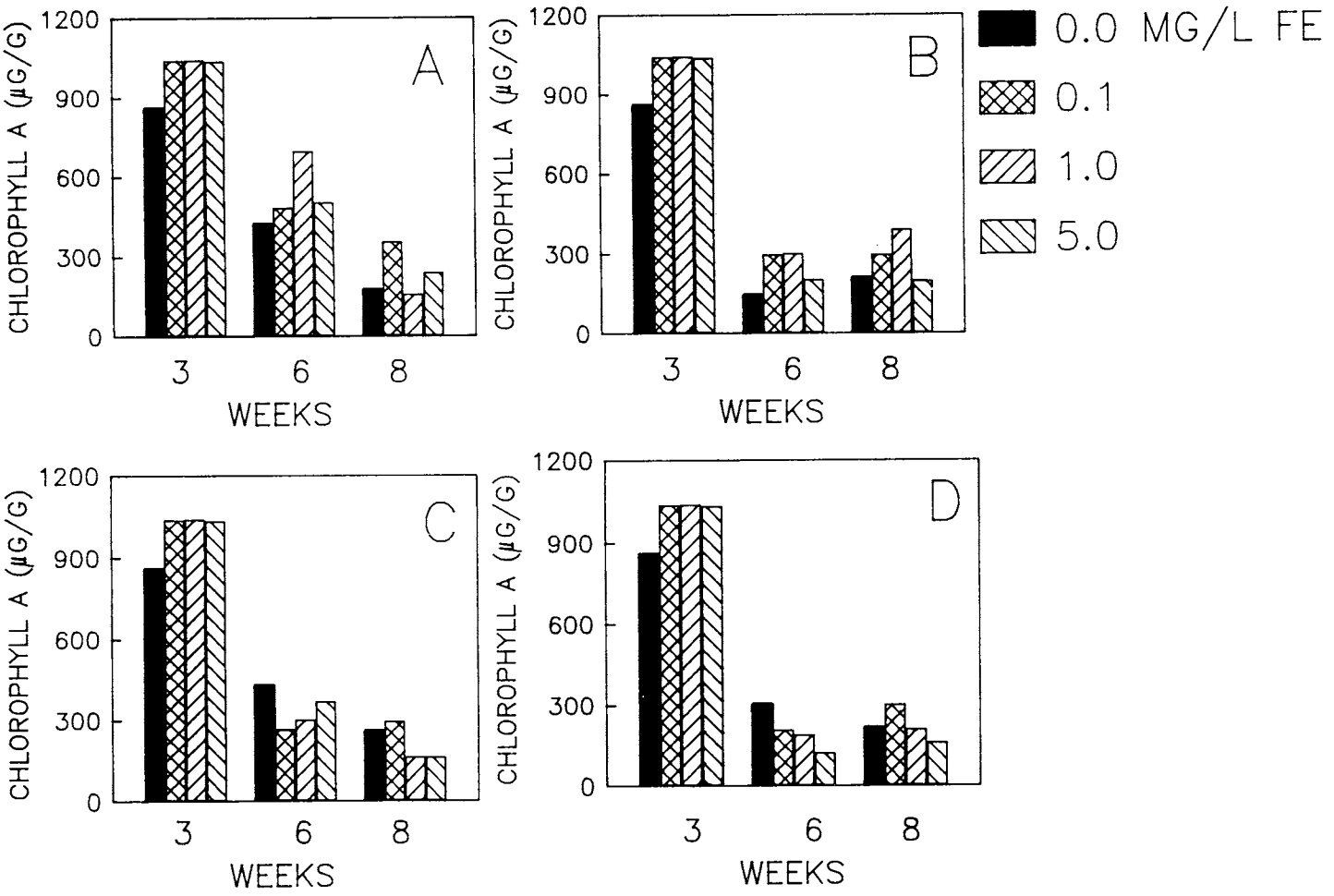

Figure 7. Chlorophyll a concentrations for hydrilla from Experiment Five. Panel A is for plants not treated with fluridone; B is for those treated with 0.05 mg/l fluridone; C is for plants treated with 0.25 mg/l fluridone; and D for plants treated with 0.50 mg/l fluridone. Plotted values are the means of 3 replicates. The 3-week sample was taken following the iron treatment, just prior to the fluridone treatment. Fluridone effects are evident by comparing the pigment concentrations at 6 weeks in panels B, C, and D with those in panel A.

suggesting that the relationship was only observed for plants in which the pigment biosynthesis pathways had been triggered. Plants with high active iron concentrations may be able to replace enzymes that are part of the carotenoid biosynthesis pathway quiker because of a greater supply of an important raw material, iron. This interpretation is consistent with information on the role of iron in pigment synthesis in algae (Price and Carell 1964; Karali and Price 1963; Carell and Price 1965).

To summarize the results of Experiment Four, we estimated the degree of recovery 24 days after the end of the fluridone treatment (as the concentration of chlorophyll a in treated plants divided by the concentration of chlorophyll a in un-treated plants; expressed as a percentage). We used this value as the dependent variable in a regression analysis with active iron and fluridone treatment concentration as the independent variables. The following equation was significant ($P < 0.001$) and yielded a coefficient of determination (R^2) of 0.93:

$$Y = 71.7 - (8.98 \times AFE) + (0.029 \times FL) + (0.35 \times AFE^2) \quad (1)$$

where Y = recovery of hydrilla chlorophyll a as % of untreated plants

AFE = active iron (µg/g) in the plant at the time of treatment

FL = fluridone concentration (mg/l)

Equation 1 describes the relationship observed for hydrilla grown under the conditions used in Experiment Four. While it may not apply to field populations of hydrilla, when coupled with information on pre-treatment concentrations of plant tissue active iron, it may be a useful first step in predicting the response of hydrilla to fluridone treatment.

Results from these experiments show that the concentration of active iron in hydrilla plants at the time of fluridone treatment influenced the plant's ability to recover. We observed evidence of recovery for plants treated 1 or 5 weeks with fluridone in Experiments One, Two, and Three. However in these experiments the exposures to fluridone were either short (1 week) or were followed or accompanied by iron treatments. In Experiment Five,

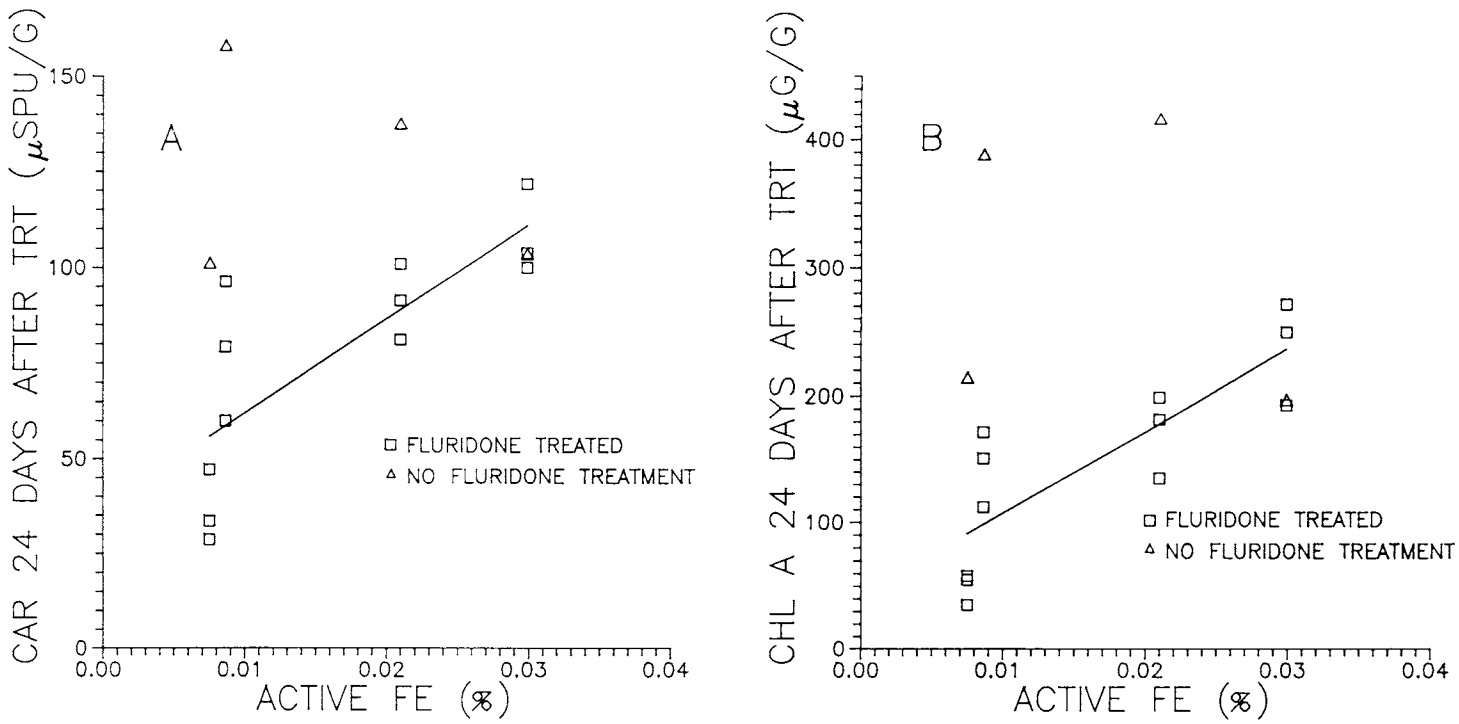

Figure 8. Relationships between carotenoid (A) and chlorophyll a (B) concentrations and active iron for hydrilla in Experiment Four.

plants exposed to fluridone for 3 weeks without later iron treatments did not recover by the end of the experiment. We conclude that hydrilla may recover from fluridone treatment, and that recovery is limited by the concentration of active iron in the plant at the time of fluridone application. To a lesser extent recovery is influenced by iron availability in the environment following treatment. High concentrations of iron in the water at the time of fluridone application do not appear to reduce fluridone's phytotoxicity. Recovery is less likely for plants exposed to fluridone for long periods or for plants growing in iron poor habitats. In this discussion, we have used recovery to refer to the return of pigment concentrations to those characteristic of un-treated plants. We recognize that pigment recovery may only be one step in the plant's complete recovery process. Data on plant weight from these experiments, suggest that there is a noticeable lag between pigment recovery and resumption of growth.

Finally, the data suggest that the analysis of field populations for levels of active iron content may yield useful information about the potential for success of fluridone applications. This needs further testing using natural populations of hydrilla. Testing this hypothesis under field conditions will not be a trivial undertaking because of problems with replication (Hurlburt 1984). However, careful measurement of tissue levels of active iron and the response of hydrilla populations to fluridone application, in several lakes characterized by different iron concentrations and fluridone half-lives may be instructive (Carpenter 1989).

ACKNOWLEDGMENTS

We appreciate technical advice provided by Mr. N. Dechoretz. Drs. F. Ryan, L. Mitich, and L. Anderson and three anonymous reviewers offered thoughtful comments on an earlier version of the manuscript.

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Influence of External Iron Concentration on Active Iron for Four Species of Aquatic Macrophytes

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ABSTRACT

Four species of aquatic plants were grown in cultures with various levels of iron in the water phase and tissue levels of total iron and 'active' iron (Fe^{2+}) were determined. Active iron accounted for 29% of the total tissue iron. The relationship between active iron and the external iron concentration was described by a rectangular hyperbola. Estimates of the external iron concentration at which the active iron fraction was one-half of the maximum 'active' iron concentration indicate that the species could be separated into two groups. Values for monoecious and dioecious hydrilla were similar to that for variable pondweed. Sago pondweed and American pondweed had values which were similar to each other but higher than for the first group. These results may be useful for predicting the efficacy of fluridone, (1-methyl-3-phenyl-5-[3-(trifluoromethyl)phenyl]-4(1H)-pyridinone), treatments.

Key words: herbicide susceptibility, iron nutrition, fluridone.

INTRODUCTION

The aquatic herbicide, fluridone, inhibits plant growth by disrupting the synthesis of photosynthetic pigments (Bartels and Watson 1978; Berard et al. 1978). Studies with wheat seedlings (Bartels and Watson 1978) and cell-free carotogenic systems from algae suggest that fluridone interferes with carotenoid synthesis. Specifically, fluridone appears to interfere with the desaturase enzyme complex which converts phytoene to gamma-carotene (Sandmann and Boger 1986). Desaturase enzyme complexes have iron as a critical component. Experimental results indicate that aquatic plants can recover from fluridone treatment (Van and Steward 1986). Recently, we have demonstrated that the extent of recovery, for hydrilla, is directly related to the tissue level of "available" or "active" iron (Spencer and

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