# Effect of Seagrass Cover and Mineral Content on *Kappaphycus* and *Eucheuma* Productivity in Zanzibar

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***Abstract*—**The productivity of two species of red algae, namely *Eucheuma denticulatum* (Burman) Collins et Harvey and *Kappaphycus alvarezii* (Doty) Doty was investigated at Paje and Uroa, two sites in Zanzibar differing in seagrass cover. The growth rate (GR) of *E. denticulatum* in Paje (low seagrass cover) was 20–75% lower than in Uroa (high seagrass cover), depending on season. Growth of *K. alvarezii* in Paje was compromised by *Polysiphonia* spp. epiphytism. Manganese, iron, copper and zinc contents of both *E. denticulatum* and *K. alvarezii* from Paje were 35–99% lower than in *E. denticulatum* from Uroa. Culturing of epiphyte-infested or healthy *K. alvarezii* in seawater fortified with the mentioned minerals improved daily GR by 10–200 %. The effect of Cu, Zn and Mn in *K. alvarezii* with epiphytic infestation and 'ice-ice' was positive only when Provasoli solution was added. The GR of *E. denticulatum* was virtually unchanged by the addition of minerals. It is suggested that Fe, Zn, and especially Mn may play an important role in conferring resistance to physical stress to the macroalgae, stress which eventually makes them more susceptible to epiphytism and/or a bacterial infection that is responsible for a disease condition known as 'ice-ice'. Ice-ice describes the texture and colour of the affected thalli. The possible role of seagrasses to the productivity of algae is also discussed.

## INTRODUCTION

The commercial mariculture of *Kappaphycus alvarezii* (Doty) Doty and *Eucheuma denticulatum* (Burman) Collins et Hervey (Solieriaceae, Gigartinales, Rhodophyta) in Zanzibar, Tanzania started in December 1989. At the experimental stage, both local Tanzanian and Philippines strains of *K. alvarezii, K. striatum* Schmitz and *E. denticulatum* were used (Mtolera et al., 1995a). The Tanzanian strains had lower growth rate than the Philippine strains and among the Philippines strains, *E. denticulatum* had a better growth rate than *K. alvarezii* and *K. striatum*, and therefore farmers preferred to cultivate the Philippines strain of *E. denticulatum*. Due to better world market prices for kappa carrageenan-producing seaweeds, a Philippines strain of *Kappaphycus alvarezii* (Doty) Doty) was introduced into Paje villages in June, 1994. Nevertheless, three months after its introduction, *K. alvarezii* was attacked by the epiphytic red algal genus *Polysiphonia* and most farmers had to return to cultivating *E. denticulatum*. It is unclear whether the *Polysiphonia* sp. was imported together with the *K. alvarezii*.

Depending on the water current, the daily growth rate of *E. denticulatum* co-cultivated with *Ulva reticulata* or *Thalassia* sp. is reduced by 10–100% (Mtolera et al., 1995a). *Eucheuma denticulatum* appears to grow best in unidirectional water currents. Thus, as reported in the Philippines (Doty, 1973), sites for *Eucheuma* farms are cleared of seagrasses. Mtolera et al. (1995a) argued that the inefficiency of *E. denticulatum* in $HCO_3^-$ utilisation could partly explain its poor growth

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when in coexistence with seagrasses or *Ulva* sp. Carbon deficiency in *E. denticulatum* could induce the production of reactive oxygen species (ROS), e.g. $H_2O_2$ and volatile halocarbon (VHC) production. Other factors playing an important role in regulating the metabolism of ROS and plant stress tolerance include water temperature and season (Collén & Davison, 2001). Although $H_2O_2$ and VHC could be helpful to algae as a defence against microbes and other algal spores (Kott et al., 1966), ROS production, e.g. superoxide radicals and excessive quantities of $H_2O_2$ and VHC in areas with poor water circulation could be harmful (Mtolera et al., 1995 a&b). Superoxide dismutase (SOD; EC. 1.15.1.1), which may exist as CuZnSOD, MnSOD and FeSOD; catalase (EC. 1.11.1.6) and peroxidases (EC. 1.11.1.7) assists plants in the disproportionation of ROS (Bannister et al., 1987; Kitayama et al., 1999) whose production may induce the production of VHC. However, there is interspecific variation in the ability to detoxify ROS (Collén & Davison, 1999).

Although seagrasses may be detrimental to the productivity of some seaweed species (Mtolera et al., 1995a, b; Davis & Fourqurean, 2001), their role in nutrient circulation could make them a necessary evil. Seagrasses are capable of taking up nutrients from sediments (Thursby & Harlin, 1982; Short & McRoy, 1984; Brix & Lyngby 1985; Moriarty et al., 1985; Moriarty & Boon, 1989) and following decomposition, releasing them into the water column. Moreover, aerobic bacteria around seagrass roots facilitate the release of nutrients into the surrounding media (Craven & Hayasaka, 1982). However, studies on the nutrient regeneration in seagrass beds are few and the status of nutrient mobilisation from the sediments to the water column in tropical eastern Africa seagrass beds is unknown.

In the study reported here it was of interest to investigate if seagrass removal to give way to *Eucheuma* or *Kappaphycus* species mono-culture and/or seagrass destruction as a result of the physical impact of farm maintenance activities has an effect on the availability of some physiologically important metals, and whether their unavailability has a negative impact on the productivity of *Eucheuma*/*Kappaphycus* farms.

## MATERIALS AND METHODS

### Plant material

*Eucheuma denticulatum* and *Kappaphycus alvarezii* were the macroalgae used in the present study. They were collected from seaweed farms at Paje and Uroa in Zanzibar, Tanzania. *Thalassia hemprichii* was growing sparsely in seaweed farms but was dense in the Uroa tidal pool. Seagrass meadows around Unguja Island are dominated by *T. hemprichii*. *Thalassia hemprichii* and *U. reticulata* samples for metal analysis were randomly picked from *Eucheuma* farms in the two villages. Both Paje and Uroa villages are important sites for the cultivation of an *E. denticulatum* strain imported from the Philippines. Studies involving *K. alvarezii* were done in Paje where its farming since introduction in June 1994 is affected by epiphytism by *Polysiphonia* species. Epiphyte infestation was found to be higher in farms located downstream, and therefore infested plants were taken from farms located downstream and healthy plants from farms located farther upstream.

### Laboratory cultivation

The algae were cultivated in Plexiglas cylinders as described by Lignell et al. (1987), at photosynthetic photon flux density (PPFD) of ca. 350 μmol photon/$m^2$/s with a 12:12 (day: night) photoregime (Mtolera et al., 1995a) using fluorescent tubes (Thorn Polylux 4000) as the light source. Growth medium was natural seawater (NSW). In cases where NSW was fortified with Provasoli medium (Provasoli, 1968) vitamins were excluded.

### Field cultivation

Plants in the field were cultivated as outlined in Lirasan & Twide (1993). Villagers in Paje and Uroa generously provided samples for metal analysis or laboratory studies. Some villagers even allowed us to take measurements of growth rate on their plants. Growth of such plants was determined as detailed in Mtolera et al. (1995a).

*Thalassia hemprichii* samples were sampled from seaweed farms where they were found growing. At Uroa, *U. reticulata* and seagrass samples were also taken from an intertidal pool where seaweed is not usually cultivated (Mtolera et al., 1995a). *Eucheuma denticulatum* and *K. alvarezii* samples were taken from plants attached to monolines. Such farmed plants and *U. reticulata* were considered suitable when growing at the site for not less than a month. Experimental *E. denticulatum* and *K. alvarezii* were replanted from seedlings taken from the same or a nearby farm.

### Metal analysis

Chemical analysis was performed by a simultaneous multi-element analysis using a direct current plasma (DCP) atomic absorption spectrophotometer at AB Lennart Månsson International, Helsingborg, Sweden. Metal content in mg/kg dry weight (DW) was analysed for *T. hemprichii*, *K. alvarezii*, *E. denticulatum* or *U. reticulata* grown in the laboratory or taken from Paje and Uroa. Samples for metal analysis were rinsed in distilled water before drying at 105 °C. Metal contact with samples was avoided.

### Effect of minerals on seaweed growth

After establishing that plants from Paje and Uroa differed significantly in some metal contents, a study of the effects of selected metals on growth of *E. denticulatum* and *K. alvarezii* was found interesting. For this study plants were taken from both Uroa and Paje, and natural sea water was taken from Paje as it was assumed to lack sufficient amount of relevant metals. To study the effects of either manganese, iron, zinc or copper, the growth medium was enriched with either $MnSO_4.4H_2O$ (80 µg/l), $FeCl_3.6H_2O$ (240 µg/l), $ZnSO_4.7H_2O$ (10 µg/l) or $CuSO_4.5H_2O$ (10 µg/l). To study the cumulative effects of the earlier metals and other nutrients such as phosphates and nitrate, Provasoli medium was added such that the sources of manganese, iron, zinc and copper remained as above. Newly prepared medium was provided every 48 hours. The effect of each enrichment on algal growth rate was assessed for two weeks of continuous growth in a given medium. The resultant mean growth rate of five such cultures run in parallel was recorded.

### Effect of epiphytes on seaweed growth

Aeration, inoculum density, pH maintenance, growth determination, and calculation of the extent of epiphyte infection were performed as detailed in Mtolera et al. (1995a). Plants free from epiphyte infestation taken directly from the field were used in the experiments. To induce 2.5–5% epiphytism, a method described in Mtolera et al. (1995a) was adopted. The effect of manganese, iron, copper or zinc to the recovery of seaweeds was studied using plants from Paje infested with both epiphytes and 'ice-ice'. Unless stated otherwise, the conditions specified above were used in all experiments.

### Data analysis

Daily growth rate, DGR as a percentage, was calculated using the formula:

$$DGR = [(W_t/W_o)^{1/t} - 1] \times 100$$

where $W_o$ and $W_t$ were initial and final biomass at day t, respectively (Lignell et al., 1987). The fresh weights were determined following a brief centrifugation (1 min). Variation in weight values using this approach was ± 0.5%.

## RESULTS

The average growth rate for the Philippines strain of *E. denticulatum* grown in Paje and Uroa were 6.5% and 8.2% in 1994 and 5% and 8.2% in 1998 respectively (Table 1a). This shows that the growth rate was lower in Paje than in Uroa and that growth rate in Paje was higher in 1994 than in 1998 by around 30%. When the Philippine strain of *K. alvarezii* was introduced in Paje in June, 1994, it had an average growth rate of 5% during June to August, 1994. After epiphyte infestation in September 1994, the growth rate was reduced to around 1.1% for plants with visible epiphyte infestation and 1.8% for those that looked relatively healthy (Table 1a).

The growth rate of *K. alvarezii* was reduced from 5% to ≤ 2% by epiphyte infestation (Table 1a). Growths rates under laboratory conditions were slightly higher, and growth rates were much higher (26–200%) in natural seawater with

**Table 1. Average growth rate for *Kappaphycus alvarezii* and *Eucheuma denticulatum* grown in the field or laboratory before and after the infestation with *Polysiphonia* sp. in September, 1994.**
**(a) Growth rate for field-growing plants sampled in 1994 and 1998.**
**(b) Growth rate of plants initially with 2.5–5% epiphyte infestation or epiphyte infestation plus 'ice-ice' or that were normal (healthy) grown for two weeks in either natural seawater (NSW) or NSW fortified with Provasoli solution containing either $Fe^{+3}$ , $Cu^{+2}$, $Zn^{+2}$ or $Mn^{+2}$.**
**(c) Growth rate of plants initially with epiphyte infestation, or with epiphyte and 'ice-ice' (E+ice-ice) or that were normal (healthy) grown in NSW fortified with either $Mn^{+2}$, or $Fe^{+3}$ or $Zn^{+2}$ or $Cu^{+2}$.**
**Values are means and standard deviations of five measurements. The range is shown in parentheses**

| | *Kappaphycus alvarezii* | | | *Eucheuma denticulatum* | |
|---|---|---|---|---|---|
| Village | Paje | | | Paje | Uroa |
| Status of the algae | Epiphytism | (E+ice-ice) | Healthy | Healthy | Healthy |
| **(a)** | | | | | |
| June–August, 1994 | No epiphytism | | 5.1 ± 0.8 (4.0–6.1) | 7.2 ± 1.2 (5.7–8.5) | 9.4 ± 0.7 (8.3–10.0) |
| Sept.–Dec., 1994 | 1.1 ± 2.3 (-1.6–3.4) | n.d. | 1.8 ± 0.6 (1.0–2.7) | 5.8 ± 0.5 (5.1–6.2) | 7.1 ± 0.6 (6.0–7.6) |
| June–August, 1998 | 3.5 ± 0.9 (2.2–4.8) | n.d. | 4.3 ± 1.2 (3.0–5.9) | 6.0 ± 0.8 (5.1–6.9) | 9.5 ± 1.2 (7.5–10.5) |
| Sept.–Dec., 1998 | 2.5 ± 0.5 (1.8–3.2) | n.d. | 3.3 ± 0.7 (2.3–4.0) | 4.0 ± 0.5 (3.2–4.5) | 7.0 ± 0.4 (6.5–7.5) |
| **(b)** | | | | | |
| Control (NSW) | l.5 ± 1.3 (0.2–3.0) | -l.l ± 3.1 (-3.9–2.5) | 2.8 ± 0.7 (1.6–3.4) | 6.2 ± 1.1 (5.1–7.6) | 7.4 ± 0.5 (6.6–8.0) |
| $Fe^{+3}$ + Provasoli | 2.7±0.7 (1.5–3.5) | Always died | 4.1 ± 1.2 (2.8–5.6) | 7.2 ± 0.9 (5.7–7.9) | 6.9 ± 1.0 (5.1–7.7) |
| $Cu^{+2}$ + Provasoli | 3.1 ± 0.8 (2.5–4.5) | 1.7 ± 1.3 (0.2–2.8) | 4.0 ± 0.9 (2.7–4.8) | 6.3 ± 0.4 (5.9–7.0) | 8.0 ± 0.9 (6.9–9.1) |
| $Zn^{+2}$ + Provasoli | 1.9 ± 1.1 (0.0–2.8) | 1.2 ± 1.2 (-0.2–2.7) | 4.3 ± 1.1 (2.8–5.6) | 5.3 ± 1.2 (4.0–6.5) | 6.5 ± 2.1 (3.1–8.8) |
| $Mn^{+2}$ + Provasoli | 4.5 ± 0.7 (3.3–5.2) | 3.2 ± 1.1 (1.6–4.6) | 5.5 ± 0.8 (4.5–6.5) | 6.6 ± 0.5 (6.1–7.3) | 8.5 ± 2.3 (4.4–9.9) |
| **(c)** | | | | | |
| Control (NSW) | 1.5 ± 1.3 (0.1–3.2) | -1.1 ± 3.1 (-3.7–2.6) | 2.8 ± 0.7 (1.8–3.6) | 6.2 ± 1.1 (5.1–7.6) | 7.4 ± 0.5 (6.7–8.0) |
| $Fe^{+3}$ | 1.7 ± 0.9 (0.6–2.7) | Always died | 2.0 ± 0.6 (1.1–2.7) | 6.4 ± 0.7 (5.3–7.2) | 7.6 ± 0.9 (6.4–8.9) |
| $Cu^{+2}$ | 2.1 ± 0.4 (1.5–2.5) | Always died | 3.3 ± 0.4 (2.8–4.4) | 7.0 ± 0.9 (5.7–8.1) | 8.2 ± 0.6 (7.4–8.8) |
| $Zn^{+2}$ | 1.4 ± 1.3 (0.1–3.3) | Always died | 4.0 ± 1.3 (2.1–5.6) | 7.1 ± 1.0 (5.5–8.2) | 7.8 ± 0.4 (7.1–8.2) |
| $Mn^{+2}$ | 3.7 ± 0.7 (3.1–4.8) | Always died | 4.5 ± 0.8 (3.2–5.5) | 8.2 ± 0.5 (7.5–8.7) | 8.7 ± 0.5 (7.8–9.1) |

n.d. = not determined.

Provasoli solution enriched with either $Mn^{2+}$, $Fe^{3+}$, $Zn^{2+}$ or $Cu^{2+}$ (Table 1b). Healthy or epiphyte-infested *K. alvarezii* grew faster in natural seawater with only $Mn^{2+}$, $Fe^{3+}$, $Zn^{2+}$ or $Cu^{2+}$. However, *K. alvarezii* affected by both epiphytes and 'ice-ice' did not survive under the latter setting (Table 1c). The growth rates for both *K. alvarezii* and *E. denticulatum* were highest when manganese was added to the culture medium.

An analysis of metal content in *K. alvarezii* (with and without visible epiphyte infestation), *E. denticulatum* and *Ulva reticulata* randomly sampled from Paje and Uroa farms shows that (with exception of Fe in *U. reticulata* from Paje) plants sampled from Uroa had 29–99% higher metal content than those from Paje (Table 2). *Kappaphycus alvarezii* infested with epiphytes had the lowest metal content (35–99% lower). *Thalassia hemprichii* from farmed areas of Uroa had respectively, 106, 160 and 69% higher iron, copper and zinc content, and 22% lower Mn content than that from Paje. The seagrass rhizomes from both study sites were richer in Fe, Cu and Zn than leaves and the reverse was true for Mn. The seagrass rhizome: leaf ratio of iron, copper, zinc and manganese contents were 1.4:1, 2.8:1, 2.1:1 and 0.5:1 for Uroa samples and 1.8:1, 1.1:1, 1.1:1 and 0.8:1 for Paje samples, respectively. *Ulva reticulata* samples from the seagrass pool at Uroa had 500, 360, 350 and 380% higher iron, copper, zinc and manganese content. The rhizomes also had high phosphorous and sulphur content (data not shown). Iron, Cu, Zn and Mn contents in *Ulva reticulata* sampled from a pool with higher seagrass cover (Uroa) were 350–500% higher than metal contents in *Ulva reticulata* from the farms where seagrasses were scattered.

## DISCUSSION

There has been a decrease in the growth rates of *E. denticulatum* farmed in Paje between 1994 and 1998 (Table 1a). These results support a general view among seaweed farmers there that the productivity of the farmed species has dropped. The reason for a higher productivity in Uroa than Paje is not yet established. However, in this study algal samples from Paje generally had lower Fe, Cu, Zn and Mn content than those from Uroa.

Plants grown in the laboratory in media supplied with Fe, Cu, Mn or Zn had 26–200% faster growth than those without, and the addition of Provasoli solution was particularly beneficial to plants. These results emphasise the importance of the minerals for seaweed growth.

In this study, *K. alvarezii* that was affected simultaneously by epiphytism and 'ice-ice' did not recover in natural seawater fortified with only metal additions (Table 1c). Neither did recovery occur in a media containing iron, natural seawater and Provasoli solution (Table 1b). A general improvement of plant growth and recovery from epiphytism and ice-ice were observed in media fortified with Mn, Cu or Zn and Provasoli solution

**Table 2. Metal content in mg/kg DW of *Thalassia hemprichii*, *Kappaphycus alvarezii*, *Eucheuma denticulatum* or *Ulva reticulata* grown in the laboratory or taken from the field (seaweed farms) in Paje and Uroa, Zanzibar. Values for *T. hemprichii* are mean values for rhizomes and leaves. Figures are averages for two samples taken randomly**

| | *Thalassia hemprichii* | | | *Kappaphycus alvarezii* | | | | *Eucheuma denticulatum* | | *Ulva reticulata* | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Uroa | | Paje | | | | | | | |
| | Paje | Farm | Pool[1] | Sick | Lab[2] | Healthy | Lab[3] | Paje | Uroa | Paje | Uroa |
| Fe | 77.5 | 160.3 | (84.0) | 21.0 | (50.0) | 72.0 | (130.0) | 32.0 | 130.0 | 91.0 | 37.5 |
| Cu | 5.1 | 13.3 | (15.6) | 11.0 | (15.0) | 4.3 | (17.0) | 9.0 | 17.0 | 5.4 | 16.5 |
| Zn | 13.0 | 22.0 | (24.0) | 13.0 | (39.0) | 53.0 | (75.0) | 22.0 | 75.0 | 23.0 | 34.0 |
| Mn | 17.5 | 13.6 | (10.6) | 0.8 | (34.0) | 62.0 | (130.0) | 1.6 | 130.0 | 22.0 | 65.0 |

[1]Seagrasses collected from an intertidal pool; [2] sick and [3]healthy *K. alvarezii* grown continuously in the laboratory for two weeks in natural sea water fortified with the shown metals and Provasoli solution.

(Table 1b). These results, apart from emphasising the importance of the cumulative effects of nutrients present in Provasoli solution, imply that minerals other than iron appear to be critical in facilitating the recovery of *K. alvarezii* from both epiphytism and ice-ice. A study to identify the physiological role of Cu, Zn and Mn in the recovery of *K. alvarezii* from epiphytism and 'ice-ice' is thus important.

In our earlier studies with *E. denticulatum* (Mtolera et al., 1995a), 'ice-ice' and epiphyte infestation were found to be associated with physical stresses such as high light intensity and pH. During such stresses the production of hydrogen peroxide and volatile halocarbons was found to be high (Mtolera et al., 1995 a & b). Mtolera et al. (1995a) associated 'ice-ice' and attack by epiphytes with a lack of sufficient protective mechanisms against the over-produced reactive oxygen species, such as hydrogen peroxide and its precursors, e.g. superoxide radicals ($O_2^{\bullet-}$), which are capable of inducing serious biochemical and physiological damage (Fridovich, 1986; Bannister et al., 1987; Keppler & Novacky, 1987; Devlin & Gustine, 1992; Collén et al., 1995; Imsande, 1999). Plant protective devices such as the enzyme superoxide dismutase rely on metals such as Cu, Zn, Mn and Fe for their activity (Bannister et al., 1987; Lidon & Teixeira, 2000). Moreover, such metal ions are important for other plant processes, e.g. $Mn^{2+}$ influences nitrogen assimilation through regulating the activity of glutamine synthase (Devriese et al., 2001) while Fe is important for optimal activities of the photosynthetic electron transfer chain (Kudo et al., 2000; Davey & Geider, 2001) and nitrate reductase (Kudo et al., 2000), and in improving the chlorophyll *a*: carotenoid ratio (Li et al., 2003).

The reason for the resistance of *E. denticulatum* to epiphyte infection in Paje is not known. Possibly this species has better defence mechanisms against epiphytes and parasites (bacteria, fungi, etc.) and/or better stress tolerance (Collén & Davison, 1999; Mtolera et al., 1995a). Despite *K. alvarezii* being farmed in Paje for more than nine years now, its growth rate and resistance to epiphytes do not seem to have improved. This possibly emphasises the need for seaweed farmers in Zanzibar to cultivate native species, such as *Kappaphycus striatum*.

In this study, *Thalassia hemprichii* samples from Paje had lower Fe, Cu and Zn content but higher Mn content compared to those from Uroa. The seagrass rhizomes from both study sites were richer in Fe, Cu and Zn than the leaves and the converse was true for Mn. Phosphorous (P) and sulphur (S) content was also higher in the rhizomes (data not shown). Nevertheless, neither the uptake route for the minerals, nor concentrations in the water column and sediments was established. In *Zostera marina* phosphorous and ammonia are taken up through both the roots and leaves (Thursby & Harlin, 1982; Short & McRoy, 1984; Brix & Lyngby, 1985; Moriarty & Boon, 1989; Davis & Fourqurean, 2001).

Paje was among the earliest villages in Zanzibar to embrace seaweed farming. One of the effects of seaweed farming using an off-bottom monoline method is the destruction of seagrasses. Although Paje and Uroa villages have farms that experience similar water movements and the seagrasses are equally disturbed, Uroa farms are close to an intertidal pool that has a dense seagrass meadow (Mtolera et al., 1995a). Metal contents in the *Ulva reticulata* that was sampled from the Uroa seagrass pool were three- to five-fold higher than those of the same species from the farms (Mtolera et al., 1995a). It is possible that seagrass density influenced the metal concentration in *U. reticulata,* or that the seagrass pool in Uroa had a positive influence on the productivity of nearby seaweed farms. However, additional studies in areas differing in seagrass cover are required to establish (a) nutrient mobilisation from the water column to the sediment pore water and vice versa and (b) cyanoprocaryota, microalgae and macroalgal growth in such areas. Davis and Fourqurean (2001) have, for example, shown a reduction of *Halimeda incrassata* density in areas with higher *Thalassia testudinum* cover. It would be useful to evaluate the optimum densities of seagrasses such as *Halimeda* for the farming of seaweeds like *Eucheuma* spp.

## CONCLUSIONS

The results of this study show that the productivity of *Eucheuma* and related seaweeds is compromised if farms are established in areas with low manganese, iron, copper and zinc contents. The role of seagrasses in mineral mobilisation warrants further studies to establish optimum density, diversity and uptake route. Aerobic bacteria may be crucial in the mobilisation of some nutrients (Craven & Hayasaka, 1982).

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