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Evidence of iron deficiency in seagrasses growing above carbonate sediments

Abstract—A comparison of available data on iron concentration in seagrass tissues shows iron concentrations in seagrass leaves growing on carbonate sediments to be below critical levels for angiosperms [$< 100\ \mu g$ Fe (g DW)$^{-1}$]. Iron concentrations of leaves in Caribbean seagrasses declined by 5–10-fold from terrigenous to carbonate sediments (inner Gulf of Mexico to the Caribbean coast off the Yucatan Peninsula). This observation provided evidence of possible iron deficiency in seagrasses, which was confirmed by an experimental demonstration that adding iron to the sediments stimulates growth of the Caribbean seagrass *Thalassia testudinum* and increases the chlorophyll *a* concentration of both *T. testudinum* and *Syringodium filiforme* growing above coralline carbonate sediments. We conclude that seagrasses growing above carbonate sediments are likely to experience iron deficiency.

Recent findings that iron-limited phytoplankton growth may occur in large areas of the ocean (e.g. Martin and Fitzwater 1988; Martin et al. 1994) have led to re-evaluation of the nature of nutrient limitation in the ocean. Interestingly, the concern for the role of iron as a major factor in oceanic production has grown parallel to similarly mounting evidence for the importance of iron as a nutrient often limiting the production of angiosperms on land (e.g. Miller et al. 1984). Whether iron deficiency may be an important factor limiting angiosperm productivity in the sea has not been, however, examined to date.

Iron deficiency of land angiosperms, characterized by a lack of chlorophyll *a*, is frequent in calcareous continental soils (e.g. Miller et al. 1984) where iron is usually trapped in a nonavailable form (Loeppert 1986). Similarly, iron limitation of seagrass productivity should be more likely above carbonated sediments, such as those that dominate the littoral zone in the tropics (Milliman 1974). Yet, current hypotheses on nutrient control of seagrass growth postulate, based on some experimental evidence (Short et al. 1990), plants growing above calcareous sediments to be phosphorus limited (Short 1987); a possible role for iron has not been considered.

Iron deficiency of the seagrass meadows growing in the Mexican Caribbean is suggested by the particular geochemical conditions at the Yucatan Peninsula, the corallinaceous origin of the sediments (~98% DW carbonate content, Merino et al. unpubl.), and the observation of very low Chl *a* concentrations in leaves of *Thalassia testudinum* growing there (Enríquez et al. 1992). The Yucatan Peninsula is a calcareous platform, where rapid infiltration of rainwater and the consequent lack of surface runoff to coastal waters (Merino et al. 1990) determine that there are no significant iron inputs—other than atmospheric and local point sources—to the coast. The sediments of the Mexican Caribbean coast have extremely low iron concentrations, with an average of 43 ppm of total Fe and <1 ppm in pore waters. Relatively higher values are observed only in sediments of highly productive environments, whether because of nutrient enrichment derived from upwelling (80 ppm of total Fe in the sediments at the Yucatan Upwelling; Botello and Villanueva unpubl. rep.) or anthropogenic inputs (192 ppm of total Fe in sediments of the eutrophic lagoons of Cancún; Botello and Villanueva unpubl. rep.).

To evaluate the range of iron concentration in seagrass leaves, we collected, between 1992 and 1994, leaf samples for a range of seagrass species growing in the Mexican Caribbean, Spanish Mediterranean, Portuguese Atlantic, the Philippine Islands (South China Sea), and on the coast of Kenya (Indian Ocean). In addition, in June 1994 we collected leaf samples for marine angiosperms (*T. testudinum, Halodule wrightii, Syringodium filiforme,* and *Ruppia maritima*) from the coasts of Veracruz (inner Gulf of Mexico) to Quintana Roo (Caribbean coast off the Yucatan Peninsula), encompassing a gradient in sediment origin from terrigenous to carbonated. To improve comparability we determined iron concentrations only in the green (mature) sections of the leaves, excluding from analyses the immature sections and those already colonized by epiphytes. Leaf sections sampled for Fe and C, N, and P analyses were dried to constant weight at 80°C. Two replicate samples (~0.5 g DW each) from each population were weighed and placed in a sealed Teflon vessel to which we added nitric acid (10 ml), chlorhydric acid (2 ml), and deionized water (3 ml). Samples were digested for 30 min in a CEM microwave oven. Deionized water was added to bring the volume of the resulting extract to 25 ml, and the Fe concentration was then read at 248.3 nm in a Varian Spectra AA-10-Plus atomic absorption spectrophotometer. The instrument was calibrated with a standard curve constructed from a 1,000 ppm Fe standard (Merck) dissolved in a matrix equivalent to the sample solution. The standard error for replicate Fe determinations was ± 22 ppm. Our measurements were merged with published reports of Fe concentrations in seagrass tissues to represent the present state of knowledge on this subject.

We examined the response to experimental iron additions of a dense, but slow-growing, shallow (−1.5 m)

T. testudinum meadow growing above carbonate sediments (carbonate content, 98% of DW) in the reef lagoon near Puerto Morelos (Mexican Caribbean, Gallegos et al. 1993). The experiment was conducted between 7 May and 2 June 1993, within the flowering period for *T. testudinum* when resource requirements are greatest. The experiment assessed the response in growth and Chl *a* concentration, a depletion of which is the main diagnostic symptom of Fe deficiency (Abadía 1992), of plants growing on control plots, plots with sediments enriched with a complete, slow-release fertilizer (N : P : Fe), and those receiving only Fe additions, as an iron chelate (Esantrene HP).

The three replicate (0.09 m^2) plots for each treatment were randomly distributed over an area of ~100 m^2 on a homogeneous meadow. In each plot, 21 *T. testudinum* shoots were used to measure growth following a modified leaf-marking technique. The shoots were tagged around their bases with a ribbon, and two holes were punched across their leaves at the level of the leaf sheath of the oldest leaf (reference level) with a hypodermic needle (Pérez et al. 1991). A complete fertilizer, which had been successfully used to enhance nutrient-limited growth of seagrasses elsewhere (Pérez et al. 1991), was added to the appropriate experimental plots by inserting 40 g of a slow-release commercial fertilizer (as bars ~5 cm long and 5 mm in diameter) to achieve a loading of ~6.19 g N, 3.2 g P, and 0.34 g Fe to each plot. Iron treatments were applied by gently injecting 60 ml of a solution containing 0.6 g of Fe of the iron chelate (Esantrene HP) dissolved in filtered seawater uniformly into the sediments at each plot. To maintain the elevated supply of Fe, we repeated the addition 19 d later, so that the total load applied to each plot was 0.12 g of Fe. Nutrients were inserted at a depth of ~10–15 cm below the sediment surface, where root biomass is highest (Duarte et al. unpubl.). Since there was no previous information on the Fe concentration of these plants, we also established plots where different Fe loadings (0.12, 0.30, and 0.72 g of Fe) were supplied to the sediments to test for changes in the Chl *a* concentration of the seagrasses growing there (*T. testudinum* and *S. filiforme*) in response to different supplies of Fe.

The marked plants were harvested 27 d after the first nutrient addition, and their growth was measured by recording the elongation of marked leaves and that of unmarked leaves, emerged after marking, during the experimental period. We also recorded the leaf width and length for all the leaves in the marked shoots. In addition to the marked shoots, we harvested leaves of unmarked shoots of *T. testudinum* and *S. filiforme* growing in the experimental plots to be analyzed for Fe and Chl *a* concentrations and to determine their specific weight.

At the end of the fertilization experiment, we used a syringe to collect samples of interstitial water from each plot to measure nutrient concentrations in the sediment pore waters. The water samples were passed through a 0.45-μm fiber-glass filter, and frozen within 30 min of collection to be stored until analyzed. Nutrient concentrations were determined with a continuous flow autoanalyzer, using established methods for nutrients in seawater as described by Mee (1986). Leaf C and N concentrations were determined for duplicate subsamples of dried material, using a Carlo-Erba CHN analyzer; P concentrations were determined colorimetrically in duplicate subsamples following wet acid digestion (Koroleff 1983). Chl *a* concentrations were measured spectrophotometrically on frozen leaf samples following pigment extraction with 80% acetone in a homogenized suspension of leaf subsamples (Dennison 1990).

The concentration of Fe in seagrass leaves ranged over three orders of magnitude, with a modal value of 340 μg $(g\ DW)^{-1}$, ~20-fold lower than those of phytoplankton and freshwater angiosperms (Table 1). This modal value is similar, albeit somewhat higher, than that for marine macroalgae and almost 3-fold higher than that for land angiosperms. Yet, some of the values encountered for seagrasses were as low as those for land plants (Table 1) where Fe limitation is widespread (e.g. Miller et al. 1984). Moreover, the lowest Fe concentrations measured in seagrass leaves and macroalgal tissues were as low [~10 μg $(g\ DW)^{-1}$, Table 1] as the lowest values reported for land angiosperms (cf. Epstein 1965). Hence, a significant fraction of the seagrasses examined had Fe concentrations below the levels [~100 μg $(g\ DW)^{-1}$] reported to cause chlorosis and associated iron-deficiency symptoms in land angiosperms and considered to be critical for balanced angiosperm growth (Epstein 1965). A substantial fraction of the macroalgae (*see* Eisler 1981) also had Fe concentrations below 100 μg $(g\ DW)^{-1}$. These low values also suggest that some macroalgae may experience Fe deficiency. Although the present sparse knowledge on the Fe requirements of macroalgae precludes reliable inferences, the possibility of Fe deficiency in macroalgae also deserves examination, particularly in habitats with carbonate sediments.

The lowest concentrations of Fe were reported for seagrasses growing in the Caribbean Sea, Arabian Gulf, and on the coast of Kenya (Table 1). Although the characteristics of the sediments beneath the Fe-deficient seagrass on the Qatar Coast were not described (Kureishy 1991), the Fe-depleted seagrasses from the Caribbean Sea and the coast of Kenya were growing above highly carbonated sediments (98% and 85% sediment DW, respectively) of coralline origin (Gallegos et al. 1993; Hemminga et al. 1994). The low Fe concentrations of the seagrasses growing in these carbonate environments is consistent with the low Fe availability predicted by geochemical models for these sediment types (Stumm and Morgan 1981), where most of the Fe should be immobilized and bound to the carbonates (Morse et al. 1985). Very high carbonate contents (> 80%) in sediments are also indicative of relatively low terrigenous inputs to coastal sediments (Milliman 1974). Hence, low Fe supply from land should be generally associated, in tropical environments, with very high sediment carbonate contents, except near industrialized areas where anthropogenic inputs can alter this pattern.

The relationship between seagrass Fe status and sediment origin was examined in more detail by comparing the leaf Fe concentrations for marine angiosperms on the Atlantic coast of Mexico along a gradient from terrigenous

Table 1. Iron concentration in seagrass leaves and rhizomes (R), and those in other plants. Range of measured values in parentheses.

Species	Location	Fe[μg(g DW)$^{-1}$]	Reference
Amphibolis antarctica	—	76–127	Harris et al. 1979, *cited by* Eisler 1981
Cymodocea nodosa	Spanish Mediterranean (5 meadows)	619.2 (230–1,073)	This study
Cymodocea serrulata	Silaqui Island (Philippines)	544	This study
Enhalus acroroides	Silaqui Island	647	This study
Halodule wrightii	Puerto Morelos (Mexican Caribbean)	52–98.7	This study
	Bojorquez lagoon (Mexican Caribbean)	59.8	Botello and Villanueva unpubl. rep.
	S. Gulf of Mexico (Mexico)	193–508	This study
	Laguna Madre (Gulf of Mexico)	50–500	Pulich 1980
Halodule uninervis	Aqaba Gulf (Jordan)	7,872 9,198 (R)	Wahbeh 1984
Halophila ovalis	Aqaba Gulf	29,126 9,922 (R)	Wahbeh 1984
Halophila stipulacea	Aqaba Gulf	10,689 6,109 (R)	Wahbeh 1984
Heterozostera tasmanica	Australia	340–870	Harris et al. 1979, *cited by* Eisler 1981
Posidonia oceanica	Medes Islands (Mediterranean)	140–1,450	Alcoverro unpubl. data
	Spanish Mediterranean (3 populations)	420 (225–777)	This study
	Aegean Sea	372 (164–815)	Malea et al. 1994
Ruppia maritima	Bojorquez lagoon	60.7–65.6	Botello and Villanueva unpubl. rep.
	S. Gulf of Mexico (Mexico)	999–2,573	This study
	Spanish Mediterranean (1 population)	419	This study
Syringodium filiforme	Puerto Morelos	35–61	This study
	S. Gulf of Mexico	140–530	This study
Syringodium isoetifolium	Silaqui Island	263	This study
Thalassia testudinum	Puerto Morelos	62.5–80.6 (93–94)	This study
	S. Gulf of Mexico	71–533	This study
	Bojorquez lagoon	12.5–57.3 77.8–43.2 (R)	Botello and Villanueva unpubl. rep.
	Puerto Morelos	51.7 129.1 (R)	Botello and Villanueva unpubl. rep.
	—	250	Stevenson and Ufret 1966, *cited by* Eisler 1981
Thalassia hemprichii	Silaqui Island	673	This study
Thalassodendron ciliatum	Chale lagoon (Kenya)	120	This study
Zostera marina	Bosphorus	2,513–2,590	Güven et al. 1993
	Newport River (USA)	810 6,000 (R)	Drifmeyer et al. 1980
	Spanish Mediterranean	734	This study
	Strait of Gibralter	1,144	This study
Zostera muelleri	—	331–1,697	Harris et al. 1979, *cited by* Eisler 1981
Zostera noltii	Spanish Mediterranean (2 populations)	711 (208–1,214)	This study
Unidentified seagrass	Qatar Coast (Arabian Gulf)	43.2	Kureishy 1991
Seagrasses	Review	340* (12–29,126)	(data above)
Phytoplankton	Review	5,900 (200–34,000)	Healey 1973
Macroalgae	Review	265* (15.2–15,470)	Eisler 1981
Freshwater plants	Review	3,170	Hutchinson 1975
Land plants	Review	140	Bowen 1966

* Modal values.

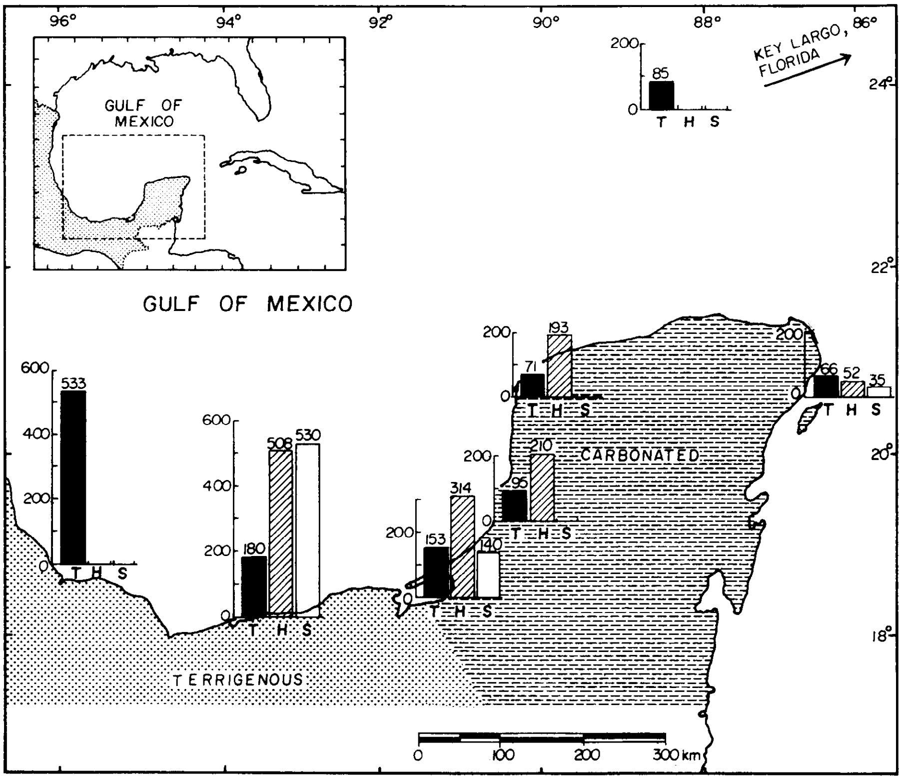

Fig. 1. The variation in leaf Fe concentration (ppm) in marine angiosperms (*Thalassia testudinum*—T; *Halodule wrightii*—H; *Syringodium filiforme*—S) growing across a range of sediment conditions in the southern Gulf of Mexico and Mexican Caribbean. The origin of each plot indicates the location of the sampling site (except for Key Largo, which is out of the frame); the nature of the sediments is also indicated on the figure. Absence of data indicates the species was not present.

to carbonate sediments (i.e. Veracruz to Quintana Roo, Fig. 1). The results indicate a clear association between sediment origin and seagrass Fe status (Fig. 1), with Fe concentrations declining 5–10-fold from seagrasses growing above terrigenous sediments to those above carbonate sediments. This pattern involved a decline in leaf Fe concentration from the inner Gulf of Mexico toward the Caribbean coast off the Yucatan Peninsula (Fig. 1), which suggests a similar gradient in the importance of Fe in controlling seagrass growth. The low Fe concentrations in carbonate sediments may have implications beyond the regulation of seagrass production. For instance, we observed very low Fe concentrations in *T. testudinum* fruits [49 μg (g DW)$^{-1}$] and seeds [31 μg (g DW)$^{-1}$], which suggest that seedlings should be particularly Fe limited and that Fe may influence the success of seedlings in establishing seagrass patches and, hence, seagrass recovery.

The sediments at Puerto Morelos had very low Fe concentrations (<0.1 ppm) and dissolved inorganic N (5.5±1 μmol liter^{-1}) and moderately low phosphate (2.7±1.1 μmol liter^{-1}) concentrations in the pore waters. Nutrients added to the sediments were mostly removed, either by biological uptake or abiotic processes (e.g. diffusion, adsorption to carbonates), by the end of the experiment. By the end of the experiment, Fe concentrations in pore waters at the plots receiving 120 mg of Fe were only ~20% greater than those in control plots, and dissolved inorganic N and phosphate in plots receiving complete fertilizer were ~40% and 100% higher than those in control plots. The N and P concentrations in *T. testudinum* leaves from control plots were 2.03±0.05% DW and 0.19±0.01% DW—close to the levels believed to be indicative of N and P deficiency (Duarte 1990). In contrast, leaf Fe concentrations in controls were 62.5±2.9 μg (g DW)$^{-1}$, well below the level [100 μg (g DW)$^{-1}$] considered critical for balanced angiosperm growth (Epstein 1965). Using the critical Fe concentration of 100 μg (g DW)$^{-1}$ reported for land angiosperms (Epstein 1965), the suggested critical N and P concentrations of 1.8 and 0.2% DW, and median C concentration of 33.6% DW for seagrasses (Duarte 1990), we propose a stoichiometric ratio of 15,800 C : 720 N : 36 P : 1 Fe for balanced seagrass growth. The ratio 25,500 C : 1,160 N : 58 P : 1 Fe observed in *T. testudinum* leaves is much higher than the proposed ratio for balanced growth, suggesting that the *T. testudinum* plants examined were more deficient in Fe than in either N or P.

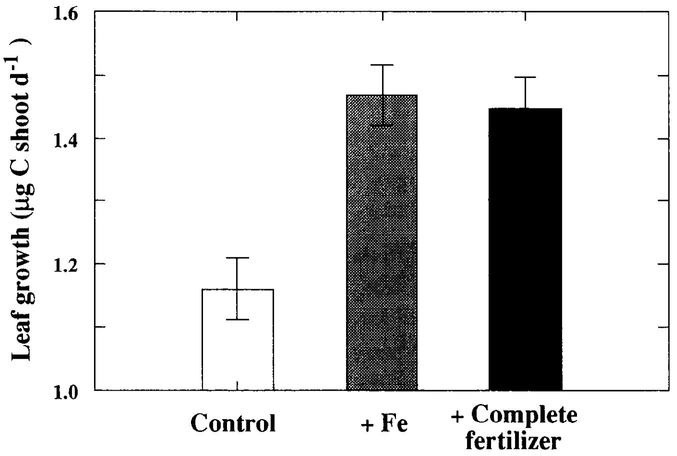

Fig. 2. The average (± SE) growth of *Thalassia testudinum* leaves in three replicate plots in response to in situ additions of Fe and complete fertilizer.

Additions of complete fertilizer to the sediments somewhat increased (~20%) the N and P concentrations in *T. testudinum* leaves (2.39±0.07% DW for N and 0.23±0.01% DW for P). The leaf P (0.26 ±0.01% DW) but not N (2.13±0.09% DW) concentration increased significantly (*t*-test, $P < 0.05$) when Fe alone was added to the sediments, suggesting that P uptake was stimulated by Fe additions. There was a tendency, although not statistically significant (*t*-test, $P > 0.05$), for the leaf Fe concentration to increase in response to Fe additions [66.6±8.4 μg Fe (g DW)$^{-1}$], with some leaves reaching very high [up to 144 μg Fe (g DW^{-1})] concentrations. The large variability in leaf Fe concentrations in plants growing above Fe-fertilized sediments suggests important small-scale differences in the availability of the added Fe to the plants over the limited timespan (~1 month) of the experiment. A small increase in Fe concentration in response to Fe additions has been also reported for Fe-deficient plants on land, for which most of the Fe they contained was in an unavailable form (Abadía 1992).

Addition of complete fertilizer to the sediments significantly (ANOVA, $P < 0.001$) stimulated the growth rate of *T. testudinum* leaves, which increased by ~30% (Fig. 2), demonstrating nutrient limitation of seagrass growth off Puerto Morelos (cf. Gallegos et al. 1993). However, Fe additions alone also produced a significant ($P < 0.001$) growth response, similar in magnitude to that achieved by adding complete fertilizer (Fig. 2), which added twice the Fe loading supplied to Fe-fertilized plots. Hence, adding Fe and complete fertilizer to the sediments significantly (ANOVA, $F = 5.25$, $P < 0.005$) increased the leaf turnover rate (0.037±0.0027% d^{-1}, and 0.031±0.003% d^{-1}, respectively) relative to that of control plants (0.027±0.0017% d^{-1}). That addition of Fe alone suffices to yield a growth response as strong as that induced by adding complete fertilizer is strong evidence that Fe was limiting *T. testudinum* growth.

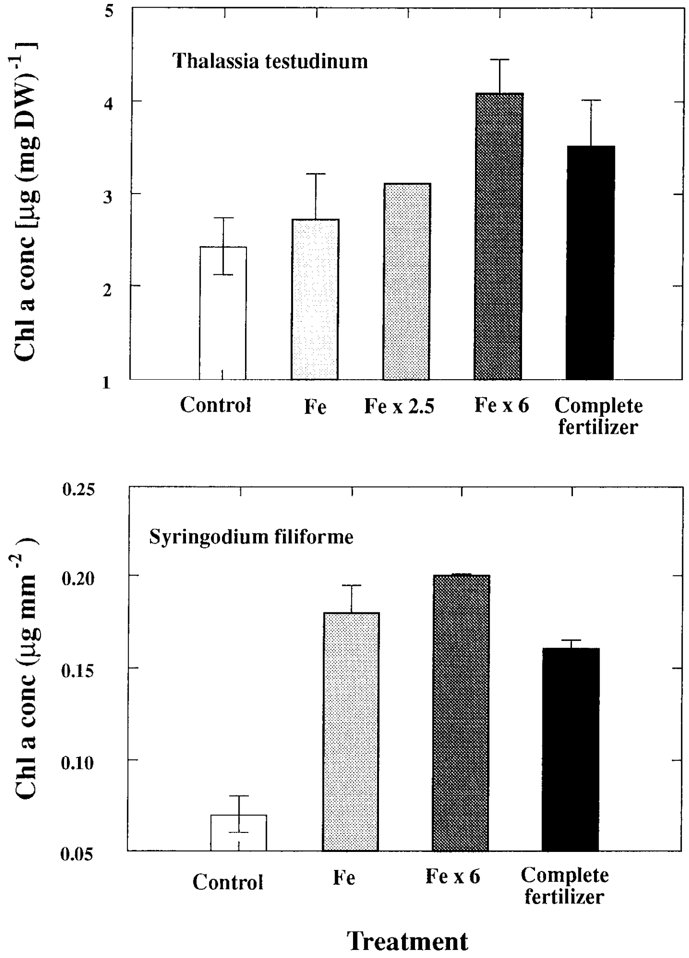

Fig. 3. The average (± SE) Chl *a* concentration in leaves of *T. testudinum* and the accompanying species *S. filiforme* in three replicate plots in response to in situ additions of Fe at different loadings and complete fertilizer.

Further evidence for the importance of Fe was obtained by examining the response of Chl *a* concentrations to Fe additions. The Chl *a* concentration of *T. testudinum* increased moderately (~15% increase) in response to Fe and complete fertilizer additions. The accompanying species *S. filiforme,* also present in the experimental plots, showed a more dramatic (~150%) increase in response to Fe and complete fertilizer additions (Fig. 3). Moreover, Chl *a* concentrations of *T. testudinum* increased steadily with increasing Fe supply and doubled at the highest Fe loading applied (Fig. 3). Accordingly, the relatively small Fe supply rate applied in the growth experiment (6-fold lower than the highest experimental supply) may not have sufficed to fully meet the plant's requirements to overcome chlorosis.

Our results provide evidence for the importance of Fe as a nutrient potentially limiting seagrass growth and pigment concentration. Examination of the distribution of Fe concentrations in seagrasses (Table 1) indicates that Fe deficiency is restricted to carbonate sediments in tropical coastal areas with low terrigenous inputs. Published Fe concentrations in macroalgae (cf. Eisler 1981) also indicate that the possibility of Fe limitation of coralline macroalgae deserves close attention. Previous hypotheses postulated P limitation of both seagrasses (Short 1987) and macroalgae (Lapointe et al. 1992) in carbonate environments. Our results extend the importance of Fe as a nutrient often limiting the growth of phytoplankton and land angiosperms to marine macrophytes growing above carbonate sediments.

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