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Uptake of Manganese in *Hydrilla verticillata* Royle

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The effect of five transition metals (Fe, Zn, Cu, Mn, and Co) on the growth of the submersed aquatic plant *Hydrilla verticillata* Royle was investigated by adding the trace metals (as EDTA salts) to Hydrilla in well water, and comparing the production of oxygen for a given period with those samples for which a given trace metal had not been added. The effect of concentration of added manganese on the rate of oxygen production by the plant was subsequently investigated, and the results follow an Eadie relationship indicating the presence of a manganese-requiring enzyme. The concentration of manganese in the plants at equilibrium was measured and the apparent concentration factor was calculated. The implications of the use of the recovered plant as mulch and fodder are considered.

Hydrilla verticillata Royle (Long and Lakela, 1971) is a perennial, submerged aquatic plant that is generally rooted by means of long, white adventitious roots which effectively anchor the plant firmly to the water bottom of lakes, rivers, and canals of the southeastern United States, but particularly in Florida. This plant is capable of forming dense mats and that portion of the plant toward the stem tips can completely occupy the top foot of the water; some plants have been observed to grow in water 20 ft deep.

The plant seems to be remarkably well adapted for survival and spreading. It reproduces primarily by vegetative processes and occasionally by seeding. It can survive as a pleustophyte or free-floating plant when up-rooted or broken from the bottom. Existence as a pleustophyte increases the survival advantage of the plant, and is one of the reasons for rapid spread and reinfestation. Hydrilla can also deposit vegetative propogules on the water bottom that can regenerate the plant, even after the rest of the parent plant has been destroyed. Finally, Hydrilla appears to spread at the expense of other plants as a result of the so-called "umbrella effect": the majority of the biomass of the plant is near the surface of the water column, in contrast to other plants, and Hydrilla can evidently gain a photosynthetic advantage over other aquatic plants (Haller and Sutton, 1975).

Aquatic weeds such as Hydrilla obstruct water flow and affect the water cycle (increasing water loss through transpiration and preventing satisfactory land drainage). The consequences of these two effects are economically significant and include: navigational loss, which can be profound when Hydrilla invades; flood control problems, which can result from up to 90% retardation of water flow in a flood control canal (Holm et al., 1969); economic costs, which include a lowering of the economic tempo of a tourist-recreation-oriented area or which include maintenance costs.

Presently, Hydrilla is controlled by chemical means, using such herbicides as 2,4-D (2,4-dichlorophenoxyacetic acid), cutrine (triethanolamine complex of copper sulfate), and other similar agents (cf. Baker et al., 1975). Unfortunately, chemical treatment also releases into the ecosystem those micronutrients that were responsible for the spread of Hydrilla originally. Biocontrol has been limited, but the use of the white amur (*Ctenopharyngodon ilella* Val.) is promising (Sutton, 1974) as a control means and as a potential food source. Mechanical control, e.g., by mowing has not been recommended because of the possibility of further proliferation.

Few studies have been concerned with understanding the micronutrient requirements of Hydrilla, but with this information available, the possibility of limitation of plant growth through management of trace-metal input would be worth considering. Past studies have indicated that two adjacent lakes in Hillsborough County are notable for the presence of Hydrilla in one and the absence in another (Martin et al., 1971). More recent studies have indicated the importance of inorganic carbon levels on the spread of Hydrilla (Martin et al., 1976) and the interesting possibility that certain levels of chelated iron may limit the growth of Hydrilla in the laboratory (Reid et al., 1974) and in the field (Martin et al., 1976).

The possibility that Hydrilla could be deprived of critical trace metal nutrients has been raised (Martin et al., 1970, 1971), but the present study is also concerned with another possibility. Could Hydrilla be regarded as a potential crop and harvested for trace metal content to be used as mulch and/or fodder? In part, utilization would depend upon trace-metal composition and/or ability of plants to accumulate trace metals. The present paper summarizes the results of a deprivation study (wherein plants were grown in trace-metal-free media with the addition or omission

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Table I. Effect of Deprivation of Selected Elements on the Growth Characteristics of Hydrilla

Metal ion omitted	Rel net dissolved oxygen (D.O.)[a]		Carboy study		
	4 days	3 days	Net D.O., ppm	Net pH increase	Biomass change,[b] %
Fe(III)	1.07 ± 0.11	0.60	6.45	2.18	+4
Mn(II)	1.09 ± 0.05	0.65	9.28	2.38	+10
Co(III)	1.13	0.81	12.12	2.00	+21
Cu(II)	1.14	1.01 ± 0.03			
Zn(II)		0.94 ± 0.08			
All present	1.00 ± 0.01	1.0	8.51	2.43	+28
Metal-free medium	0.96 ± 0.01				

[a] ΔD.O. system/ΔD.O. "all present" system, ± $((\text{rel. dev.})_a^2 + (\text{rel. dev.})_b^2)^{1/2}$. [b] Wet weight basis.

of five trace metals added as EDTA complexes). As a result of this study, manganese was chosen for further study because omission of manganese appeared to have an unfavorable effect on plant growth.

EXPERIMENTAL SECTION

Plant Sources. Hydrilla plants were collected from the Hillsborough River, Tampa, Fla. All plants were thoroughly washed with tap water, and cultured in deep well water for at least 1 week prior to initiation of studies.

Reagents. EDTA compounds were used as the sources of metals, and Na[Fe(EDTA)], Na_2[Zn(EDTA)], and Na_2[Cu(EDTA)] were obtained from Eastman Chemical Company (white label), while K[Co(EDTA)] was a standard preparation (Dwyer and Garvan, 1960). Finally, Na_2Mn(EDTA) was formed by adding $MnCl_2 \cdot 4H_2O$ (1.97 g, 0.01 mol) in a minimum amount of 95% ethanol to an equal volume of aqueous Na_2EDTA (3.72 g, 0.01 mol). The precipitate that formed was collected by filtration and air dried to give a 92% yield of a pale pink solid, mp 233–236 °C. Anal. Calcd for $Na_2Mn(C_{10}H_{14}N_2O_8) \cdot 4H_2O$: C, 29.42; H, 5.43; N, 6.86; Mn, 13.46; H_2O, 17.6. Found: C, 29.80; H, 5.15; N, 7.00; Mn, 13.22; H_2O, 15.2.

Manganese was determined by atomic absorption spectrophotometry (vide infra), water content was determined by weight loss following drying at 110 °C, 24 h, and other microanalyses were performed by Galbraith Laboratories, Inc.

Deprivation Studies. Systems were devised to determine the effect of deprivation of selected trace metals at natural water concentrations on plant growth. The basic medium was deep well water filtered through Millipore (0.45 μm) membrane filter and treated with sodium Chelex-100 cation exchange resin (Davey et al., 1970). The EDTA salts of iron, zinc, copper, manganese, and cobalt were added, omitting one metal from each flask. The concentrations studied, respectively, were Fe, 120; Zn, 52; Cu, 14; Mn, 16; and Co, 1 ppb. Two control sets were included: (1) "all present" (to which all five EDTA complexes were present) and (2) "metal-free medium" (to which no EDTA compounds were added). Study systems (in triplicate) were 500-ml stoppered flasks (Corning), inverted in 3 in. of water and lighted by one 14-W fluorescent "Daylight" lamp. Each vessel contained 30 cm of plant that had been cultured 2 weeks in well water and rinsed thoroughly with deionized water. Dissolved oxygen was measured initially and finally after 3 or 4 days (cf. Table I). Subsequently, results with 20-l. carboys were checked.

Effect of Manganese on Plant Growth. Study systems consisted of 20-l. Pyrex glass carboys closed to the atmosphere and attached via clamped tubing to matching polyethylene reservoirs. Manganese was added to deep well water in the systems as Na_2[Mn(EDTA)] in the range 15–150 ppb of Mn. All systems contained 40 g of plant, were illuminated 13 h/day by two 40-W "cool-white" fluorescent lamps, and were stirred continuously. Dissolved oxygen was measured at daily intervals using the Winkler method (Martin, 1972), and these data were used to calculate the pseudo-first-order rate constant for the production of oxygen, k_{O_2} (Martin and Reid, 1974). The study systems were also sampled on selected days and analyzed for manganese. Manganese was determined by the colorimetric, leuco-base method (Martin, 1972) at 615 nm against standards prepared from the EDTA complex. Pertinent results are summarized in Table II.

Manganese Content of Hydrilla. Plant samples were collected from duplicate studies, dried at 110 °C for 24 h, ground to a fine powder (4–5 g), and decomposed in a well-ventilated hood by heating in 100 ml of concentrated HNO_3 until about 25 ml remained. Heating was continued with dropwise addition of $HClO_4$ (72%) until dense white fumes appeared above the mixtures or until the mixtures were colorless (ca. 10 ml). [Details on the safe handling of perchloric acid have been provided by Smith (1953, 1955, 1965) and by the Analytical Methods Committee of the Society for Analytical Chemistry (1959)]. Residual volumes were heated to near dryness and diluted with enough water to effect quantitative transfer into a fritted glass funnel. Any slight amount of white residue was washed with double-distilled water, and the clear colorless filtrate was transferred to a volumetric flask and diluted to 250 ml with double-distilled water.

Manganese was determined using a Perkin-Elmer Model 403 atomic absorption spectrophotometer (at 289 nm). Samples were compared with stock manganese solutions (Martin, 1972). All unknown concentrations were evaluated using a linear interpolation program (Wang 370 calculator using a card reader) and using standards that bracketed the unknown concentration. Pertinent data are summarized in Table III.

RESULTS AND DISCUSSION

Metal ion deprivation studies (Table I) indicated that iron and manganese had the more obvious effect on plant growth, as indicated by the net increase in dissolved oxygen (Table I) in the absence of these two elements. Manganese, as $Mn(EDTA)^{2-}$, was selected for further study; additional information was available for the effect of iron on growth of Hydrilla (Reid et al., 1975) that could be used for comparison with manganese.

The variation of first-order growth constants for the production of oxygen, k_{O_2}, with increasing amounts of added trace metal can provide useful information. For iron, as $Fe(EDTA)^-$, the values of k_{O_2} increased with increasing amounts of added iron, up to a maximum (0.1–0.15 ppm), beyond which it appeared that inhibition occurred (Reid et al., 1975). An examination of the data in Table II indicates that the same pattern is observed for manganese. The precision of the specific rate constants has also been calculated, and the relative standard deviation was about 10%.

Table II. Summary of Growth Characteristics for Hydrilla in Water Enriched with Manganese in a Standard System

Bottle no.	Added Mn, ppb[a]	Dissolved oxygen, ppm			pH			Plant wt, wet, g			No. of roots (initial = 0)	Mean growth constant[c] k_{O_2} day^{-1}
		Initial	Final (max)	Net	Initial	Final (max)	Net	Initial	Final	Net		
1	15	7.35	14.17 (same)	6.82	7.40	8.35 (same)	0.95	40.25	47.35	7.11	69	0.071 ± 0.008
2	30	7.00	19.17 (same)	12.17	7.54	8.41 (same)	0.87	39.84	46.43	6.59	72	0.128 ± 0.007
3	60	7.40	24.16 (same)	16.76	7.60	8.28 (same)	0.70	39.75	48.56	8.81	86	0.170 ± 0.02
4	90	6.99	19.78[b] (same)	12.79[b]	7.52	8.25 (same)	1.13	39.90	48.51	8.61	95	0.197 ± 0.03
5	120	7.30	22.50 (same)	15.20	7.58	8.22 (same)	1.12	40.11	47.11	7.00	87	0.170 ± 0.01
6	150	7.59	15.70[b] (same)	8.11	7.63	8.20 (same)	1.04	39.76	47.28	7.52	70	0.139 ± 0.017

[a] Added as $Na_2Mn(EDTA)$; concentration of manganese in initial water = 0.006 ppm. [b] Value for day 7 only (final = day 10), system malfunctioned day 10. [c] $k = 1/\Delta t \ln (C_f - C_i)/(C_f - C_t)$; systems 1 and 6 calculated from $C_f = 20.00$.

Table III. Uptake of Manganese[a] by *Hydrilla verticillata* Royle in Well Water

Sample no.	Dissolved manganese, ppm		mg of Mn/kg of dry plant	Apparent concn factor[b]
	Added	Actual		
35-1	0	0.006	81.6	13 600
35-2	0.015	0.021	155	7 380
42-1	0.015	0.021	173	8 240
35-3	0.030	0.036	206	5 720
42-2	0.030	0.036	156	4 330
42-3	0.060	0.066	306	4 640
35-4	0.075	0.081	389	4 800
42-4	0.090	0.096	282	2 938
35-5	0.100	0.106	428	4 038
42-5	0.120	0.126	473	3 753
35-6	0.125	0.131	472	3 600
42-6	0.150	0.161	512	3 180

[a] Added as $Na_2Mn(EDTA)$; actual value based upon initial day analysis. [b] A.C.F. = (mg of Mn/kg of dry plant)/(mg of Mn/kg of solution).

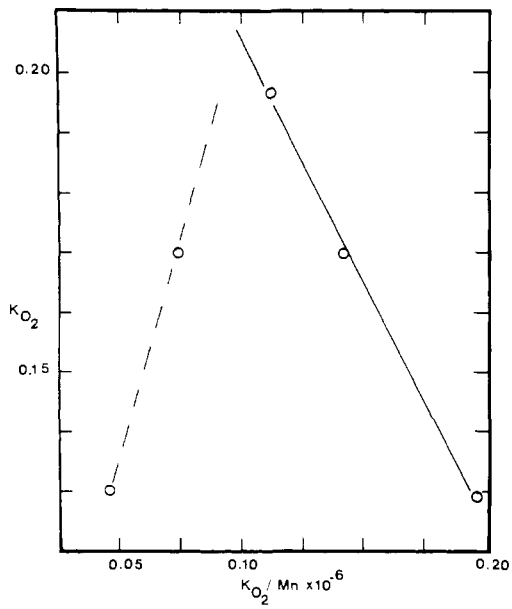

Figure 1. Eadie plot for Hydrilla: first-order growth constants for oxygen production, k_{O_2}, as a function of k_{O_2}/[Mn], where [Mn] is the molar concentration of manganese(II) for a typical study.

The rate data from Table II were subjected to an Eadie plot (Eadie, 1942) to determine the presence of metal-requiring enzymes. From the data presented in Figure 1, it appears that k_{O_2} for Hydrilla depends upon the amount of added manganese, that the plant contains an enzyme that requires manganese, either as a constituent or as a co-factor, and that inhibition occurs above a concentration of 1.75×10^{-6} M Mn (or 0.1 ppm of Mn). A similar Eadie dependence has also been observed for iron (Reid et al., 1975). From the slope of the Eadie plot, a Michaelis constant can be calculated and it is 0.84×10^{-6} M for manganese (Figure 1); the corresponding value for iron is 0.75×10^{-6} M.

Another part of the study was concerned with the concentration of manganese in Hydrilla. Plants in two studies (35 and 42, Table III) were collected after 3 weeks and once equilibrium had been established as evidenced by a constant level in the amount of dissolved oxygen. Plants were analyzed for manganese content, expressed as milligrams of manganese per kilogram of dry plant, and it is evident that the manganese content increases in a general way with the amount of added manganese. A more

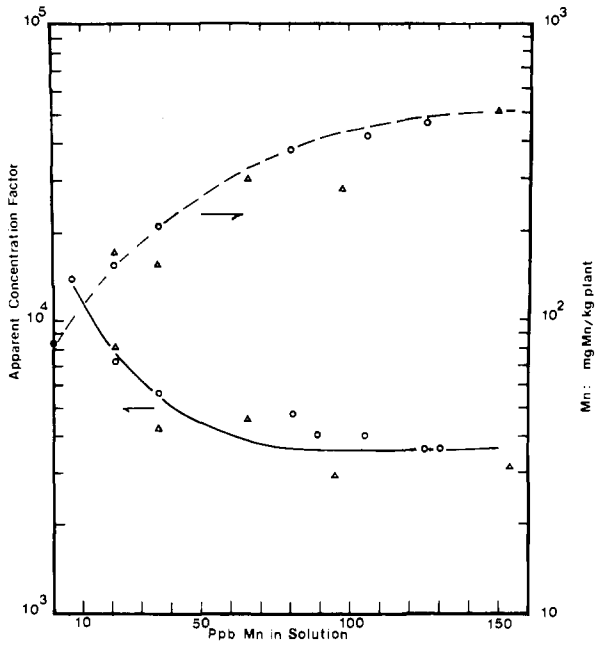

Figure 2. Semilogarithmic relationships between concentration of manganese in Hydrilla samples (log concentration, mg of Mn/kg of dry plant, right ordinate) and apparent concentration factor (log A.C.F., left ordinate) as a function of the amount of manganese(II), ppb, present in solution. Two series of standard runs are indicated. A.C.F. = (mg of Mn/kg of dry plant)/(mg of Mn/kg of solution).

quantitative treatment is possible and the apparent concentration factor may be defined (cf. Table III). If the manganese content, as defined above, is divided by the concentration of added manganese (expressed as parts per million) then the apparent concentration factor is obtained (footnote *b*, Table III).

The concentration of manganese in plants and the apparent concentration factor are presented as a function of the concentration of manganese in solution, Figure 2. The semilogarithmic relationship indicates an upper limit is approached for the amount of manganese taken up, that the concentration factor asymptotically approaches a limit, and that good agreement was obtained between the two studies. Interestingly enough, the limits for uptake and concentration factor occur beyond the inhibition concentration.

Manganese uptake apparently differs from iron uptake in two respects. The absolute concentration of manganese is greater and the concentration factors are also greater. The maximum concentration observed for iron was about 196 mg of Fe/kg of dry plant, and the concentration factor was about 1300. The mobility of iron appears to be much less than phosphorus or manganese, and a previous study (Reid and Martin, 1975) indicated that iron tends to become immobilized in roots and not to become translocated, despite the presence of a chelating agent.

The present study would indicate the possibility of using Hydrilla to remove manganese from natural waters and to concentrate this element and iron in the plant. Clearly, there are more obvious sources of either element, but the apparent concentration factors would suggest that Hydrilla should be physically removed from certain natural waters, such as lakes and canals, and not treated chemically to degrade and re-release the elements. The question of the incentives for plant removal quickly arises, and the possibility of using noxious aquatic weeds as a crop arises. The proliferation of this exotic plant probably came as a result

Table IV. Nutrient Concentrations in Hydrilla (mg/kg of Dry Plant) and in Land Forages

Element	Hydrilla[a] mean	Land forages[b]
Ca	10 800	3 000-6 000[c]
P	3 200	1 200-6 600
K	27 000	10 000-300 000
Mg	5 900	1 000-5 000
Na	11 700	100-1 400
Fe	1 438	
Cu	36	5-12
Zn	50	∿13-50
Mn	158	96-85

[a] Cf. Easley and Shirley, 1974. [b] NRC (1971); Thomas et al. (1955); Beeson et al. (1947). [c] Land grasses; legumes are greater by 3×.

of its being used as a crop, in this case as an aquarium plant. The possibility of using it as a mulch or livestock feedstuff might provide an incentive for removal.

Possible use as a crop (cf. Boyd, 1968) requires a more detailed analysis of the constituents of Hydrilla. Easley and Shirley (1974), for example, considered the possible use of Hydrilla and other aquatic plants as for utilization for feedstuff for livestock. The nutrient levels of Hydrilla obtained from Kings Bay, Crystal River, Fla., are compared with nutrients in typical land forages in the United States (Table IV). In general, it can be seen that the mean value compares favorably, with a few exceptions. The calcium–phosphorus ratio should be about 2:1 though values as high as 7:1 are tolerable for cattle (NRC, 1970). It also appears from personal experience that much calcium may be absorbed on the plant leaves. Also the iron levels may be higher than those normally recommended, though previous data (Reid et al., 1975) would indicate that this could be controlled by the levels of iron in the natural waters. The copper levels per kilogram of dry plant appear to be a little low in comparison with those recommended (NRC, 1970) for a 300-kg steer to gain 1.1 kg/day. For most other nutrients 1 kg of dry plant would provide adequate nutrition.

Our results with manganese indicate that the apparent concentration factors are significant, and that the level of manganese is also significant; the maximum level obtained in the present study (500 mg/kg of dry plant) was not the potential maximum. Easley and Shirley (1974) found a maximum concentration of 346 mg/kg of dry plant over a 1-year study, and many healthy pastures may contain less than 100 ppm of Mn (Undergood, 1966).

In summary, it appears that aquatic weeds as an unintential crop may be a generally unconsidered resource. At present, this Hydrilla and the related genera *Egeria* and *Elodea* are thought to be confined to the Southeast, though, in fact, representatives of the three genera cover much of the United States (Solymosy and Gangstad, 1974). And if the spread of aquatic weed problems may be anticipated, perhaps the utilization of these plants in agriculture should be anticipated as well.

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Response of Harvested Avocado Fruits to Supply of Indole-3-acetic Acid, Gibberellic Acid, and Abscisic Acid

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Satisfactory penetration and distribution of growth regulators in harvested avocado (*Persea americana* Mill.) fruits were achieved by infusing growth regulator solutions through the pedicel. Indole-3-acetic acid (IAA) greatly accelerated ripening and inhibited abscission of the ripe fruit but only when applied at a very high dosage (10^{-2} M). Gibberellic acid (GA_3) had no influence upon abscission and ripening processes even though it seemed to inhibit the ethylene production of the fruit at abscission. Abscisic acid (ABA), when given in a 100-ppm solution, accelerated abscission but not ripening, while a 1000-ppm solution accelerated both. The rate of ethylene production at abscission time was in all cases much lower than in control fruits.

Three plant hormones are usually considered to interact or influence the production and effects of ethylene: auxin, gibberellin, and abscisic acid (Dilley, 1969; Leopold, 1971). The effect of auxins on accelerating endogenous ethylene production in plant tissues has been established (Burg and Burg, 1968; McGlasson, 1970). Thus, induction of flowering (Burg and Burg, 1966) and of fruit ripening (Hansen, 1946; Mitchell and Marth, 1944) was achieved indirectly by auxin treatments. On the other hand, auxin delayed ripening of pears in spite of the increased production of ethylene (Frenkel and Dyck, 1973). The gibberellin effects were shown to be antagonistic to those of ethylene (Babbitt et al., 1973; Dostal and Wilcox, 1971; Scott and Leopold, 1967; Sharples, 1973), although in some cases gibberellin application accelerated ethylene production and abscission (Becka, 1973; Wittenbach and Bukovac, 1973). Exogenous ABA promoted ethylene production in fruits (Cooper and Henry, 1971; Cooper and Horanic, 1973; Cooper et al., 1968) and disks of orange peel (Gertman and Fuchs, 1972), while it inhibited ethylene production in cut flowers (Mayak and Halevy, 1972) and pea seedlings (Gertman and Fuchs, 1972).

When studying fruit response to exogenously supplied growth regulators, one of the main problems is its penetration and distribution within the fruit. Insufficient penetration and uneven distribution of an auxin, applied by immersion to banana, accelerated the rate of ripening; however, application by vacuum infiltration to banana slices, a method providing even distribution, inhibited ripening (McGlasson, 1970; Vendrell, 1969, 1970).

In the present work we used an infusion method through the pedicel (Adato and Gazit, 1974a) to achieve satisfactory penetration and distribution of plant hormones in the fruit. Using this method we have attempted to clarify the effect of three hormones on ethylene production, abscission, and ripening behavior of avocado fruits.

MATERIALS AND METHODS

Plant Material and Infusion Method. Ten-month-old mature Hass avocado (*Persea americana* Mill.) fruits were used for the experiments with indole-3-acetic acid (IAA) and gibberellic acid (GA_3); 7-month-old mature fruits of the same variety were used for the abscisic acid (ABA, *R,S*, cis–trans) experiment.

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