FINAL REPORT

An assessment of seagrass survival and functioning in response to manipulations in sediment redox at Nyali Lagoon, Kenya.

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By

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Abstract

Thalassodendron ciliatum was studied during two monsoon cycles of the year 2001/2002 to determine the interactive effects of experimentally elevated redox potentials on *in situ* plant structure and shoot-root (S/R) biomass allocation patterns. *Thalassodendron* plants from shallow back-reef tidal pools were substrate manipulated under ambient field conditions for 90 days on each monsoon cycle. Plant sampling was done from quadrats impacted with organic substrates at three different concentrations (proxies to induce differential redox potentials). Our data show clear differences (at ANOVA, $p < 0.05$) in *Eh* and plant traits from 2 treatment effects and from monsoon seasonality effects. *Thalassodendron* had relatively higher canopy cover, shoot density, shoot blade density, and absolute shoot and root biomass at control sites than at two substrate-impacted sites. Between the monsoons, the same plant traits were higher during the North-East Monsoons (NEM) than they were during the South-East Monsoons (SEM). *Thalassodendron* beds experienced negative carbon balances within 3 weeks of impaction and were dead by 2 months, which coincided with periods when daytime redox potential values consistently lower than –70mV. S/R ratios were relatively higher at high substrate impacted sites and during the South-East Monsoons (SEM), both conditions also coinciding with higher reducing conditions. Final S/R ratios were 0.32 and 0.34 during NEM and SEM periods respectively at control sites, and 0.33, 0.42, and 0.55, and 0.34, 0.38 and 0.60 at zero, mid and high substrate impacted sited during NEM and SEM depth respectively. About 60% and 95% of root biomass were distributed in the top 10-cm and top 20-cm of soil respectively. Our findings support our hypothesis that reduced redox concentrations would increase plant stress and, consequently, decrease investments in growth capacity.

Keywords: Biomass Production, Kenya, Monsoon Cycle, Organic Substrates, Redox conditions, Sediment Rhizosphere, Shoot-Root (S/R) Ratio, *Thalassodendron ciliutum.*

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Introduction

Kenyan seagrasses grow abundantly in shallow-water environments, mostly within the inshore lagoon ecosystems (Aleem, 1984; Heip *et al.*, 1995; UNEP, 1998; Dahdouh-Guebas *et al.*, 1999). Majority of these lagoons are aligned more or less parallel to a continuous fringing coral reef platform (Hartnoll, 1976). The fringing reef platform is known to break strong waves (Kirugara, 1998, Angwenyi, 2002), thereby calming waters in the back reef lagoons, which promote seagrass colonization and growth. In East Africa and indeed worldwide, seagrass meadows are of considerable ecological importance in coastal and marine ecosystems where they play significant roles in several ecological processes and provide resources for nearshore coastal ecosystems (Howard *et al.*, 1989; Poiner *et al.*, 1992; Hemminga *et al.*, 1995a & b). They are important in the production of organic carbon in the oceans (sequesters of CO_2) (Larkum et al. 1989; Hemminga *et al.*, 1995a; Bjork *et al.*, 1997; Schwartz, *et al.*, 2000; Duarte *et al.*, 2002); promotion of biological interactions (e.g., influence of grazing, detritus production and epiphyte production) (Little *et al.*, 1988; Marguillier, *et al.*, 1997; Mariani and Alcovero, 1999), and consequently supporting high biodiversity (Brakel, 1981; Little, *et al.*, 1988; Larkum *et al.,* 1989; MacArthur and Hyndes, 2001), including supporting two endangered species in Eastern Africa, the green turtle, *Chelonian mydas*, and the dugong, *Dugong dugong* (Frazier, 1975; Kendall, 1986; Wamukoya *et al.*, 1996; 1997). Seagrass beds also offer protection of coastal environments from storm surges (vertical stems/shoots acting as breakwaters) thereby offering natural shoreline protection/stabilization (Fonseca and Fisher, 1986; Fonesca, M.S. and Kenworthy, J. 1987).

In addition, seagrass beds support important biogeochemical processes such as oxygenation of water column (Duarte and Cebrian, 1996; Gattuso and Frankignoulle 1998; Gattuso *et al.*, 1998a & b), sedimentation of suspended particles (Phillips and Menez 1988; Fonsea, 1989; Miyajima, 1998), and regeneration of nutrients (Hemminga 1991, 1994, 1999, 2000). Though the effects of seagrass metabolism on above-ground water column properties are fairly known, the scenario obtaining within the sediment layer where they are rooted is poorly understood, especially for tropical seagrass (Hemminga 1998). In Kenya, although low organic loading is a feature that is common in well-flushed lagoons, eutrophic conditions and high bacterial contamination in the sheltered and semi-enclosed creeks have been reported (Mwangi *et al.*, 2001). This is a recipe for anaerobic processes and the corresponding elevated oxygen demand and soil anoxia. The implication of this to the survival and functioning of local seagrass communities is, however, not known. Some studies from high latitude regions have shown that many seagrass roots are capable of responding to moderate fluxes of anoxia. For instance, some seagrass roots release free oxygen through the rhizosphere to the surrounding sediments, which help maintain some aerobic processes and oxidative chemical reactions (Armstrong *et al.*, 1979; Kuhn, 1992; Pedersen *et al.*, 1998, 1999; Connell, *et al.*, 1999; Terrados, *et al.*, 1999). This free oxygen may also modify redox conditions within the rhizosphere. But when oxygen supply becomes limiting, as happens in highly reducing sediment, anaerobic processes replace aerobic respiration (Koch *et al.*, 1989, 1989, 1990). Under anoxic conditions, inorganic ions such as sulfates ($SO4^{-2}$) are known to serve as the principal terminal electron acceptors in oxidative phosphorylation (Hines *et al.*, 1989).

Due to an abundance of sulfates in seawater, the breakdown of deposited organic mater will largely be accomplished by sulfate reducing bacteria that release free sulfide ions into the

sediment environment which may be stressful, if not toxic to plants (Howarth and Teal, 1979). The resultant sulfide toxicity, together with the reducing conditions obtaining within sediments, may make seagrass growth and survival very difficult. It has been established that increased rates of organic matter deposition and decreased rates of re-oxidation from photosynthetic oxygen diffusing from seagrass roots and rhizomes to rhizosphere (e.g., Carlson *et al.*, 1994) promote the precipitation of sulfides in seagrass sediments. Short-term increases in sediment sulfide levels can affect seagrass photosynthesis-respiration balance more towards the latter (e.g., Copeland, 2001), but over a longer term, decreased seagrass photosynthesis may lead to other cascading effects culminating in plant death (see review by Hemminga 1998). Declines in seagrass cover, species composition, growth vigour, and health status, therefore, may indicate slow but important changes in their environment. Seagrass structural complexity indices (e.g., community structure and health status) have been used variously as sensitive bioindicators for both water and sediment quality in some places (Pergent-Martini, 1998; Pergent *et al.*, 1999; Fourqurean and Cai, 2001).

Like elsewhere in the developing world, although natural events are also responsible for some large-scale and local losses of seagrass habitats, recent evidence suggests that human population expansion and tourist developments are now the most serious cause of seagrass habitat degradation in East Africa (Shah *et al.*, 1989; Saunders *et al.*, 1990; Johnson and Johnston 1995; Abal and Dennison 1996; Kenya-ICAM 1996; Richmond, 1997; WWF, 2001, 2002). This is especially important to the coastal cities and peri-urban regions which are experiencing rapid developments along the their coasts, especially attributed to tourism development which result in organic-laden waste discharges into the lagoons neighbouring these facilities (CDA, 1995; Kenya-ICAM 1996, Ochieng 1996). A study in Kenya has shown that a seasonal blooming of two species of seaweeds, *Enteromorpha* and *Ulva*, occurred at sites that experienced sewage outfall from hotel establishments and municipal sewage (Mwangi *et al.*, 2001). There is, therefore, a wide shared concern over the sustainability of goods and services from urban and peri-urban seagrass beds due to such cases of environmental degradation. Despite the limited documented cases of seagrass threats and declines for the Kenyan region (e.g., Wakibya 1995; Ochieng 1995; CDA, 1995; Kenya-ICAM 1996; Ochieng and Erftemeijer 1999; Ochieng and Erftemeijer 2002; WWF 2001, 2002), there are no studied reports that pin points the incidence of degradation of seagrass communities to measured effects of their causal agents. There are even no published data on estimates of area loss or degradation in this region (Johnston, 1995; Bandeira and Bjork, 2001), making even the crudest estimates very difficult. This study addresses this gap partially. The current study was, therefore, designed to address and test the vulnerability of a common tropical seagrass species to stress from organic deposition into its environments.

The objectives of this study, therefore, were to quantify and to evaluate the effects of reduced redox potentials associated with organic sedimentation on *in situ* plant structure and functioning. It was hypothesized that reduced redox concentrations would increase plant stress and, consequently, investments in growth capacity would decrease. The null hypotheses tested were that there would be no significant effects of reduced redox concentration on plant health. The independent variable was differential redox concentration; the dependent variables were the various plant characteristics and biomass levels in shoot and root compartments.

Methods:

Study site

The back-reef tidal pools of Nyali Lagoon were selected for the study (Figure 1). The area is within the Mombasa Marine Park and Reserve, which is part of a larger Nyali-Bamburi-Shanzu Lagoon (about 20km^2). The environmental and oceanographic conditions of this site are fairly well known (Turyahikayo 1987; Maclanahan 1988; Odido 1994; Nguli, 1994; Heip *et al.*, 1995; Kenya-ICAM, 1996; Kirugara, 1998, Tack & Polk, 1999; Angwenyi, 2002). The biophysical environment encompasses clear-water subtidal habitats with a maximum depth of about 6-m at the channels during spring low tides. Mixed seagrass communities (dominated by *Thalassodendron ciliatum*) and associated seaweeds cover about 60% of the lagoon (Muthiga, 1996). The tidal amplitude is large, about 4-m at spring tides (Maclanahan, 1988, Odido 1994; Nguli, 1994; KPA, 2001, 2002), creating a wide littoral environment towards the beach, where patchy seagrass beds are to be found, majority occurring within shallow depressions retaining pools of water at low tides (known also as tidal pools). The tidal pools and the extensive lagoons, are protected from the open sea by a continuous fringing reef platform lying about 0.5 - 1km offshore and parallel to the coastline (Figure 1), and experiences more turbulent water motions in comparison to closed bays and creeks. At some locations, narrow channels connect the lagoons with the open sea during low tides, but high waters pass over the reef crest into the lagoon so that water exchange is very effective, and the spatial and temporal concentrations of nutrients and chlorophyll-*a* do not reach eutrophic levels because the lagoon is well flushed.

The environmental and oceanographic conditions experienced locally are partly under the broader influence of a seasonal monsoon cycle driven by the annual north-south migration of the Inter-Tropical Convergence Zone (ITCZ), and also under the impact of the recently discovered Indian Ocean Dipole (IOD) phenomenon (Anderson 1999, Behera *et al.*, 1999 Saji *et al.*, 1999 Webster *et al.*, 1999) on the interannual variability of the Indian Summer Monsoons. The influence of the IOD on the Indian Monsoons is reported to be opposite to the effect of El Niño/Southern Oscillation (ENSO), and the IOD-monsoon rainfall relationship varies complementarily to that between the ENSO and monsoon rainfall. Two main climatic conditions occur creating two monsoon events, southeast monsoons (SEM) and northeast monsoons (NEM), driving local differences in the physical, chemical and biological oceanographic conditions of coastal waters. During SEM, the coastal currents move northwards along the coast driving the waters onshore, under conditions associated with high wind energy, high cloud cover, high rain (and therefore high sedimentation from increased river discharge or surface run-offs), and low water temperatures. As a consequence of SEM conditions, reduced productivity and a relative higher abundance of benthic algae are generally experienced in coastal waters. During NEM, the reverse is true: the coastal currents move southwards along the coast driving waters offshore, under conditions associated with high radiation, low wind energy, low cloud cover and, therefore, productivity is much higher (Maclanahan, 1988, Odido 1994; Nguli, 1994).

Seasonality differences also occur in tidal cycles and water circulation patterns (Turyahikayo 1987; Odido 1994; Nguli, 1994) between the two monsoon events, and these differences may have significant impacts on plant functioning (Ochieng and Erftemeijer 1999). Tidal data for the study site in the year under investigation were: highest astronomical tide = 4.1m; lowest astronomical tide = -0.1m; MHWS = 3.5m; and MSL = 1.86m [all heights were referenced to Datum of the largest scale Admiralty Charts of Kilindini Port of Mombasa, Kenya, (KPA 2001, 2002)]. Tides at the site have been described as semi-diurnal with two low and two

high tides per day and characterized by asymmetries in sea level and current cycles (Turyahikayo 1987; Odido 1994; Nguli, 1994; Kirugara 1998; Angwenyi, 2002). The lowest tides occur during NEM due to the prevailing winds that drive waters offshore. Also, the lowest tides occur during daytime during NEM, while the lowest tides occur at night during SEM, meaning desiccation stress due to day-time exposure times differ between the two seasons. It has also been shown that there are two different wave-induced net water circulation patterns in neap and spring tides, which may also differ between the two monsoons (Turyahikayo 1987; Kirugara 1998; Angwenyi, 2002). The seasonality effects of tides and monsoon winds have been reported to drive a differential seagrass loss: detachment of seagrass blades (or plant fragments) from their stems/rhizomes by the surge effect from waves. The most intense accumulations (up to 1.2 x 10^{-6} kg dry wt. in a 9.5-km stretch encompassing Jomo Kenyatta Public Beach (Fig.1)) were shown to occur during SEM (Ochieng and Erftemeijer, 1999) which corresponds to periods when wind speeds and current speeds, water column mixing and wave heights are usually greatest (Turyahikayo 1987; Odido 1994; Nguli, 1994; Kirugara 1998; Angwenyi, 2002).

The study site was species rich in Kenyan seagrass species with 8-species reported in past studies including our candidate species *T. ciliatum* (Kamermans, 2001, 2002; Alcoverro & Mariani, 2002), out of the regional 12 species (Isaac, 1968, Aleem AA, 1984; Coppejans *et al.,* 1992; Hemminga *et al.,* 1994, 1995a, Wakibya 1995; Uku *et al.,* 1996; Ochieng and Erftemeijer 1999; Ochieng and Erftemeijer 2000). The study site plots were spatially located within about 30 to 80-m from the beach line (high spring water-mark), behind which were two tourist hotels (Reef Hotel and Bahari Club). Experimental study plots were interspersed within an area covering about 100m-squared (Figure 2). This area had few individual sea urchins (a total of 16 were encountered in plots; these were removed prior to set-up). Removal of sea urchins was considered important to avoid experimental bias due to their grazing and movements. The common sea urchin here, *Tripneustes gratilla*, for instance, can graze at a rate of 1.8 seagrass shoots/m^2/day at fronts that support a sea-urchin abundance of 10.4 individuals/m^2 (Alcoverro & Mariani, 2002). Experimental plots were set out in shallow tidal pools (permanently submerged pools) so that plots had at least 10-cm immersion water depth at spring low tides. This ensured sites experienced more-or less similar immersion times.

Experimental set-up

Field experimental plots were set up in a spread of three days for each of the monsoon phases: 7th to 9th October 2001 for SEM, and 3rd to 5th May 2002 for NEM. Plots selected for SEM studies were different from those selected for NEM studies, to avoid historical bias of treatment effects. Several assistants were on hand at the sites to enable specific timeline schedules to be completed in time as detailed below. For each set-up, separate field assistants were stationed at different replicate sites to enable treatment effects to be applied simultaneously, thus avoiding possible confounding effects of different experimental start-up times. Prior to field set-up program, organic substrates for experimental treatments were prepared in the lab as follows:

a) **Organic substrate preparation (lab work)**

   This was made from industrial granular sucrose and powdered industrial starch. This was mixed in equal volume proportions, and then further mixed with sieved medium sand particles (retained by sieve mesh size 0.250-mm or phi-2) to produce a sand-sucrose-starch complex used as the organic substrate for the experiments.

b) **Substrate applicator (pipette) preparations (lab work)**

Organic substrate applicators were made from 10-ml plastic pipettes (about 10-cm long) pre-perforated with fine-needle (about 0.1-0.2 mm diameter) along their lower tapering 6-cm lengths at approximately a hole every 3-mm, and 6 columns down. Pipettes were then stuffed with the sucrose-starch complex to the tip and stoppered on the open ends with small rubber cocks. Such a design would allow pipettes, when inserted in sediments (insertion depths were 7-cm to conceal the 6-cm length pipette perforations) to transfer, at continuous rates, the sucrose-starch cocktail to the rhizosphere (rooting soil compartment). Pipettes were rubber stoppered to prevent possible dissolution loss of sucrose-starch cocktail via the end sticking into the water interface, diffusion only occurring via the perforations opening into sediments.

The field experiment proceeded as follows:

c) Block designs (day-1)

A randomized (discrete) block design was set up on day-1 of the experimental cycle. Four blocks (representing 4 replicates) were established within *T. ciliatum* meadows (each block separated from each other by about 10-m strip of meadow), and each block occupied an area of about 4m-squared and comprised four (0.4 x 0.4m^2) experimental plots at least 1-m apart from each other (Figure 2a). To establish the experimental plots, 0.16m^2 stainless steel metal quadrats were secured to the sediments using thin plastic pegs, and appropriately numbered with plastic twines and bright labels for easy re-find.

d) Treatment procedures (day-2 & 3)

In each block, experimental plots were randomly assigned to one of the three-substrate treatments: 1) Treatment-1 (T-1): nil substrate application (all sand-filled pipettes); 2) Treatment-2 (T-2): low-level substrate application (50% sand-filled pipettes + 50% substrate-filled pipettes, uniformly distributed spatially); and 3) Treatment-3 (T-3): high-level substrate applications (100% substrate-filled pipettes, uniformly distributed spatially) (Figure 2b & 2c). Pipettes were placed at 5-cm from each other, and the boundary ones were 2.5 cm from the quadrat walls. An extra fourth plot (Treatment-0 (T-0) was set and left un-manipulated as a control unit. Treatments were replenished regularly at two-weekly intervals for all applications. These replacement times were pre-determined in a preliminary trial study undertaken earlier. All four plots within a block were completed before the next block was started and two blocks were set up per day. Experimental blocks were replenished/sampled in the same order as they had been established.

e) Plant and soil activity sampling and monitoring

(i) Soil redox (*Eh*) measurements:

Microelectrode profiling for redox (*Eh*) conditions were done on experimental plots and bare sites adjacent to the plots (bare sites selected had a surface area at least 4-m^2 and the shortest diameter at least 1.5m). In experimental plots, redox measurements were always done ahead of plant sampling, but on same day. Redox measurements were made *in situ*, at intervals of beginning of the experiment, Day-3, Day-7, and thereafter weekly, for 90 days. Redox measurements were conducted just before sunrise (earliest sunrise time in NEM was 5.57am and 6.19am in SEM) and again daytime at high irradiance time (i.e. between 11:00 and 15:00 h). Redox potentials were measured using a heavy-duty combined redox and sulphate electrode probes coupled to a millivolt (Mv) meter via long watertight conducting cables (Microscale Measurements, De Hague, Netherlands).

Each electrode had an insertion length of 50-cm, which was further graduated in 1-mm scales. For maximum performance, electrodes were always calibrated with a redox standard solution (phosphate buffer) at 25°C in the laboratory prior to sampling. Sediment redox potential values were obtained by carefully inserting electrode points into sediment, starting from the sediment-water interface and going down to deeper sediment layers sampled at graded depths of surface-0, 2, 5, 10 15, 20, 25, and 30-cm depths. At each measurement point/depth electrodes acclimated for about one minute to the sediment conditions before readings were taken in the mV meter. Duplicate measurements (made at different points) were taken at each experimental plot on each sampling day. Redox measurements were corrected to obtain Eh values relative to the standard hydrogen electrode.

(ii) Grain-size and organic matter determination:

At the beginning of the experiment, duplicate sediment core samples (up to 20-cm depth layer) were collected from strips separating the plots by corers (clear PVC tubes, 6-cm diameter and 40-cm long) to characterize sediments. At the end of the experiment, new cores were taken, but from within the experimental plots and next to biomass cores described in (iii) below. Cores were sectioned into 5 cm slices in the field, placed in plastic bags (double bagged), and stored in cool boxes until return to lab facilities at KMFRI, Mombasa. At the lab, each section was homogenized and about half of each core was wet sieved. The other half was frozen as an archive for future analyses, part of which was for organic matter content.

For grain-size determinations, each sub-sample fraction was first oven-dried (60°C for 24 h) and weighed, followed by wet sieving. Stainless steel sieves (Wenton scale series 2000mm to 38 μm mesh, or phi scale of –1.0 to 5.0) were used in wet sieving. Sieves were coupled together over a large bucket and samples were washed first through the top 2000mm mesh sieve. Samples were then sequentially washed into and through the succeeding sieves with tap water. After wet sieving, each fraction was lyophilized, weighed, and discarded. For organic content analyses, sections from second sub-sample series were oven-dried (60°C for 24 hr), weighed and then combusted in an electric furnace (500°C for 6 hours).

(iii) Plant form and S/R ratios measurements:

At each experimental plot, plant samplings/monitoring were done at Day-1, 3, 7, and thereafter weekly, and continued for up-to 90 days. All samplings/monitoring were made at low tide during the day. When daytime water levels in the plots were relatively high (neap tides), sampling was undertaken by snorkelling and/or SCUBA. For plant data, visual estimates for percentage cover were done per quadrat, and counts were made for total number of shoots (shoot density). From each plot, and on each sampling day, 10 shoots were randomly chosen and measured for data on leaf dimensions (stainless steel veneer caliper measurements, 2nd youngest leaf), and leaf blade density (number of blades per shoot).

At the end of the experiment, data on average leaf blade density, epiphyte-free 2nd youngest leaf dimensions and biomass (dry wt), and shoot density

(shoots/m^2) were determined from plots and controls prior to coring for biomass estimations. Above ground biomass was harvested from the sediment surface layer within a 20-cm diameter ring placed at the central inner parts of the experimental plots (to ensure that comparison of differences between treatment plots was not affected by sampling location within plots), and stored in labelled bags. For belowground parts, plant corers (20-cm diameter, 50-cm long) were used to get rooted tissues from depth. Plant core samples were sectioned into 10-cm slice fractions and analysed for root biomass present in the various fractions. All tissue categories were oven-dried (60°C for 24 h), to determine their dry weight biomass.

Statistical analyses:

Graphical techniques were applied to define sediment characteristics. Kruskal-Wallis Test, a nonparametric method that tests the assumption that the medians of different samples are similar, was performed to see if significant differences existed in sediments from different treatment sites. One and two-way analysis of variance (ANOVA) were used to assess the magnitude of variability on *T. ciliatum* variables from different treatment sites and between the two monsoon periods. A significance level of $p = 0.05$ was set in all tests.

Results:

Sedimentary environment

Pre-treatment grain size data characteristics are presented in Table-1. Eight weight fractions (corresponding to the sieve fractions used) were produced representing different sediment types. Generally, very coarse and coarse fractions contained mostly shells and some fragments of seagrass, and the finest fraction contained only fine-grained silt/clay. The overall sediment type is described as medium sand [sediment type based on classification of Folk (1974): median diameter 1.9 ϕ (i.e., about 2 ϕ which corresponds to 250mm)]. Medium sands and fine sands alone accounted for about 70% of the total sediment weight, hence they broadly defined the sediment type. Sediments in which *T. ciliatum* grew mostly comprised fractions between 125 to 250 mm. Organic matter was generally low in the sediments: about 3.64 % (±1.83) for *T. ciliatum* sediments and about 0.89% (±0.34) from the bare sites. The sediment characteristics were not peculiar to *T. ciliatum* sediments; they applied more-or-less to other seagrass vegetated sites like *Cymodocea serrulata* and *Syringodium isoetifolium* sediments (Table-1and Fig. 3). Results of Kruskal-Wallis test (performed on sediment data from experimental plots at the end of experiment) showed that there were no significant differences in sediment median diameter between the plots attributable to treatment effects (Table-2, Kruskal-Wallis test, $p > 0.05$). Hence, sediment grain characteristics were independent of treatment effects. There was also no significant difference in sediment characteristics between the two NEM-SEM seasons (Table-1 and 2, ANOVA, $p > 0.05$).

Redox potentials

Only data for NEM are given. Poor weather on some days did not allow consistent redox measurements in SEM, and so SEM redox data were disjunct in places. Positive redox potentials were recorded only in daytime measurements and within the top 10-cm sediment

depths. At dark (dusk measurements) all redox potentials had negative *Eh* values (Table-3, Figure 4). Dark time redox potentials were more negative than day values, and similarly down a depth profile redox potentials were also more negative. Ambient dusk vs day average redox potentials at the start-up time were –40.4 vs +28.2, -72.2 vs –14.0, -93.5 vs –24.6, and –103 vs –73.4 mV in the 0-2, 2-10, 10-20, 20-30 cm soil depths respectively in vegetated plots. These were taken as baseline redox levels for normal seagrass functioning at those depths. Normal functioning of *T. ciliatum* meadows seems to cope with build-ups in negative redox conditions in sediments up to around -110mV (at dark) so long as these can be cleared by daytime. In the study, the clearing effect by seagrass in normal functioning (difference between dark and day values on Day-1) were +68.6, 91.2, 68.9, and 30.3 mV in the 0-2, 2-10, 10-20, 20-30 cm soil depths respectively in vegetated plots. The lowest difference was at depths below 20-cm that had relatively higher negative values coinciding with low root biomass as will be seen later. Within three weeks (Day-21), diurnal differences were highly variable within experimental plots from below +40mV in 02-10, 10-20 and 20-30cm soil depths of T-2 and T-3 plots to above + 70mV in surface sediments (all plots) and above + 60mV in 2-10 and 10-20 cm soil depths of T-0 and T-1 plots. By Day-90, differences in day and dark redox values were lowest at 10-20 and 20-30cm depths in T-2 and T-3 plots. Most seagrass plots where death occurred coincided also with daytime redox potential values consistently lower than –70mV within the 2-10 and 10-20 cm soil depths. Redox variability at 20-30cm soil depths was hard to explain in our results, as it was very variable here with or without treatment impactions.

There were also other important observations in redox potentials between seagrass meadows and bare sites: one, relatively more positive potentials were recorded at 10-20cm soil depths within seagrass rhizosphere than from unvegetated (bare) sites which were relatively more negative (Table-3, Figure 4); two, while surficial sediments from bare sites had relatively higher redox potentials than those at depth, surficial vegetated sites (0-2cm) consistently had lower redox potentials than at 10-20cm soil depths; three, at 20-30 cm soil depths, *Eh* values between vegetated and non-vegetated (bare) sites were highly erratic; and four, on Day-56 and 90, there was also small differences between daytime *Eh* potentials and those obtainable at dusk, both coinciding with massive reductions in plant canopy cover and biomass (Figure. 6a & 6b). As more above ground biomass (and its corresponding root biomass was lost as the experiment matured in days, there was a substantial increase in rhizosphere redox potentials (see days 56, and 90 in Figure. 4).

Leaf and canopy characteristics

Standing blades in mature shoot at the beginning of the experiment in NEM peaked at 10 blades per shoot with a mean of 7.6 ± 0.64 blades per shoot. Many shoots, however, had standing leave blades of 8 (median values) in NEM (Table 4; Figure 5a). During this time, meadows had maximum development with a cover approximating 100% (Figure 5b). At the end of experiments in NEM period, the population of standing leaf blades averaged from highs of 7.65 ± 0.21 blades per shoot in un-manipulated plots (T-0) to lows of 3.32 ± 0.98 blades per shoot in the highly substrate impacted plots (T-3). At the end of experiments, the maximum standing leaf blade populations ranged from high maxima of 10 and medians of 8 blades per shoot (T-0; T-1) to a low maximum of 5 and medians of 3 blades per shoot in the severely impacted plot (T-3). There was a reduction in standing leaves and canopy shoots with exposure to substrate impaction (Figure 6b). During SEM, leaf and canopy characteristics had a trend similar to NEM's. A notable difference between the two monsoon

periods was the apparent relatively low absolute standing blades per shoot: whereas maximum blades per shoot were 10 for NEM shoots, they were mostly peaked at 9 for SEM shoots. But like NEM traits, at the end of experiments, final standing blade populations averaged from highs of 7.23 ± 0.63 and 6.48 ± 0.62 blades per shoot in T-0 and T-1 plots to lows of 4.45 ± 0.39 and 2.69 ± 0.43 blades per shoot in T-2 and T-3 plots respectively. For both NEM and SEM measurements, mean standing leaves in the populations at the start and end of the experiment were more or less similar in the controls (T-0) and T-1 plots, but were significantly different in T-2 and T-3 plots (ANOVA, $p<0.05$ Table-4).

At the same time, NEM seagrass canopy cover did not change between start and end of experiments in T-0 and T-1 plots (average change in cover less than 1.3%), while in SEM canopy cover remained unchanged only in T-0 (average change in cover less than 2.0%), but were slightly reduced in T-1, albeit insignificantly (average reduction in cover less than 10.8%). Canopy cover was significantly changed in T-2 and T-3 plots in both seasons (ANOVA, $p<0.05$, Table-4). In NEM, cover in T-2 plots reduced from about 97% to 48% (representing average reduction in cover of 50.7%), and in T-3 plots they changed from about 97% to 27% (representing average reduction in cover by 71.9%). In SEM, they reduced from 93% to 36% and 93% to 21% in T-2 and T-3 plots respectively (representing average reduction in cover by 70.0% and 77.2% in T-2 and T-3 plots respectively). Canopy cover and shoot standing blades were insignificantly changed in all plots between Day-1 and Day-21 (cover change less than 17%, median standing blades 7 – 8 blades per shoot; ANOVA, $p > 0.05$), but were significantly different in plots T-2 and T-3 on Day-56 and Day-90 (cover change between 20 - 80%, median standing leaves between 6 – 3 blades per shoot; ANOVA, $p <0.05$; Table-4).

Blade measurements in the 2nd youngest leaf blade populations over time differed only very marginally. Initial blade lengths in NEM averaged 8.9 ± 1.28cm long (all plots), but in individual plots they varied within a range from 9.90 ± 1.54 (T-2 plots) to 8.56 ± 1.35 (T-0 plots). In T-0 and T-1 plots, lengths changed little over time, and initial and final values were 8.56 ± 1.35 cm vs 8.58 ± 1.14 cm in T-0 and 8.70 ± 1.68 vs 8.50 ± 0.67 cm in T-1 respectively. In T-2 and T-3 plots, blade lengths were reduced with exposure to substrate impaction, and initial and final measurements were 9.90 ± 1.54 cm and 8.70 ± 0.95, and 8.60 ± 0.87 and 8.10 ± 0.90 cm long in T-2 and T-3 plots respectively. Initial blade lengths in SEM were 9.2 ± 0.97cm long (all plots), but in individual plots varied between 10.29 ± 0.74 (T-2 plots) to 8.74 ± 1.20 (T-3 plots). Final SEM blade lengths were highly variable and, unlike in NEM blades, T-0 and T-1 had a slight increase in blade lengths, while T-2 and T-3 had a slight reduction in blade lengths (Table-4).

Initial width measurements in NEM were 13.4 ± 1.41mm wide (all plots), but final widths were highly variable, with T-0 and T-1 having small increases in blade widths, while T-2 and T-3 had slight reductions. Initial width measurements in SEM were 14.0 ± 1.11mm wide (all plots), but with time under exposure to organic substrate impactions, widths were reduced in all plots over time save for T-0 which had a small increase. A general trend was observed in T-2 and T-3 plots where blades got thinner with increasing tone of stress. A comparison of shoot blades of T-0 plots (controls) in NEM and SEM revealed that blades had relatively bigger surface areas (higher length-width values) in SEM than they were in NEM (Table-4). However, despite these apparent changes, initial and final blade dimensions of 2nd blade leaves at the two observation times were statistically insignificant in all plots and between treatment effects (ANOVA, $p > 0.05$, Table-4).

Similarly, differences in biomass of 2nd blade leaves at the start and at the end of the experiment were statistically insignificant in T-0, T-1 and T-2, but were at least significant in T-3 treatment effects in NEM (ANOVA, $p < 0.05$), but not so for SEM. Leaf biomass data for 2nd youngest blades, which were chosen because they were epiphyte free, were not significantly different between T-0, T-1 and T-2 treatment groups in NEM and SEM (ANOVA, $p > 0.05$). When compared to biomass in the controls, biomass in the heavily substrate impacted plot (T-3), was the only category that differed from the control group, and even then only for NEM measurement periods.

Shoot and root characteristics:

Initial shoot densities averaged 932 and 873 shoots/m^2 in NEM and SEM respectively representing about 96-98% cover (Table 5; Figure 5b). Over the history of treatments, shoot densities became variable and at Day-90 they ranged from highs of 920 ± 46.03 and 950 ± 55.09 shoots/m^2 in T-0 and T-1 plots to lows of 413 ± 71.92 and 249 ± 55.64 shoots/m^2 in the highly impacted T-2 and T-3 plots (NEM experiments), and from highs of 896 ± 69.90 and 745 ± 77.44 shoots/m^2 in the T-0 and T-1 control plots to lows of 346 ± 48.05 and 163 ± 67.90 shoots/m^2 in the highly impacted T-2 and T-3 plots (SEM experiments). The initial and final shoot densities changed by 1% in T-0 and T-1 plots in NEM, and by 1% in T-0 and 10% in T-1 in SEM experiments. In T-2 and T-3 plots they changed by 44 vs 39% and 27 vs 18% in the NEM and SEM experiments respectively. Initial and final shoot density changes in T-0 and T-1 were insignificant, but those in T-2 and T3 plots were significant (ANOVA, $p < 0.05$) in both NEM and SEM experiments (Table 5). NEM shoot densities were little changed in all plots between Day-1 and Day-21 (% change less than 10%), but in SEM, changes in plots T-2 and T3 were larger (about 17% reduction in canopy cover) and were significant (ANOVA, $p < 0.05$). Shoot densities on Day-56 and Day-90 were always significantly different from each other in plots T-2 and T-3 (% change about 30%). Like with blade populations, shoot densities in NEM were slightly higher than those in SEM.

Final NEM shoot biomass was high in T-0 and T-1 plots, at 196 ± 18.03 and 204 ± 23.76 gDW/m^2 respectively, but low in T-2 and T-3 plots, at 96 ± 23.53 and 24 ± 23.05 gDW/m^2 respectively. Corresponding SEM final shoot biomass were 206 ± 23.74, 193 ± 20.71, 65 ± 17.12, 24 ± 16.03 gDW/m^2 in T-0, T-1, T-2 and T-3 plots respectively. NEM final aboveground biomass (AGB) values were 371, 393, 242, 135 gDW/m^2 in T-0, T-1, T-2 and T-3 plots, while in SEM they were 399, 363, 168, 148 gDW/m^2 in T-0, T-1, T-2 and T-3 respectively. Shoot biomass accounted for over 50% of AGB in T-0 and T-1 plots, but only between 40% and 16% of aboveground biomass in T-2 and T-3 respectively in both seasons. Living stems contributed about 36 – 38% of AGB in T-0 and T-1 plots, but only between 29% and 6% of AGB in T-2 and T-3 at both seasons. Likewise, stems without shoots (dying stems) accounted for between 9 to 12% of AGB biomass in T-0 and T-1 plots, while they accounted for between 32% and 78% of aboveground biomass in T-2 and T-3 at both seasons. Unlike shoot and blade dynamics, final biomass values in all component parts considered here (shoots, live stems, dead stems and AGB) were significantly different from each other (ANOVA, $p < 0.05$). But between the different treatment days, for both T-2 and T-3 plots, treatments significantly changed AGB dynamics, and the final biomass were significantly different (ANOVA, $p < 0.05$) from their initial values. This was true at both NEM-SEM experiments (Table 5).

Root biomass is synonymous with belowground biomass (BGB) as root/rhizomes are the only category found below ground. Total NEM BGB values were 6.3, 6.2, 2.3, and 0.4 gDW/cm^3 in T-0, T-1, T-2 and T-3 plots respectively, while in SEM they were 5.4, 5.0, 1.7, and 0.4 gDW/m^3 in T-0, T-1, T-2 and T-3 respectively. *T. ciliatum* roots extended mostly to the 20-cm deep layers, and were very rare at 30-cm deep layers (Table 5; Figure 4). 50% of BGB in T-0 and T-1 plots was accounted for in top 10-cm soil depth, while up to 90% of BGB was present in the top 20-cm soil depth. In T-2 and T-3 plots, top 10-cm and top 20-cm soil depths accounted for between 67 and 87% of BGB (NEM), and between 70 and 84% of BGB (SEM) respectively. Only 4 – 6 % of biomass was present in the last fraction (20 – 30cm depths) in T-0 and T-1 plots (both seasons), and only between 5% and 0.3% (NEM), and between 3% and 0.8% (SEM) of BGB in T-2 and T-3 plots respectively. Like AGB dynamics, final BGB in sediment fractions considered (0-10, 10-20, and 20-30 cm depths) were significantly different from each other and from the controls (ANOVA, $p < 0.05$) in the four plots (Table 5). But between the different treatment days, only in T-2 and T-3 plots were final BGB values significantly different (ANOVA, $p < 0.05$) from their initial values. This was true for both NEM and SEM experiments. Hence BGB followed similar trends to that of shoot densities and biomass: they were relatively similar in T-0 and T-1 plots, but in highly impacted plots (T-2 and T-3) they showed large variation from the rest. Moreover, final root biomass was more in NEM than they were in SEM (Table 5).

The shoot to root biomass ratio (S/R) in T-0 and T-1 plots were 0.31 vs 0.34, and 0.33 vs 0.34, in NEM vs SEM periods respectively (Table 5). This implies that about one-third of plant biomass is shoot (=leaf) biomass. As more reducing substrate was applied into treatment plots (T-2 to T-3), S/R increased to 0.41 vs 0.37, and 0.55 vs 0.55 in T-2 and T-3 at NEM vs SEM treatments respectively, meaning a differentially more allocation to shoots than to roots. The ratio of above ground to below ground biomass (AG-BG) followed the same trend: increasing ratios as the exposure period and intensity to organic substrates gets longer and/or stronger (T-2 to T-3) and relatively higher ratios in SEM than in NEM. This is consistent with a relative reduction in root biomass with increases in intensity of reducing conditions (reflected as higher S/R ratio).

Discussion

The results here suggest that the development, growth, morphology, biomass allocation, and canopy space occupation by *T. ciliatum* meadows is adversely affected by high sedimentary organic sedimentation that in effect induces reducing conditions more severe than normal for seagrass functioning. Under intense exposure to reducing conditions, reductions in space occupation (canopy clonessnes) were realized more in the aboveground plant form and structure, while biomass decline was particularly evident in the belowground (root) depth fractions, both conditions indicating negative carbon balance detrimental to growth capacity. Reduced sediment conditions also resulted in localized seagrass death indicating a net negative carbon balance at *Eh* levels consistently above levels normally cleared by plants at daytime after diurnal day-night fluxes. These conclusions are supported by our data which revealed (i) reductions in plant blade standing leaves, leaf surface area, and shoot densities with increasing redox potentials (Figure 5); (ii) general reductions in plant biomass, but relatively high reductions in root biomass relative to shoot biomass, and increase in S/R ratios with reducing redox potentials (Figure 5 & 6a); and, (iii) sustained reductions in plant cover

and ultimate death in plots consistently subjected to continuous substrate treatment effects, and whose day-time redox values were in excess of –70mV. Our results, therefore, suggests that organic discharges in to lagoon waters, where most seagrass grow, are likely to impact negatively on seagrass beds.

Within the water column, organic discharges should induce light competition between seagrass and other marine flora by lowering periods and intensity of incident light, but within the sediments, they would impact directly on seagrass communities by inducing more negative redox potentials and associated stress from free sulphides toxicity arising from organic matter decomposition by sulfate reducing bacteria, possibly leading to seagrass declines and death, if not cleared, as has been shown to occur under similar circumstances (Azzoni *et al.,* 2001, Enríquez *et al.,* 2001). The effects of seagrass on ameliorating negative sediment redox conditions and the processes governing them are still not well known, particularly in comparison to the knowledge already available on the metabolic interactions between seagrass leaves and the water column. However, since seagrass-sediment interactions must have important contributions to the functioning of seagrasses in the ecosystem, judging from the enormous biomass invested within the belowground parts, the reductions of its biomass under deleterious sediment reducing conditions might be an important survival strategy. Root biomass in *T. ciliatum* meadows were up to one-and-half times greater than shoot biomass (634 and 400 g DW m^{-2} for root and shoots biomass respectively in control plots). This implied *T. ciliatum* invested heavily on root network within the sediments; this despite the obvious respiratory demands it puts on the carbon balance for the plant. It has been pointed out that seagrass roots play a vital role in exploiting nutrient stocks from sediments in the otherwise nutrient poor coastal environments (Hemminga, 1998, 2000). Nutrient concentrations in sediment compartments are generally at least one order of magnitude higher than the concentrations within the water columns; this means seagrass roots are a definite asset as they help in directly accessing this nutrient-enriched medium. But under severe reducing conditions, the opportunity costs of retaining them must be higher than those of shedding them off for the seagrass to remain alive, hence the differential biomass allocation patterns observed.

Normal functioning of *T. ciliatum* meadows was shown to cope with negative redox conditions in sediments up to around –110mV so long as these are not persistent and get cleared by daytime. In fact lower redox potentials in excess of –70mV (dusk values) were raised to higher potentials (above –30 in top 20-cm depths which had over 90% of root biomass) during daytime normal functioning, possibly by way of photosynthetic oxygen release via roots as has been reported for other species (Pedersen , *et al.,* 1998, 1999; Connell *et al.,* 1999; Terrandos *et al.,* 1999; Enríquez: *et al.,* 2001). Under sustained low redox potentials (below -70mV even at daytime), the additive effects of these resulted in the negative impacts felt by *T. ciliatum*. The impact of these strenuous (highly reducing) conditions were reductions in canopy cover, reductions in root biomass and a corresponding reductions in shoot biomass, accompanied with increases in S/R to values approaching one (Figure 6a) and ultimate death (Figure 6b). The negative effects were obvious by three weeks, and about 25 - 44% canopy death (canopy reductions) was accomplished within two months of continuous exposure. It is possible that the negative effects on plant functioning within the first three weeks were already severe but were masked by some form of acclimation by *T. ciliatum* to reduced redox potentials, similar to plant acclimations that are reported to occur in other conditions such a low light (van Tussenbroek, 1995; Enríquez: *et al.,* 2001). In support of these findings, a study by Wilfredo *et al.* (in press) has shown that reduced sediment conditions largely reduced belowground biomass and increased respiratory demand in

Thalassia hemprichii. Our redox results are in agreement with other similar studies of root-sediment interactions (Kenworthy *et al.* 1982, Isaksen & Finster 1996, Holmer & Nielsen 1997, McGlathery *et al.* 1998), that suggest that seagrass roots play a role in controlling some aspects of sediment biogeochemical conditions, thereby affecting also the life of sediment infauna and key processes for the cycling of carbon and nutrients in these ecosystems.

That *T. ciliatum* meadows were found over high carbonate-derived sandy sediments with low organic matter content, would suggest that all sites were subject to strong hydrodynamic turbulence. Within adjacent bare areas, this could have induced greater instabilities within surface sediments, thus explaining their relative high redox potentials (bare sites compared to vegetated sites) similar to what has been observed in similar environmental settings (e.g., Terrados and Duarte, 1999), whereby re-suspension of surface sediments would enhance the exchange of pore water with overlying oxygenated waters. Within the surface sediments on seagrass beds, on the other hand, we hypothesize that the buffering effects by *T. ciliatum* meadows on water currents aids resident soil microflora to act on organic matter deposited from senescing leaves and from other particulate organic matter trapped by seagrass meadows from overlying waters, and these should induce greater respiration on surface sediments leading to relatively more reduced conditions. High leaf loss rates have been reported for this site (Ochieng and Erftemeijer 1999). Given the low sedimentary organic matter content values found in the study, organic enrichment from detachment sources should be of less concern, and microbial degradation must be an active component in the biogeochemical cycles therein. However, elevated organic inputs from human-related activities might be of concern in cases where, because of low flushing rates in particular near0shore coastal settings in parts of lagoons, biochemical compounds' concentration levels might get higher, or in sheltered microhabitats with low hydrodynamic conditions, such as those obtainable in seagrass-sheltered tidal pools like the once in this study, which may favour a high accumulation of sedimentary organic matter. In Kenya where human activities are increasing in coastal areas, anthropogenic driven organic discharge into lagoonal areas may be expected to lead to seagrass declines.

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Annex 1: List of Tables (p25-29)

Table 1. Sediment data from *Thallasodendron ciliatum* sites (pool from all plots, two NEM-SEM seasons)[1] prior to treatments. Data from *Syringodium isoetifolium, Cymodocea serrulata* and bare sites added for comparison. Core depths 20-cm deep.

	Grade (mm)	Phi scale	Sediment type	*Thallasodendron ciliatum* (n=16)		*Syringodium isoetifolium* (n=8)		*Cymodocea serrulata* (n=8)		*Unvegetated (bare)* (n=6)	
				Sieve wt. (%)	Cum %	Sieve wt. (%)	Cum %	Sieve wt. (%)	Cum %	Sieve wt. (%)	Cum %
Sieve data	2000	-1.0	Granule/shells	4.6	4.6	1.7	1.7	3.1	3.1	4.1	4.1
	1000	0.0	Very coarse sand	3.4	8.0	1.7	3.4	2.9	6.0	3.9	8.0
	500	1.0	Coarse sand	9.7	17.7	8.0	11.4	8.6	14.6	9.8	17.8
	250	2.0	Medium sand	33.4	51.2	27.2	38.6	30.8	45.4	33.4	51.2
	125	3.0	Fine sand	36.6	87.8	42.1	80.7	39.4	84.8	35.7	87.0
	63	4.0	Very fine sand	5.5	93.3	7.8	88.6	7.6	92.4	6.3	93.3
	38	5.0	Coarse silt	0.8	94.0	0.9	89.5	1.2	93.6	1.1	94.3
	Ettrited	> 5	Fine silt/clay	6.0	100.0	10.5	100.0	6.4	100.0	5.7	100.0
Descriptive data				100.0		100.0		100.0		100.0	
	Median diameter (Md) (phi)			1.9		2.3		2.2		1.9	
	Quartile deviation (Qd)			0.7		0.6		0.7		0.7	
	Skewness (Skq)			-98.1		-97.8		-98.0		-98.1	
	Sediment type* (Folk, 1974)			medium sand		medium-fine sand		medium sand		medium sand	
	Coarse sediment fraction (%)			33.43		27.19		30.81		33.42	
	OM (%)			3.64 (1.83)		3.03 (0.46)		2.67 (1.12)		0.8 (0.34)	
NEM vs SEM ANOVA (*p*-value)[2] for T-0				*0.90*		*0.68*		*0.57*		*0.82*	

[1] = there was no significant difference in grain size between SEM and NEM plots; phi = $-^2 \log d$ where d is the diameter of the particle size (mm); Cum % = cumulative %; Md = 50% point in cum %; Qd = difference of 75% & 25% points in cum %; Skq = sum of 75% & 25% points less the Md in cum %; Sediment type* is based on the classification of Folk (1974); OM = organic matter (SE numbers in parenthesis); NEM vs SEM ANOVA comparisons (*p*-value)[2] only for control plots (T-0).

Table 2. Summary of Kruskal-Wallis test for post-treatment effects on sediments characteristics in *T. ciliatum* plots

Grade (mm)	phi scale	Sediment type	Mean pre-treatment sieve weights (n=16)	Mean post-treatment sieve weights (n=16)	*p*-values for Kruskal-Wallis tests (individual plot tests) T-0 (n=4)	T-1 (n=4)	T-2 (n=4)	T-3 (n=4)	Decision (p < 0.05)
2000	-1.0	Granule/shells	4.6	4.9	0.34	0.74	0.95	0.38	Significant; accept
1000	0.0	Very coarse sand	3.4	4.1	0.82	0.85	0.94	0.59	"
500	1.0	Coarse sand	9.7	8.9	0.19	0.26	0.77	0.14	"
250	2.0	Medium sand	33.4	35.3	0.34	0.35	0.55	0.48	"
125	3.0	Fine sand	36.6	33.5	0.55	0.32	0.61	0.52	"
63	4.0	Very fine sand	5.5	6.7	0.66	0.45	0.56	0.37	"
38	5.0	Coarse silt	0.8	0.9	0.91	0.51	0.19	0.15	"
Ettrited	> 5	Fine silt/clay	6.0	5.7	0.28	0.26	0.34	0.11	"
Median diameter (Md)			*1.9*	*1.8*	0.35	0.74	0.91	0.68	"
NEM vs SEM ANOVA (*p-value*)* for T-0			*0.75*	*0.58*					

Significance level was set at $p = 0.05$ for Kruskal-Wallis test (testing the null hypothesis that grain medians within the four plots is the same); *p*-values were significantly lower than 0.05 level, and therefore, all are significant and accepted; NEM vs SEM ANOVA comparisons (*p*-value)* only for control groups (T-0).

Table 3: Redox measurements from experimental plots, control and bare sites (NEM data only)

		Day-1 (n=8)* (*Eh* in mV)			Day-21 (n=8)* (*Eh* in mV)			Day-56 (n=8)* (*Eh* in mV)			Day-90 (n=8)* (*Eh* in mV)		
Depth (cm)[1]	Plot	Dusk	Day	Difference	Dusk	Day	Difference	Dusk	Day	Difference	Dusk	Day	Difference
Surface	Bare	-37.5	52.25	89.8	-41.5	42.75	84.4	-39	27.25	66.3	-38.75	26.75	65.5
	T-0	-41.5	28.5	70.0	-49	21.25	70.3	-52.75	0	52.8	-47.75	5.5	53.3
	T-1	-46.5	32.65	79.1	-48	42.5	90.5	-54.75	17.75	72.5	-44.5	17.25	61.8
	T-2	-34	28.15	62.1	-69.25	5.5	74.8	-66.25	-14.5	51.8	-79.75	-14.75	65.0
	T-3	-39.75	23.75	63.1	-73.5	2	75.5	-75	-25	50.0	-79	-27	52.0
	Avg	-40.4	28.2	68.6									
02-10	Bare	-70	-23.25	46.8	-79.5	-55.25	24.3	-78.5	-61	17.5	-76.5	-63	13.5
	T-0	-74.25	24.5	98.8	-71.75	23.25	95.0	-84	31.25	115.3	-88.25	32.75	121.0
	T-1	-79.25	18.5	97.8	-95.75	19	114.8	-84.25	22.5	106.8	-89	40	129.0
	T-2	-76	7.5	83.5	-97.75	-60.75	37.4	-105	-82	23.0	-104.25	-61.75	42.5
	T-3	-79.25	5.375	84.6	-83	-63	20.0	-101.75	-88	13.8	-128.5	-87.25	41.3
	Avg	-77.2	14.0	91.2									
10-20	Bare	-102.5	-92.75	9.8	-108.5	-92.25	16.3	-100.5	-91.5	9.0	-102.5	-97.5	5.0
	T-0	-96.25	-19.75	76.5	-101.75	-14.5	87.3	-106	-15.75	90.3	-103.5	-17.5	86.0
	T-1	-94.25	-26.5	67.8	-120.5	-16.75	103.8	-113.75	-12.75	101.0	-102	-37.5	64.5
	T-2	-91.25	-34.5	56.8	-128.75	-91.25	37.5	-119.75	-105.5	14.3	-130.5	-99.25	31.3
	T-3	-92.25	-17.5	74.8	-118.75	-96.75	22.0	-126.75	-110	16.8	-127	-117.5	9.5
	Avg	-93.5	-24.6	68.9									
20-30	Bare	-110	-113.5	-3.5	-116.25	-100	16.3	-119.75	-110	9.8	-109.75	-97.25	12.5
	T-0	-103	-69.75	33.3	-119.75	-70.25	49.5	-123.75	-76.75	47.0	-109.75	-71.75	38.0
	T-1	-106	-78.25	27.8	-124	-64	60.0	-130.25	-67.75	62.5	-119.75	-68	51.8
	T-2	-108.75	-71.75	37.0	-134	-90.75	43.3	-129.5	-112.5	17.0	-126.5	-106.25	20.3
	T-3	-97.25	-74	23.3	-134.25	-120.25	14.0	-133.75	-117.75	16.0	-133.25	-123.75	9.5
	Avg	-103.8	-73.4	30.3									
Summary data													
Vegetated	MIN *Eh*	-108.8	-78.3	23.3	-134.3	-120.3	14.0	-133.8	-117.8	13.8	-133.3	-123.8	9.5
	MAX *Eh*	-34.0	32.6	98.8	-48.0	42.5	114.8	-52.8	31.3	115.3	-44.5	40.0	129.0
Bare	MIN *Eh*	-110.0	-113.5	-3.5	-116.3	-100.0	16.3	-119.8	-110.0	9.0	-109.8	-97.5	5.0
	MAX *Eh*	-37.5	52.3	89.8	-41.5	42.9	84.4	-39.0	27.3	66.3	-38.8	26.8	65.5

Depth[1] = averages of micro-depths at 0, 2, 5, 10, 15, 20, 25, 30 cm depths; * = for each plot area and each depth, n=8 obs (4 replicates, 2 readings for each point)

Table 4. Canopy, stand and leaf characteristics of *T. ciliatum* from four experimental plots subjected to different treatment effects (NEM and SEM)

Variable	Max lvs[1] shoots/obs) (n=10)	Standing lvs (median blades/shoot) (n=10 shoots/obs)* (Seagrass cover (%) in parenthesis) (n=4 plots/obs)					Standing lvs (avg; no/shoot) (n=10 shoots/obs)* (SE values given in parenthesis)			2nd blade dimensions (avg; L-W) (n=10) shoots/obs)* (SE values given in parenthesis)					2nd blade biomass (avg; mg/leaf) (n=10 shoots/obs)* (SE values in parenthesis)		
	Start-End	Day-1	Day 21	Day 56	Day-90	*p*-values[2]	Start	End*	*p*-values[2]	L (cm)s	W (mm)s	L (cm)e	W (mm)e	*p*-values[2]	Plots-End	Control-End	*p*-values[2]
NEM Avg[3]	10 - 10	8 (97.25)					7.6 (0.64)			8.9 (1.28)	13.4 (1.41)						
NEM -T-O	10 - 10	8 (97.59)	8 (98.61)	8 (98.85)	8 (97.47)	0.95	7.61 (0.50)	7.65 (0.21)	0.98	8.56 (1.35)	12.89 (1.00)	8.58 (1.14)	12.93 (0.55)	0.88	33.46 (6.29)	33.46 (6.29)	1.00
NEM -T-1	10 - 10	7 (97.15)	7 (96.52)	8 (97.33)	8 (97.86)	0.78	7.54 (0.66)	7.45 (0.70)	0.69	8.70 (1.68)	13.10 (0.82)	8.50 (0.67)	13.30 (0.33)	0.76	32.44 (5.39)	33.46 (6.29)	0.12
NEM -T-2	10 - 6	8 (97.38)	7 (90.69)	6 (75.80)	4 (48.02)	0.01	7.49 (0.38)	4.26 (0.87)	0.02	9.90 (1.54)	14.00 (0.65)	8.70 (0.95)	12.48 (0.85)	0.59	30.35 (4.06)	33.46 (6.29)	0.08
NEM -T-3	10 - 5	8 (96.88)	7 (91.17)	5 (65.89)	3 (27.34)	0.00	7.68 (0.47)	3.32 (0.98)	0.00	8.60 (0.87)	13.50 (0.70)	8.10 (0.90)	12.85 (0.89)	0.20	31.19 (7.91)	33.46 (6.29)	0.03
ANOVA *p*		0.69	0.81	0.01	0.00		0.72	0.00		0.76	0.64	0.28	0.26		0.01		
SEM –Avg[4]	9 - 9	7 (91.85)					7.2 (0.49)			9.2 (0.97)	14.0 (1.11)						
SEM -T-O	9 - 9	7 (92.71)	8 (93.23)	8 (93.41)	8 (94.57)	0.82	7.32 (0.41)	7.23 (0.63)	0.72	9.21 (1.01)	14.12 (0.82)	9.50 (1.27)	14.30 (0.73)	0.94	34.21 (5.37)	34.21 (5.37)	1.00
SEM -T-1	8 - 9	7 (88.15)	8 (94.04)	8 (91.60)	7 (78.65)	0.15	7.15 (0.58)	6.48 (0.62)	0.62	8.68 (0.88)	13.98 (0.96)	8.97 (0.87)	12.75 (0.78)	0.86	33.73 (5.78)	34.21 (5.37)	0.37
SEM -T-2	9 - 6	8 (93.44)	7 (78.13)	6 (66.66)	4 (36.46)	0.00	7.27 (0.35)	4.45 (0.39)	0.04	10.29 (0.74)	14.11 (0.83)	10.23 (0.65)	13.01 (0.88)	0.62	32.42 (4.15)	34.21 (5.37)	0.14
SEM -T-3	9 - 5	7 (93.11)	7 (80.94)	4 (54.62)	3 (21.19)	0.00	7.22 (0.55)	2.69 (0.43)	0.00	8.74 (1.20)	13.85 (1.10)	7.75 (0.86)	12.10 (0.61)	0.21	28.54 (8.47)	34.21 (5.37)	0.07
ANOVA p NEM vs SEM[5]		0.76	0.68	0.03	0.00		0.66	0.00		0.83	0.74	0.39	0.44		0.04		
ANOVA p	0.04	0.07	0.08	0.04	0.01		0.05	0.07		0.71	0.95	0.86	0.72		0.68	0.74	

[1] = median max leaf blades present; *p*-values[2] for ANOVA comparisons between initial (day-1) and final (day-90) measurements; NEM-avg[3] and SEM avg[4] values from start/controls data; NEM vs SEM[5] AVOVA-*p* from ANOVA comparisons for significant differences between NEM and SEM values in controls (T-0); Legend: L (cm)^s = length in cm at start; W (mm)^s = width in mm at start; L (cm)^e = length in cm at end; W (mm)^e = width in mm at end; end* refers to Day-90. For each trait and in each plot, n=10 shoots/blades except for seagrass cover where n=4.

Table 5: Summary of canopy features and final aboveground and belowground biomass from *T. ciliatum* plots subjected to different treatment effects (NEM and SEM)

Variable	Shoot density on different days (avg, no/m^2) (n=4 plots/obs)					Final above-ground biomass (avg; g/DW/m^2) (n=4 plots/obs)					Final below-ground biomass (avg; mg/DW/cm^3) (n=4 plots/obs)						S-R ratios		Final sediment characteristics (n=4 plots/obs)		
	Day-1	Day-21	Day-56	Day-90	P^1	Shoot	Live stems)[a]	Dying stems[b]	Total AGB	P^1	0 to10	10 to 20	20 to 30	Total BGB (mg/cm3)	Total BGB (g/m2)	P^1	S-R^2	S-R^3	Grain size (ϕ)	Coarse %	OM (top 20)
NEM Avg[4]	932.0																				
NEM -T-O	914.0 (48.64)	918.7 (54.03)	923.9 (65.64)	920.1 (63.41)	0.65	195.5 (18.03)	3.74	36.0 (21.69)	370.9	0.87	3.7 (0.23)	2.3 (0.23)	0.4 (0.09)	6.34	634.0	0.79	0.308	0.528	1.84	31.79	3.74
NEM -T-1	949.0 (55.09)	856.8 (65.03)	943.7 (53.60)	951.2 (64.12)	0.68	204.2 (23.76)	3.27	46.7 (24.51)	393.4	0.69	3.5 (0.19)	2.5 (0.13)	0.3 (0.11)	6.21	621.4	0.67	0.329	0.558	1.72	30.35	3.27
NEM -T-2	942.1 (57.38)	861.6 (68.60)	689.7 (77.43)	413.0 (71.92)	0.01	95.5 (26.23)	2.51	77.0 (32.69)	241.9	0.00	1.5 (0.17)	0.7 (0.14)	0.1 (0.03)	2.30	230.0	0.04	0.415	0.717	2.26	32.11	2.51
NEM -T-3	923.0 (46.03)	873.0 (72.03)	622.8 (74.03)	249.1 (55.64)	0.00	23.9 (23.05)	2.08	95.9 (32.88)	134.7	0.00	0.4 (0.19)	0.1 (0.17)	0.0 (0.04)	0.44	43.8	0.00	0.545	0.888	2.13	34.92	2.08
ANOVA p^5	0.83	0.18	0.01	0.00		0.00	0.00	0.04	0.03		0.01	0.02	0.01	0.00	0.00						
SEM –Avg[6]	872.8																				
SEM -T-O	881.8 (45.81)	894.5 (50.24)	891.6 (57.80)	896.3 (56.90)	0.77	206.2 (23.74)	145.4 (37.06)	47.3 (20.61)	398.9	0.94	3.05 (0.20)	2.07 (0.28)	0.28 (0.12)	5.40	610.1	0.95	0.338	0.576	1.95	28.54	5.01
SEM -T-1	827.8 (58.45)	874.5 (52.45)	841.2 (62.45)	744.9 (77.44)	0.56	193.6 (20.71)	137.4 (23.01)	31.7 (17.81)	362.7	0.50	2.92 (0.47)	1.86 (0.22)	0.18 (0.16)	4.97	566.8	0.52	0.342	0.584	1.76	27.96	4.21
SEM -T-2	896.8 (48.63)	746.8 (61.89)	636.8 (54.14)	346.1 (48.05)	0.00	64.8 (17.12)	44.3 (9.81)	59.1 (37.28)	168.2	0.02	1.2 (0.48)	0.5 (0.16)	0.1 (0.13)	1.73	172.8	0.01	0.375	0.631	2.31	31.22	3.58
SEM -T-3	885.0 (46.53)	774.3 (54.25)	505.0 (66.23)	162.6 (67.90)	0.00	24.2 (16.03)	8.8 (8.06)	115.2 (18.08)	148.2	0.00	0.3 (0.09)	0.1 (0.37)	0.0 (0.13)	0.41	40.9	0.00	0.592	0.807	2.05	32.58	2.74
ANOVA p^5	0.96	0.15	0.03	0.00		0.00	0.00	0.03	0.04		0.01	0.05	0.02	0.01	0.01						
NEM vs SEM ANOVA p[7]	0.18	0.10	0.15	0.25		0.02	0.06	0.09	0.19		0.47	0.83	0.54	0.17	0.17						

SE values in parenthesis; p^1 for ANOVA comparisons between final control and final experimental values; live stems^a = with green colour and flaccid, and with shoots; dead stems^b = shootless stems (green, brown, or black, and sometimes brittle); S/R^2 = shoot biomass to below ground biomass (stems omitted); S/R^3 including stems; NEM-Avg^4 and SEM Avg^6 for all plots averages; ANOVA p^6 gives ANOVA values between different treatments in T-0, T-1, T-2, and T-3; NEM vs SEM ANOVA p^7 values from ANOVA test for significant differences between SEM and NEM values in controls (T-0).

Annex 2: List of Figures (p30-39)

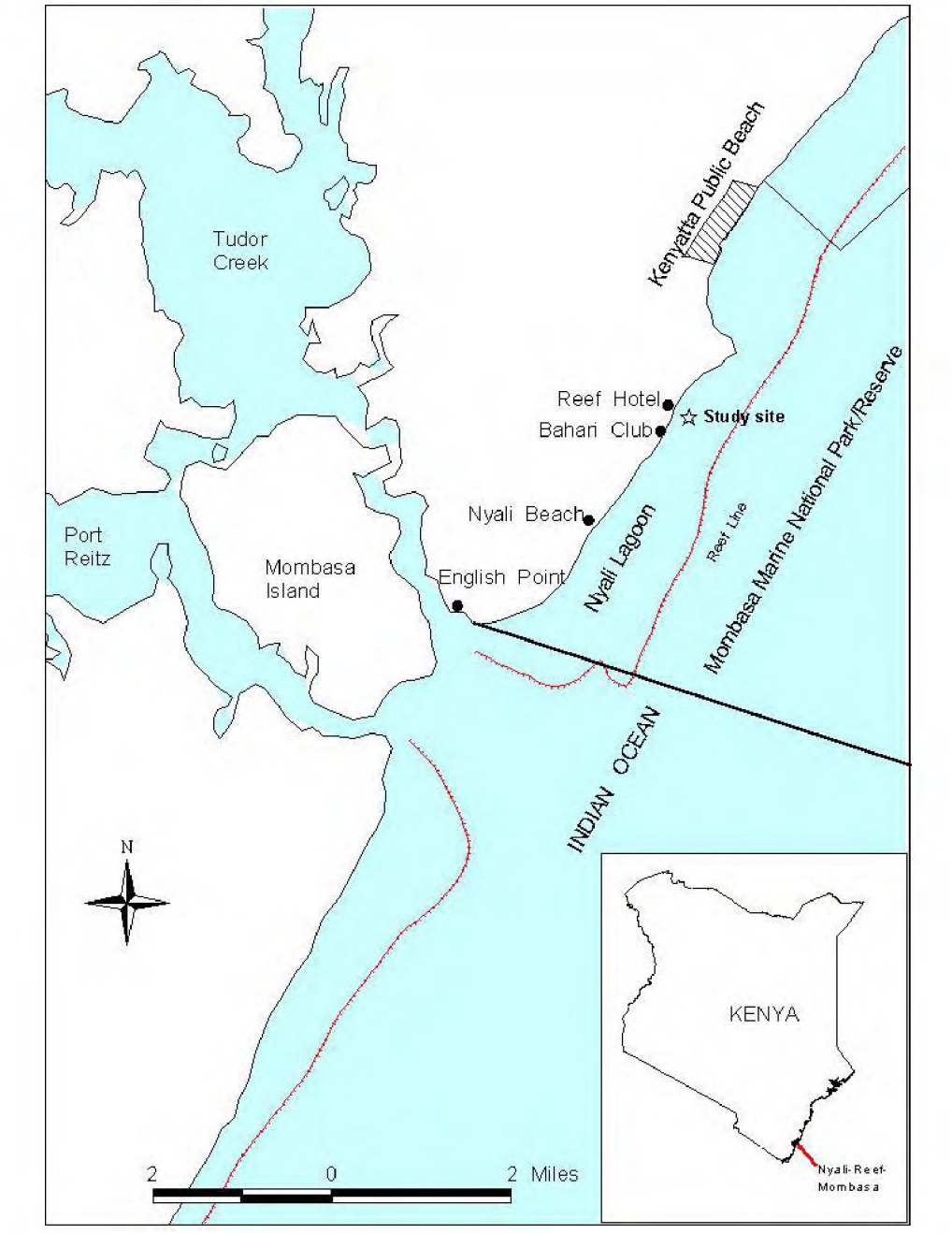

Figure 1. Map of the Nyali Lagoon showing location of Reef Hotel and the sampling site. Study site falls within the Mombasa Marine National Reserve.

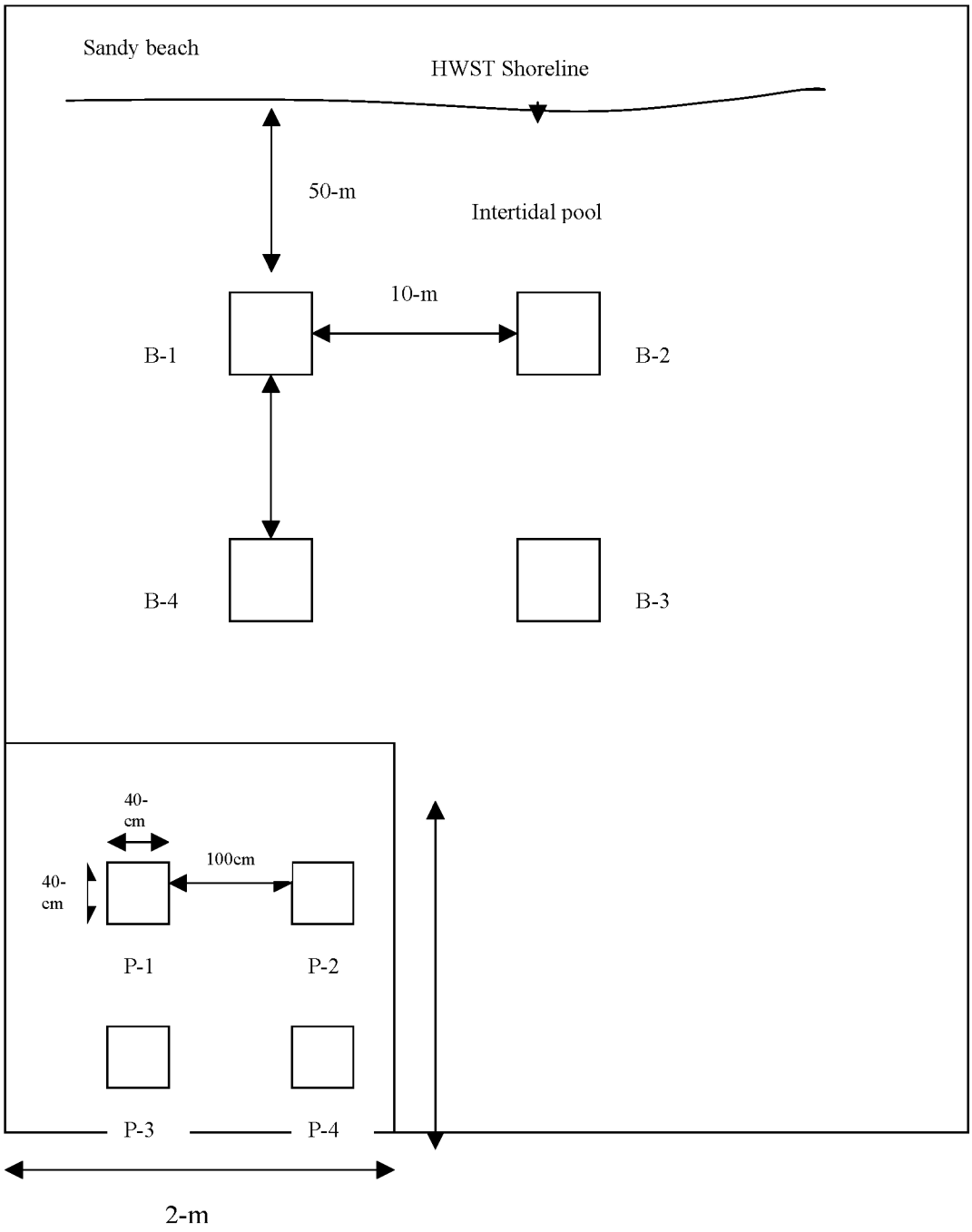

Figure 2a: Schematic representation of spatial arrangement of experimental blocks at the site (B-1 to B-4) and experimental plots (P-1 to P-4) within a block. Each of the experimental plots were randomly assigned to one of the three-substrate treatments: 1) nil substrate application (all sand-filled pipettes), 2) low-level substrate application (50% sand-filled pipettes + 50% substrate-filled pipettes), and 3) high-level substrate applications (100% substrate-filled pipettes). The fourth plot was un-manipulated and acted as a control unit. Drawing not to scale.

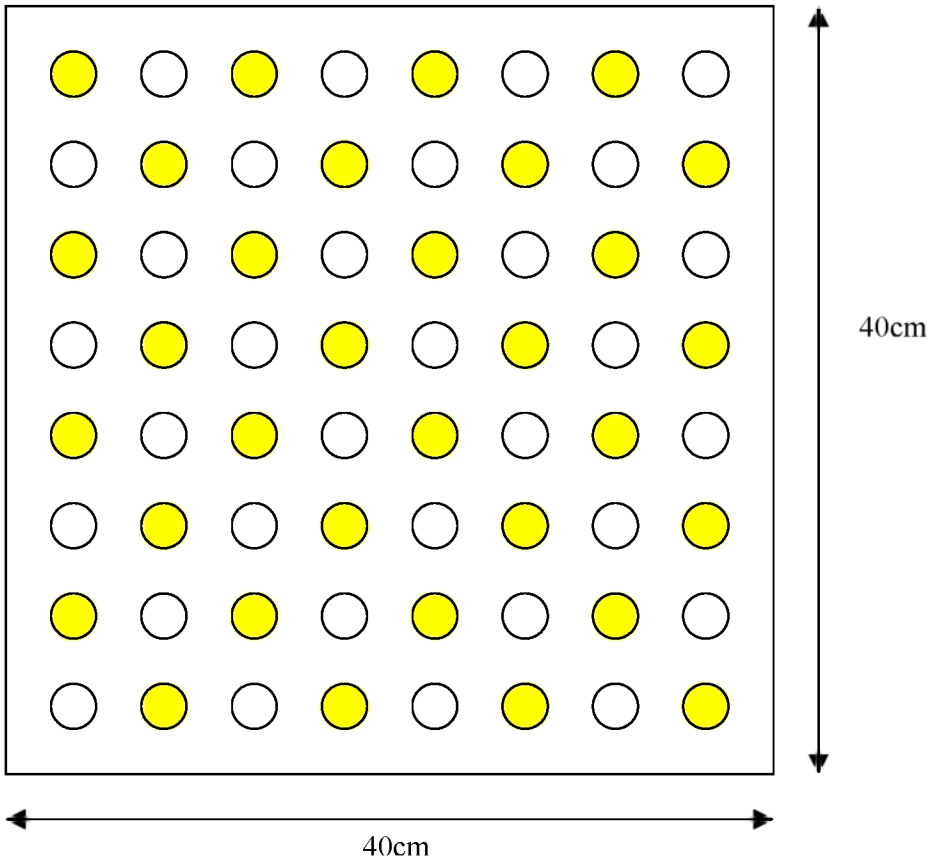

Figure 2b: Schematic representation of the spatial application points for substrate in the plot quadrats. In the nil substrate application, all pipettes were sand-filled and placed at all the points (all circles). In the low doze category only half of pipettes had substrates (shaded circles) and the other half had sand (clear circles). In the high doze category all pipettes had substrates (clear and shaded circles). Pipettes were placed at 5-cm from each other, and the boundary ones were 2.5 cm from the quadrat walls. Figure not drawn to scale.

Figure 2c: quadrat used to guide pipette insertion points being lowered into shallow back reef experimental plot where *T. ciliatum* response to substrate impaction was investigated [mid-ground: buckets holding pipettes; background: exposed sites at low tide; notice experimental plot with knee-high tidal water at spring low tide (arrow)].

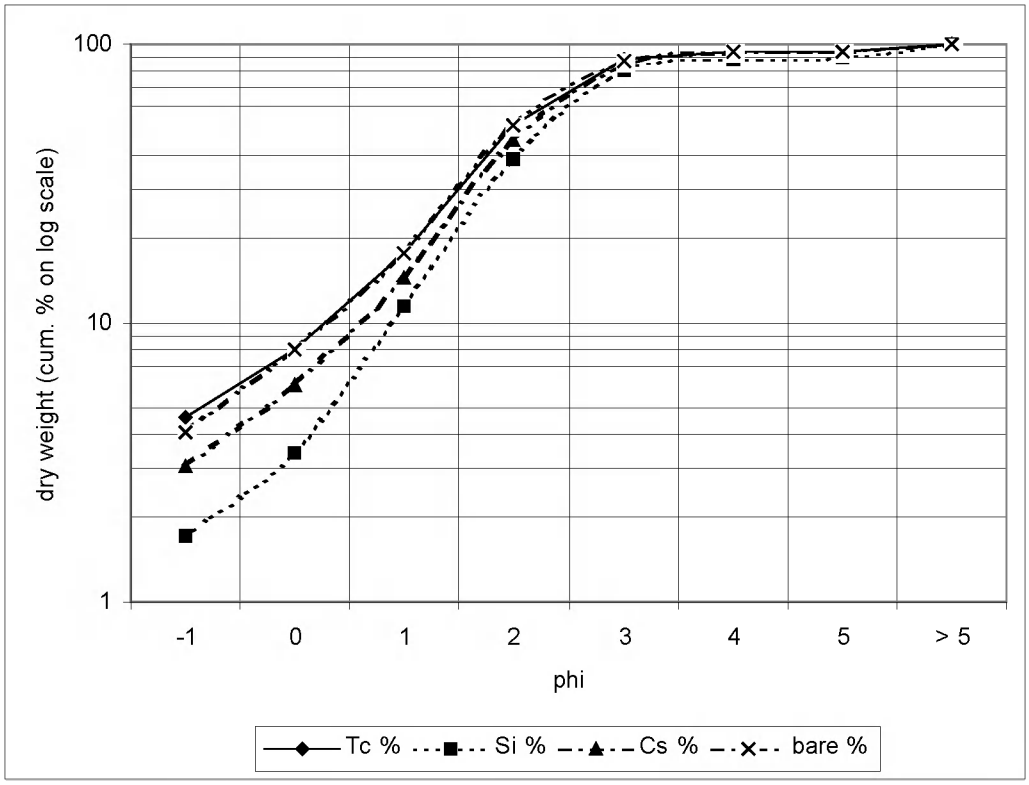

Figure 3. Dry weight curves of sediment (cum % on log scale) in *T. ciliatum* sites. (Distributions in *S. Isoetifolium, C. serrulata* and bare sites added for comparison). Data is pooled for SEM and NEM periods). Cum % greater than 5 were not graded, as these were washed out with water through the last sieve (mesh 38 microns).
phi = $-^{2}$ log *d* where d is the diameter of the particle size (in mm). Sample size as follows: Tc (16), Si (8), Cs (8), and bare (6). Cum % = cumulative %. Key: Tc - *Thallasodendron ciliatum*; Si = *Syringodium isoetifolium*; Cs = *Cymodocea serrulata*.

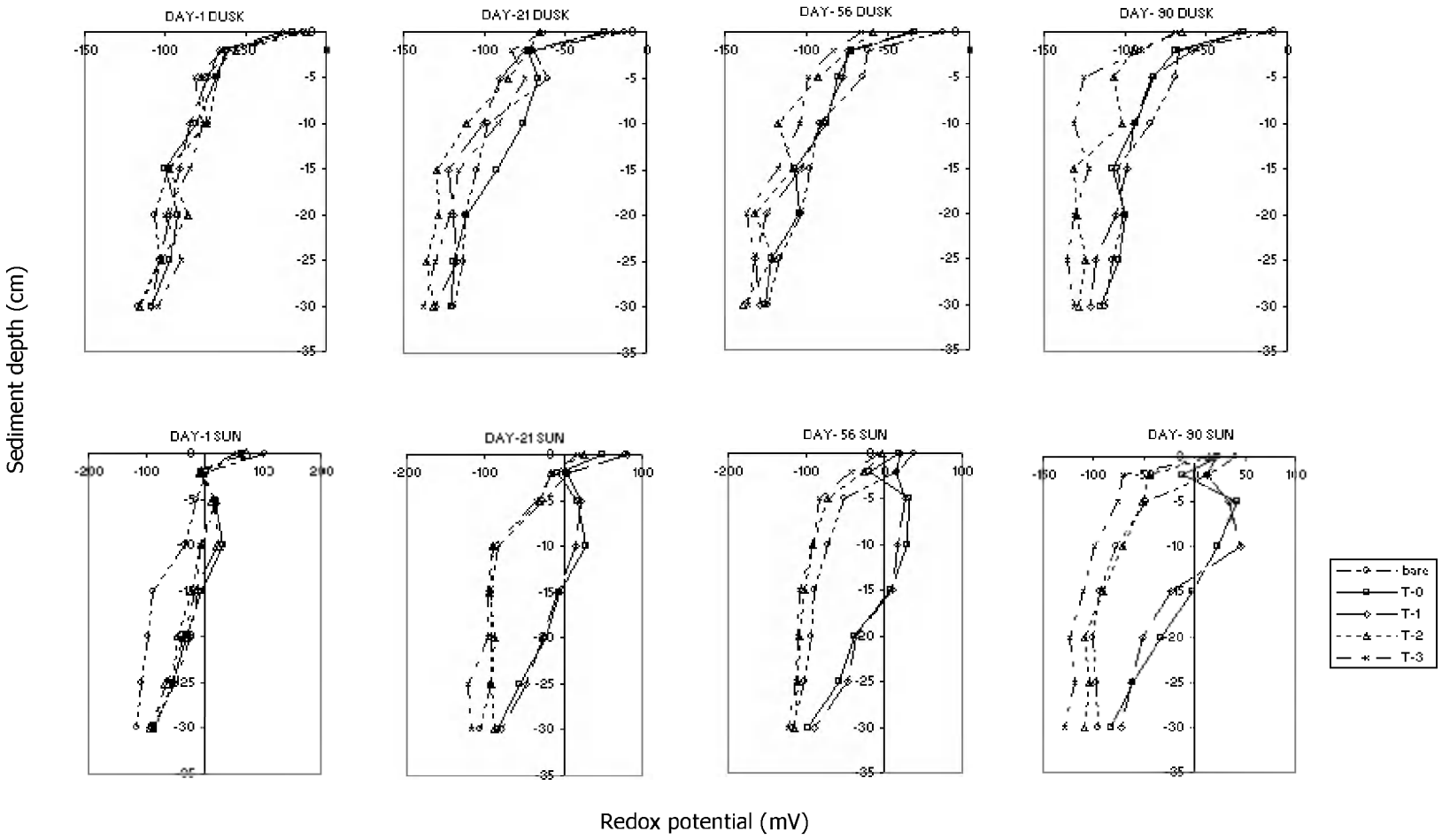

Figure 4. Depth profiles of mean redox potential in four experimental plots and bare sediments adjacent to them during the NEM period of 2001.

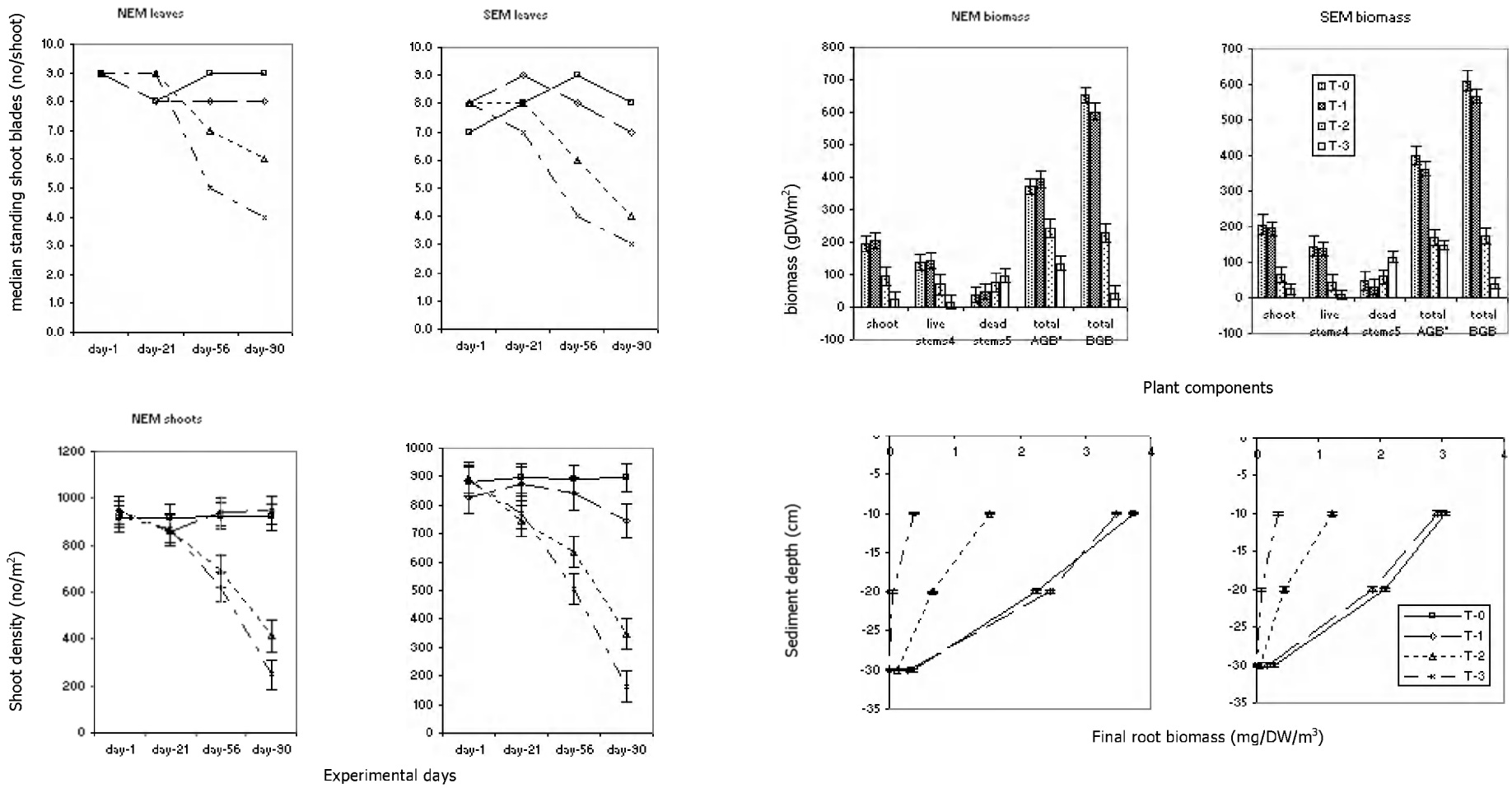

Figure 5a. *T. ciliatum* characteristics and biomass levels at different experimental stages and at different soil depths during NEM and SEM experimental phases.

Figure 5b. Well-developed *T. ciliatum* beds in one of the substrate impaction sites. Notice the clonessness in canopy (97% cover). Most shoots had 8-10 blades at this stage.

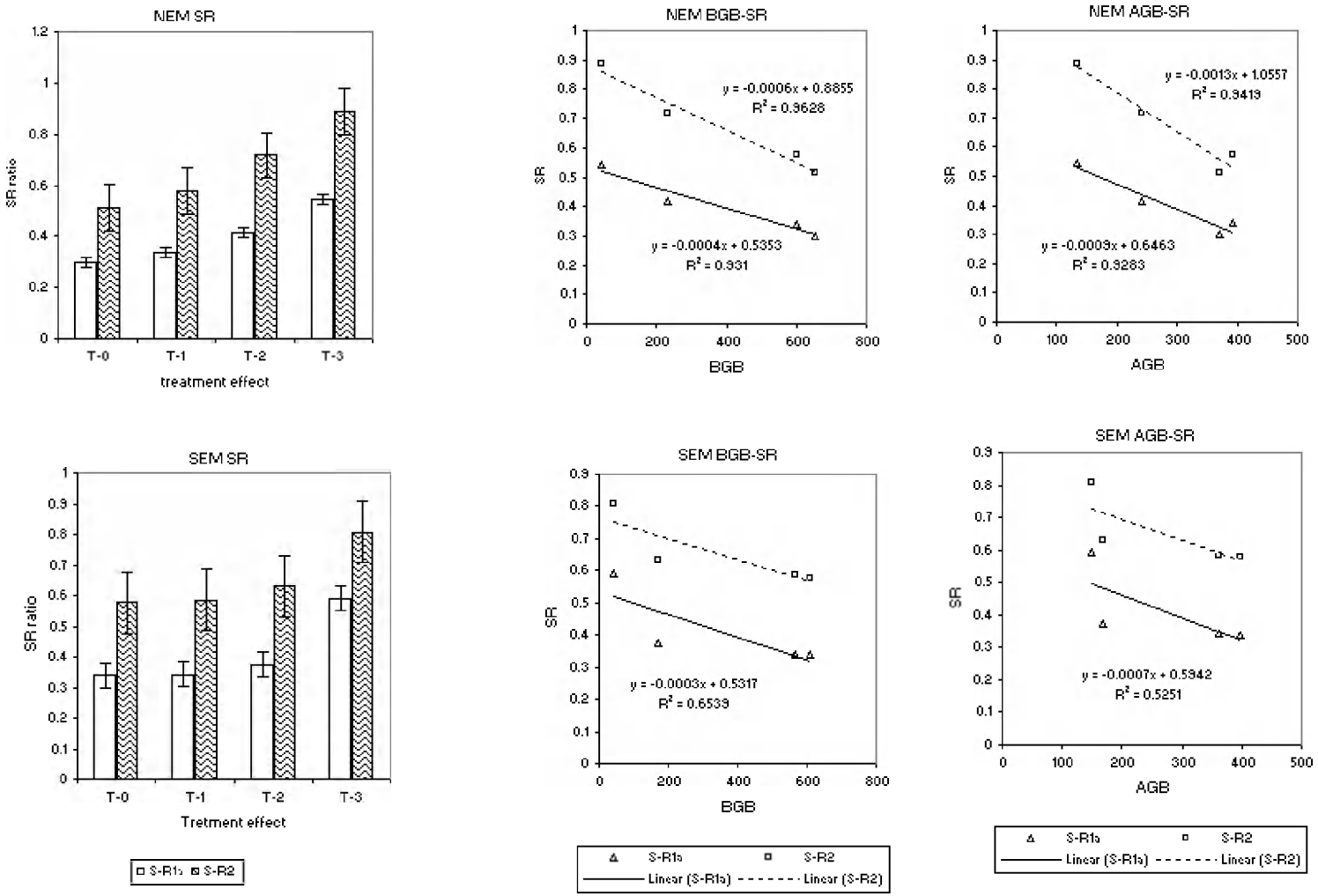

Figure 6a. The relation between treatment effects and shoot-root ratio in *T. ciliatum* sites at two monsoon periods.

Figure 6b. Moderate degradation in canopy cover, reductions in leaf blade densities and local death in *T. ciliatum* shoots site shown earlier (Fig. 5b) at Day-56. Arrow showing shoot with 5 blades.

END.