FACTORS LIMITING GROWTH AND PRODUCTION OF TROPICAL SEAGRASSES: NUTRIENT DYNAMICS IN INDONESIAN SEAGRASS BEDS.

PAUL ERFTEMEIJER

FACTORS LIMITING GROWTH AND PRODUCTION OF TROPICAL SEAGRASSES: NUTRIENT DYNAMICS IN INDONESIAN SEAGRASS BEDS.

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"De mens heeft het web van het leven niet geweven,
Hij is slechts één draad ervan. Wat hij met het web
doet, doet hij met zichzelf. Alle dingen hangen samen.
Wat er met de aarde gebeurt, gebeurt met de kinderen
van de aarde."

Opperhoofd Seattle, 1854.

Communication number 660 of the
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Aan mijn ouders

CONTENTS

CHAPTER ONE

GENERAL INTRODUCTION

Aerial view of Barang Lompo island.

GENERAL INTRODUCTION

Seagrasses are marine angiosperm plants with well-developed rhizome-root systems. They occur in a wide range of intertidal and subtidal marine and estuarine habitats throughout the world. Worldwide, more than 50 species have been described, belonging to two different families, the Potamogetonaceae and the Hydrocharitaceae (den Hartog, 1970). In Indonesia, 7 genera and 12 species are present. Here, they occur as monospecific as well as mixed-species beds on substrates ranging from consolidated dead coral to fine muddy sediments in the vicinity of mangroves, and at depths ranging from the upper intertidal down to 40 m.

Seagrass beds are generally acknowledged to be important in stabilizing sediments, thus preventing coastal erosion and reducing siltation of coral reefs, and as nursery grounds for many fish and crustacean species, including several of economic importance. They support complex trophic food webs and rank among the most productive of submerged aquatic ecosystems. Yet, large-scale losses of seagrass habitat are being increasingly reported from various parts of the world. Human-induced eutrophication is considered among the most frequent causes of seagrass decline.

Information on seagrass communities in the tropical Indo-West Pacific region is very scarce in comparison with the tropical Central American - Caribbean seagrass beds, even though these are much less diverse. Recent studies during the Indonesian-Dutch Snellius-II Oceanographic Expedition in 1984-85 in Eastern Indonesia (Lindeboom and Sandee, 1989; Nienhuis et al., 1989) and by Brouns and Heijs (1986) in Papua New Guinea, have provided a considerable amount of information on various structural and functional aspects of Indo-West Pacific seagrass beds, that has formed the basis of the aims and objectives of the present study.

Dense and well-developed seagrass beds in the Banda Sea may have a maximum biomass of up to 700 g AFDW m^{-2} with a coverage of up to 95%, and may consist of a mixed vegetation of up to 8 species competing for light, space and nutrients. Full-grown stable seagrass beds appear to show little seasonal variation in biomass, while growth rates and decomposition seem to be equally balanced. Mean community respiration was found to be about 80% of the total maximum gross primary production (5 g C m^{-2} d^{-1}) in seagrass beds in the Flores Sea. Nutrient concentrations in the water column above the seagrass beds were found to be very low.

These data have led to the hypothesis that the tropical seagrass ecosystem is a highly productive self-sustaining ecosystem in a nutrient-poor environment. It seems that the major part of the high primary production is used within the ecosystem for various consumption purposes (respiration, mineralization). Net export of nutrients or organic matter to adjacent ecosystems, such as mangroves and coral reefs, is probably small. The high productivity implies a high nutrient demand which appears to be met by a highly efficient recycling of nutrients through rapid decomposition within the bed and through internal remobilization from older plant parts during senescence. Although this hypothesis characterizes the tropical seagrass beds as energetically self-sustaining in terms of nutrient cycles, this does not imply absence of important biotic interrelations with other ecosystems. For example, it is well-documented, that many coral reef animals spend certain periods of their life-cycle in seagrass beds.

The key to the understanding of the functioning of tropical seagrass ecosystems is located in the factors regulating production and decomposition of organic matter. Although light is regarded as one of the primary factors limiting growth and production of seagrasses in temperate regions (Verhagen and Nienhuis, 1983; Giesen et al., 1990), there are no indications that the seagrass populations in the Indonesian waters, which have their optimum growth in the lower intertidal and upper subtidal zone, are limited by the availability of light in these generally very clear tropical oceanic waters. The growth, abundance and morphology of these seagrasses are more likely to be limited by the availability of nutrients. Nutrient dynamics play a key role in the functioning of seagrass beds and adjacent coral reefs (Patriquin, 1972) but hardly anything on this is known from the Indo-West Pacific region.

Several authors have addressed the issue of nutrient limitation of seagrass growth in temperate and tropical Caribbean regions, some of which reported on the effects of in situ fertilization of the sediment. Short (1987) stressed the importance of geochemical characteristics of the sediment in the study of nutrient limitation of seagrass growth. He concluded that seagrasses growing in temperate terrigenous sedimentary environments are often more typically nitrogen limited, whereas seagrasses occurring in tropical carbonate sedimentary environments generally experience phosphorus limitation.

In order to achieve an appropriate testing of Short's limitation theory in an area in the Indo-West Pacific region, as well as to test the more general hypothesis of the tropical seagrass bed as a self-sustaining ecosystem characterized by a highly efficient recycling of nutrients, I have collected a substantial set of data with regard to production rates, nutrient pools and concentrations, and environmental variables, which is presented in this thesis.

The present study was carried out in the Spermonde Archipelago and adjacent coastal areas in South Sulawesi (Indonesia) in the framework of the Buginesia Programme, an Indonesian-Dutch cooperative research programme in marine science. Previous studies within this cooperative framework have focussed on the geology and morphogenesis of the area (De Klerk, 1983), zonation and diversity of scleractinian corals (Moll, 1984), systematics and ecology of mushroom corals (Hoeksema, 1990), and stabilizing and decomposing components of coral reefs (Verheij, 1993). All these projects, as well as the present study, were financially supported by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO).

The present thesis describes the results of the Buginesia 4 project, which was carried out from August 1989 to August 1993. Of this period, two years (1990-1991) were spent in Indonesia, after permission was granted from the Indonesian Institute of Sciences (LIPI). The first year in Indonesia was spent largely to study nutrient concentrations and resources, environmental variables, growth and primary production in seagrass beds at several selected localities, the results of which are described in chapters 2 and 3. Chapter 4 deals with sediment-nutrient interactions, and describes the major geochemical processes that regulate the availability of nutrients in sediment porewaters to seagrass growth. Chapter 5 describes the results of three in situ fertilization experiments that were carried out during the second half of 1990 and first half of 1991. These experiments were done to study the long-term (6 months) effects of experimental nutrient enrichment on the biomass, nutrient incorporation and production of seagrass beds on different sediment types. In chapter 6 the seasonal dynamics in two contrasting intertidal seagrass beds are discussed. This chapter describes the changes in biomass, nutrient contents and production of the seagrasses that were monthly monitored between February 1991 and February 1992, and tries to determine what environmental variables are responsible for the observed dynamics. In Chapter 7 the main results of the previous chapters are summarized and discussed in relation to the hypothesis and in relation to other studies. The overall importance of sediment geochemistry and terrigenous influences to the nutrient dynamics in seagrass beds is discussed, and the implications of the high nutrient demand and observed nutrient resources to the site of nutrient uptake, water column turn-over, decomposition rates and internal nutrient recycling, is evaluated.

CHAPTER TWO

DIFFERENCES IN NUTRIENT CONCENTRATIONS AND RESOURCES BETWEEN SEAGRASS COMMUNITIES ON CARBONATE AND TERRIGENOUS SEDIMENTS IN SOUTH SULAWESI, INDONESIA.

Jene Berang river mouth and plume, showing significant input of suspended sediment and organic material into the ocean (photograph taken: April 1982).

Erftemeijer, P.L.A.
Bulletin of Marine Science 54 (1): in press.

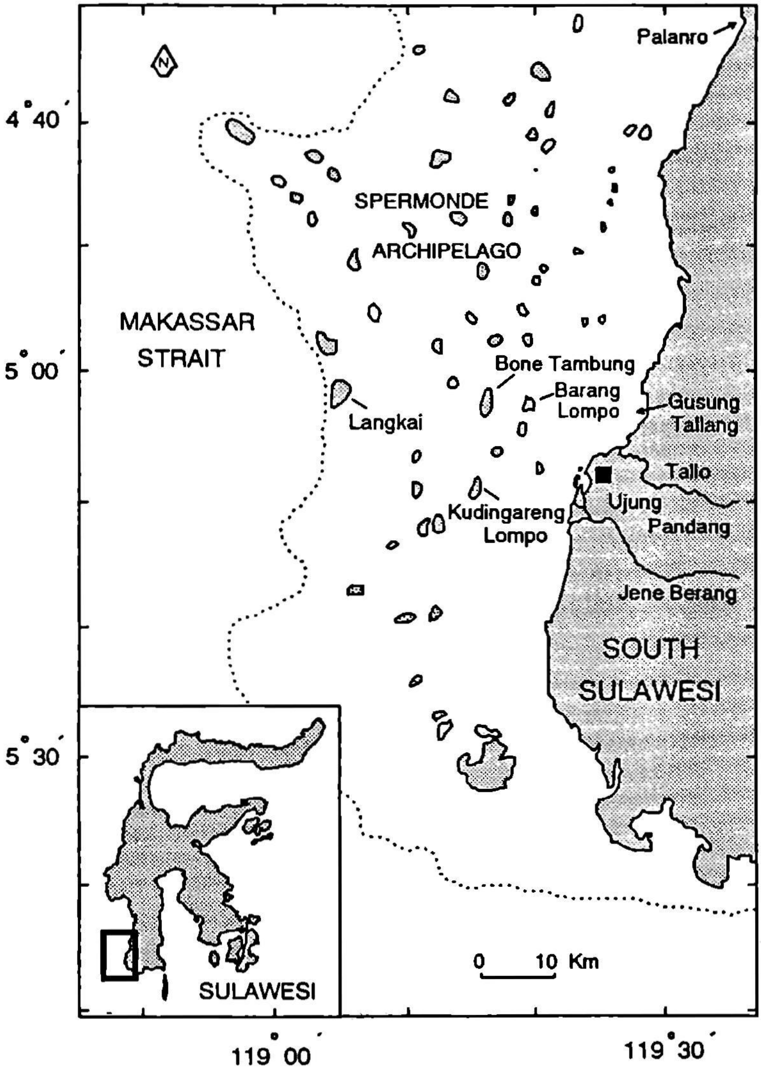

Fig. 2.1 Map of the study area, showing the locations mentioned in the text. (dotted line is approximate edge of continental shelf)

DIFFERENCES IN NUTRIENT CONCENTRATIONS AND RESOURCES BETWEEN SEAGRASS COMMUNITIES ON CARBONATE AND TERRIGENOUS SEDIMENTS IN SOUTH SULAWESI, INDONESIA.

ABSTRACT

Water column, sediment and plant parameters were studied in six tropical seagrass beds in South Sulawesi, Indonesia, to evaluate the relation between seagrass bed nutrient concentrations and sediment type. Coastal seagrass beds on terrigenous sediments had considerably higher biomass of phytoplankton, epiphytic algae and macro-algae, if compared to seagrass beds growing on carbonate sediments in oligotrophic reef-flat environments. The size of leaves of seagrass plants of the same species was considerably larger at terrigenous sites than at carbonate sites. Seagrasses in carbonate-rich environments had invested considerably more in below-ground biomass relative to above-ground biomass than those growing on terrigenous sediments. Elementary composition of plant material indicated a richer nutrient supply of both N and P at the terrigenous sites (C:N:P = 340:19:1) than at carbonate sites (C:N:P = 565:18:1). Concentrations of dissolved reactive phosphate, ammonium, and nitrate+nitrite were low (< 2 µM) in the water column at all sites, often below detectable limits, but considerably higher in sediment porewaters. Porewater phosphate concentrations (3-13 µM) were comparable between the two sediment types, but exchangeable phosphorus contents were 2 to 5 times higher in carbonate sediments (18.6-23.6 mg P_2O_5 100 g^{-1} versus 4.4-10.9 mg P_2O_5 100 g^{-1} in terrigenous sediments). Porewater phosphate concentration decreased with increasing sediment depth in carbonate sediments. The relatively coarse composition of these sands might have limited the adsorption of phosphate onto the carbonate mineral surfaces. Carbonate sediments were extremely low in organic matter, compared to terrigenous sediments. Both biogeochemical properties of the sediment type and the degree of influence from terrigenous run-off were found to be important factors affecting the availability of nutrients to seagrass growth and determining the response in morphology, biomass and chemical composition of the seagrass material.

INTRODUCTION

Seagrass beds are known to be important as nursery areas for many fish and crustacean species including several of economic importance (Pollard, 1984; Bell and Pollard, 1989; Heck and Weinstein, 1989; Parrish, 1989; Chester and Thayer, 1990; Orth and Van Montfrans, 1990). They are also considered to be of great importance in stabilizing sediments (Phillips, 1978; Fonseca and Fisher, 1986; Fonseca, 1989) thus reducing coastal erosion and siltation of coral reefs, with which they are often associated.

One of the most striking features of the Indo-Pacific region is the occurrence of multi-species vegetations. Mixed seagrass beds may contain up to eight different species, each of which may dominate alternatively (Brouns & Heijs, 1991). This situation is different from that in the Caribbean, where monospecific vegetations dominate (Zieman, 1987). In contrast with the seagrass communities of the Caribbean and temperate regions, ecological information available on the tropical Indo-Pacific region is limited, notwithstanding the fact that in Indonesia alone they cover an area of roughly 40,000 km^2 (estimated). Some information on community structure, production and associated macrofauna was gathered during the joint Indonesian-Dutch Snellius-II expedition in 1984 (Brouns, 1985c; Lindeboom & Sandee, 1989; Nienhuis et al., 1989). Kiswara and Hutomo (1985) reported on the distribution of seagrasses in Indonesia and Hutomo and Martosewojo (1977) described the fish community associated with seagrass beds at Pari Island (Java). Brouns and Heijs (1986) studied various structural and functional aspects of Indo-Pacific seagrass beds (mainly in Papua New Guinea).

Available information (Nienhuis et al., 1989) suggests that a large part of the gross primary production in tropical Indo-Pacific seagrass beds is used within the seagrass ecosystem for several consumption purposes (respiration, mineralisation). Nutrients are captured in the large seagrass biomass and are re-used efficiently. The seagrass ecosystem seems to a large extent energetically self-sustaining and transport of nutrients to adjacent coral reefs seems insignificant or episodic.

Information on nutrient concentrations and nutrient dynamics in seagrass beds from the Indo-Pacific region is virtually lacking. Detailed information on nitrogen pools is available from seagrass beds in adjacent tropical and subtropical waters of Australia but data on phosphorus are scarce (Boon, 1986; Moriarty and Boon, 1989). Various studies in temperate regions have demonstrated that the availability of nutrient resources affects the growth, distribution, morphology and seasonal cycle of eelgrass (Zostera marina) populations (Orth, 1977; Kenworthy et al., 1982; Short, 1983a), but comparable data on (sub-)tropical seagrasses are scarce (Powell et al., 1989; Powell et al., 1991; Fourqurean et al., 1992).

Earlier research indicates that seagrass communities on carbonate and terrigenous sediments display physical and biological characteristics specific to the substrate type. Short (1987) noted the importance of sediment geochemistry in seagrass beds in determining nutrient limitation of seagrass growth. He concluded that seagrasses growing in terrigenous environments are more often typically nitrogen limited, whereas seagrasses occurring in tropical carbonate environments generally experience phosphorus limitation. Short (1987) reported differences in (1) seagrass growth, abundance and morphology, (2) the chemical composition of seagrass plant material (C:N:P-ratio's), and (3) porewater nutrient concentrations, between terrigenous and carbonate environments. The present study was set up to test Short's (1987) hypothesis for tropical seagrass communities on carbonate and terrigenous substrates in Sulawesi, Indonesia.

MATERIALS AND METHODS

Study area

The study was conducted in the Spermonde Archipelago and adjacent coastal areas of South Sulawesi, Indonesia, and concentrated on six sites; (Fig. 2.1) four coral reef islands (Barang Lompo, Bone Tambung, Kudingareng Lompo, Langkai) and two localities along the coast (Gusung Tallang and Palanro). Maximum tidal amplitude in the area is 120 cm. Data were collected between May and November 1990. The number of visits, replicate samples and measurements was set by logistic limitations. A variable-oriented approach was followed, studying variable after variable for all localities within minimum time intervals, rather than locality after locality for all parameters. To exclude possible seasonal effects, the study was performed in the dry period, during which day-to-day fluctuations are considered minimal (tropical conditions).

Terrigenous sediments in the study area originate from fluvial transport and consist of erosion material from the (mainly volcanic) mainland of Sulawesi. They vary in particle size distribution from sand to sandy muds. A major proportion of these sediments consists of weathered silici- and volcanoclastics. Heavy mineral analysis of some sediment samples from the same area by Storm (1989) indicated a dominance of augite and some basic hornblende. Storm (1989) found that the influence of riverine terrigenous sediments is restricted to a zone parallel to the coastline with a general extension of 4 kilometers.

The reefflats of the many coral islands in the study area are covered by carbonate sediments. These sediments are biogenic, mainly consisting of skeletal components eroded from the coral reefs by wave action. All carbonate sediments in the study area are of a relatively coarse composition with usually over 40% of the particles larger than 312 µm, indicative of the rate of exposure of the sediment.

Water column parameters

14 l samples of surface water were collected in opaque bottles at each site and transported on ice. Within 6 hours of sampling, the water was filtered over Whatman GF/C glass fiber filters (0.45 µm). The filters had previously been extracted for 6 h with acetone, dried for 12 h at 250 °C and weighed prior to use. After filtration the filters were rinsed with distilled water, dried for 48 h at 80 °C and stored dry. These filters were used to determine seston, particulate organic

carbon (POC) and particulate organic nitrogen (PON) with a Carlo-Erba NA 1500 CN-analyser. To determine chlorophyll-a levels the filters were not treated or weighed prior to use. After filtration they were stored frozen at approximately -40 °C (14 days maximum). Chlorophyll-a was determined spectrophotometrically, using a Shimadzu UV-240 spectrophotometer, according to Parsons et al. (1984).

Separate water samples were filtered in the field over 0.2 µm Minisart NML disposable syringe filters and transported on ice, of which six replicate 5 ml subsamples were directly analysed spectrophotometrically, using a Nanocolor 100D-MN filter photometer, for phosphate, ammonium, and nitrate + nitrite (10 ml samples were used for the reduction of nitrate to yield 5 ml samples for the nitrite determination) according to Strickland & Parsons (1972). Blanks of artificial seawater were produced from triple-distilled water and salts.

Salinity and temperature were monitored in the field with a YSI 3466 (model 33) salinity meter. pH was measured at the laboratory with a 7004104 Electrofact pH meter. Some approximate data on current velocities was collected with a PVC-floating body (Hayes, 1978). Turbidity was monitored with a secchi disk (d = 12 cm), which at the reef sites was operated in deeper waters adjacent to the reef flat.

Sediment parameters

Sediment samples were taken with small hand corers (d = 6 cm) to a depth of 10 cm while snorkling. Each core was separated into 2 cm sections. The coinciding sections of every 12 successive cores were combined to reduce spatial heterogeneity and treated as one sample. Two series of 12 sediment cores were collected at each site, representing two replicates per sediment section within each site (one visit per locality). These samples were transported on ice in sealed plastic bags for further treatment in the laboratory. Plant parts, shells and large stones were removed prior to further treatment. Within a maximum of 4 h after sampling, porewaters were extracted by filtration of the samples over Schleicher & Schüll membrane filters (0.45 µm) under high pressure using nitrogen gas, following a slightly modified technique of Kelderman (1985). Porewater samples were filtered over 0.2 µm filters and phosphate, ammonium and nitrate + nitrite were analysed spectrophotometrically on the same day according to Strickland and Parsons (1972).

Samples of the top 10 cm sediment layer were taken to determine water contents by measuring the weight loss after drying the samples for 48 h at 100 °C. Microphytobenthos (expressed as mg Chl-a m^{-2}) was determined in series of nine replicate samples of the top 1 cm sediment layer for each location. Sampling was done according to Wolff (1987). Samples were taken with small hand-cores (surface area: 4.5 cm^2) and transported on ice. The upper (1 cm) layer was sliced off from each sediment core and stored for maximum 14 days at -40°C. Chlorophyll-a in these samples was determined spectrophotometrically (Parsons et al., 1984). Separate samples of the top 10 cm sediment layer were taken to study grain-size distribution, calcium carbonate content, total carbon, organic carbon, total nitrogen, total phosphorus and exchangeable phosphorus. These samples were dried for 48 h at 80 °C and plant parts, shells and macroscopic fauna were removed prior to storage and further treatment. Grain-size distribution was determined by laser diffraction on a Malvern Particle Sizer 3600 Ec. $CaCO_3$ content was analysed by gasvolumetry (Hulsemann, 1966).

Treatment of the sediment samples with HCl vapours in small aluminium containers in an exsiccator, as often used in C and N determinations of sediments with low $CaCO_3$ contents, as well as ashing at approximately 500 °C, did not reveal satisfactory results in the determination of organic carbon contents, given the extremely high $CaCO_3$-contents of most of the samples. Therefore, an adapted methodology was applied (Nieuwenhuize, in prep.): 10 replicate sediment samples (20 mg) were treated with several drops of 25 % HCl (2 times 20 µl) in small silver (Ag) containers to remove all inorganic C from $CaCO_3$, and then heated (60-100 °C) to remove all remaining HCl. Organic carbon (after treatment with HCl drops), total carbon (without such previous treatment) and total nitrogen (no treatment) were determined on a Carlo-Erba NA 1500 CN-analyser. Values for organic carbon obtained with this adapted method showed a high degree of reliability with small sd-values.

Total phosphorus was analysed by a strong oxidizing acid digestion (hydrochloric acid + nitric acid + perchloric acid) followed by a standard colorimetric phosphate determination of the digest solution (Allen, 1974). Exchangeable phosphorus or P_2O_5 (i.e. the fraction of P in the sediments that is most readily exchangeable with the dissolved P in the porewater) was analysed by a weak oxidizing acid extraction (ammonia + lactic acid + acetic acid) and a standard colorimetric phosphate determination (op.cit.).

Seagrass parameters

At each of the six localities quantitative samples of the seagrasses were collected haphazardly in densely vegetated areas (cover > 50%) by wading or snorkling, using an aluminium frame (surface area 0.0625 m^2) and a spade. The samples were transported on ice and stored in a refrigerator at 4 °C. At the laboratory, samples were rinsed with freshwater and divided into above-ground (leaves, sheaths, generative parts) and below-ground (roots, rhizomes) plant parts. Epiphytes were removed from leaves by scraping. Associated macro-algae (if present in a sample) were treated separately. The plant parts were dried at 60-80 °C to constant dry weight (DW) and stored for determination of ash-free dry weight (AFDW) by ashing at c. 550 °C, and total C, N and P (see sediment

Table 2.1
Water column data for each locality. Values are averages (± sd) of replicate samples or measurements. The number of replicates (n) were equal for each locality. Values below detectable limits are presented as 0. (Localities: BL=Barang Lompo, BT=Bone Tambung, KL=Kudingareng Lompo, Lk=Langkai, GT=Gusung Tallang, Pal=Palanro).

		Carbonate sites				Terrigenous sites	
	n	BL	BT	KL	Lk	GT	Pal
seston (mg l^{-1})	3	5.8 ± 0.3	5.5 ± 2.1	5.2 ± 0.2	6.4 ± 2.1	26.2 ± 4.4	7.3 ± 0.3
POC (mg l^{-1})	3	0.19 ± 0.01	0.18 ± 0.03	0.16 ± 0.04	0.16 ± 0.02	0.54 ± 0.12	0.28 ± 0.08
PON (mg l^{-1})	3	0.03 ± 0.01	0.03 ± 0.01	0.03 ± 0.01	0.02 ± 0.01	0.08 ± 0.01	0.04 ± 0.01
Chl-a (µg l^{-1})	3	0.5 ± 0.2	1.3 ± 0.1	1.0 ± 0.1	0.7 ± 0.1	2.9 ± 1.5	1.1 ± 0.1
Secchi (m)	5	18.2 ± 3.2	22.8 ± 3.6	21.4 ± 4.7	20.8 ± 3.1	1.2 ± 0.6	8.8 ± 5.1
salinity (S)	3	34.2 ± 0.6	34.8 ± 0.4	35.7 ± 0.3	36.2 ± 0.2	31.5 ± 2.0	33.3 ± 0.5
currents (m s^{-1})	3	0.05 ± 0.02	0.05 ± 0.02	0.23 ± 0.14	0.02 ± 0.01	0.04 ± 0.01	0.03 ± 0.02
PO_4 (µM)	6	0.8 ± 0.4	0.2 ± 0.1	-	0.2 ± 0.1	1.7 ± 0.1	3.3 ± 1.1
NH_4 (µM)	6	1.4 ± 0.6	2.7 ± 0.5	-	0	1.4 ± 0.4	0
NO_3+NO_2 (µM)	6	0.9 ± 0.1	0	-	0.5 ± 0.2	0.6 ± 0.5	1.5 ± 0.2

analysis). Shoot densities were determined by counting those present in the biomass samples. For species with an irregular distribution in densily vegetated areas (e.g. Enhalus acoroides), counts were made within aluminium frames (50x50 cm) thrown arbitrarily in the seagrass bed. The leaf lengths and widths of Thalassia hemprichii and Enhalus acoroides were measured in fresh material from several sites to study morphological variation. These values were used together with data on shoot density to calculate leaf-area indices (LAI; both sides).

Data analysis

Comparisons between the different localities for the various parameters were statistically tested by a one-way analysis of variance (ANOVA), followed by a Tukey (HSD) multiple comparison test ($p < 0.05$). Each locality was tested relative to each of the other localities. Replicate numbers of samples (n) refer to different visits to the localities, unless specified otherwise. Data collection of a parameter was done at each of the localities within reasonable time limits (days or weeks), excluding possible seasonal effects among localities. Data were not blocked for time in ANOVA; all data were considered as pure random samples. Data were tested for heteroscedacity by a Bartlett test for homogeneity prior to ANOVA. Data that scored significant for heteroscedacity (seston, Chl-a, S, secchi, PO_4, NO_3, and above-ground : below-ground biomass ratio) were log-transformed, which considerably improved the data (no longer significant at 1% level in Bartlett test), while ANOVA results remained consistent with those obtained by the analysis of non-transformed data. Reports of ± refer to standard error of average throughout the text.

RESULTS

Water column parameters

Table 2.1 summarizes data on environmental parameters measured in the water column above the seagrass beds for each locality. All coral reef island sites were characterized by clear water with high secchi-disk readings (14 to 26 m). Chlorophyll-a concentrations were usually low (<1.5 µg l^{-1}), so were seston, POC and PON with no considerable differences between sites. In contrast, the mud-dominated terrigenous site of Gusung Tallang was characterized by turbid water with low secchi-readings (0.7 to 2.0 m) and high levels of seston, chlorophyll-a, and particulate organic matter (POC & PON). The sand-dominated terrigenous bay at Palanro showed a water column environment comparable with that of the reef islands, although secchi depth was significantly smaller at this site.

Nutrient concentrations were low in all water column samples (Table 2.1) often below detectable limits. In general, the concentrations of ammonium, phosphate

Table 2.2
Sediment data for each locality. Values are averages (± sd) of replicate samples or measurements. The number of replicates (n) were equal for each locality. Localities: see Table 1. (P exchang. = exchangeable phosphorus)

		Carbonate sites				Terrigenous sites	
	n	BL	BT	KL	Lk	GT	Pal
particle size range: (% dry wt)							
< 63 µm	2	11.3 ± 1.1	11.2 ± 1.1	13.7 ± 2.9	17.8 ± 0.4	39.1 ± 3.0	26.0 ± 1.6
> 312 µm	2	46.1 ± 0.8	28.7 ± 3.9	41.6 ± 6.1	43.7 ± 1.8	3.5 ± 3.1	8.3 ± 1.5
water contents (%)	5	27 ± 2	30 ± 5	28 ± 3	29 ± 2	47 ± 2	23 ± 2
micro-phytobenthos (mg Chl-a m^{-2})	9	13.6 ± 3.1	22.8 ± 3.4	20.4 ± 4.2	49.8 ± 15.4	9.7 ± 2.5	37.2 ± 9.9
$CaCO_3$ (%)	10	98 ± 5	99 ± 2	100 ± 3	97 ± 3	10.8 ± 3.7	7.5 ± 0.2
total C (%)	10	12.05 ± 0.06	11.92 ± 0.11	12.05 ± 0.06	12.07 ± 0.11	6.72 ± 0.06	1.45 ± 0.06
organic C (%)	10	0.29 ± 0.05	0.36 ± 0.05	0.34 ± 0.04	0.29 ± 0.05	1.89 ± 0.05	0.58 ± 0.03
total N (%)	10	0.04 ± 0.01	0.04 ± 0.02	0.04 ± 0.01	0.05 ± 0.02	0.08 ± 0.03	0.05 ± 0.02
total P (mg P_2O_5 g^{-1})	2	0.65 ± 0.01	0.60 ± 0.17	0.68 ± 0.01	0.64 ± 0.01	2.33 ± 0.02	2.57 ± 0.08
P exchang. (mg P_2O_5 100 g^{-1})	2	20.1 ± 0.9	18.6 ± 1.3	20.0 ± 0.7	23.8 ± 0.4	4.4 ± 0.3	10.9 ± 0.6

and nitrate in the water column were very low (at least < 2 µM), and no significant differences could be found between carbonate and terrigenous sites. Phosphate concentrations seemed higher at terrigenous sites, but the heterogeneity of variance for PO_4 data was too large (even after log-transformation) to determine significant differences between localities.

Salinity values were relatively constant and averaged 34 ‰S. Minimum values (down to 21 ‰S) were measured at Gusung Tallang during the rainy season, indicating a considerable influence of the mainland at this site. Surface water temperature varied between 26.5 and 32.5 °C, but may rise up to 38 °C in shallow pools in depressions on reefflats at spring low tide during the daylight period. pH was relatively constant at all sites, ranging from 8.1 to 8.4. Surface irradiance showed a maximum of 1900 µE m^{-2} s^{-1} (daylight from 6 AM to 6 PM). At sites with low turbidity, irradiance at 15 m depth may still reach as high as 400 µE m^{-2} s^{-1} at noon (Langkai: September, 12). In contrast, at the turbid coastal site Gusung Tallang, the irradiance may be below 200 µE m^{-2} s^{-1} at 1 m depth (June, 27). The light extinction coefficient averaged 0.3 ± 0.1 at Barang Lompo and 1.4 ± 0.7 at Gusung Tallang (data 1991; n=18 at both sites).

Surface water current velocities varied considerably as a result of tidal fluctuations and winds. A maximum velocity of 0.6 m s^{-1} was measured along the edge of the reef at Langkai in September, but on the reefflats of the islands and at the terrigenous sites values were usually below 0.1 m s^{-1} (Table 2.1).

Practically all water column parameters differed significantly ($p < 0.05$) between Gusung Tallang and the rest of the localities, without significant differences among the other sites. The only exceptions were currents, ammonium and nitrate+nitrite concentrations, which showed no significant differences between any of the six localities.

Sediment parameters

Table 2.2 summarizes data on sediment parameters. Sediment samples collected from the seagrass beds on the reefflats of the coral islands Barang Lompo, Kudingareng Lompo, Bone Tambung and Langkai all consisted of nearly 100% $CaCO_3$. Calcium carbonate levels were significantly lower ($p < 0.05$) in the sediments of the two terrigenous sites, with lowest $CaCO_3$ in the sand from Palanro (7.5%).

Sediment particle size distribution was roughly comparable between samples collected from the various coral islands. These sediments consisted of a mixture of coarse, medium and fine carbonate particles, with particles under 63 microns contributing only 11-18% and particles over 300 microns usually contributing more than 40% to the total dry weight of a sediment sample. The terrigenous sediment

Table 2.3
Porewater nutrient concentrations at each of the localities. Values are averages (± sd) of two sample series. Localities: see Table 1.

Sediment		Carbonate sites				Terrigenous sites	
interval		BL	BT	KL	Lk	GT	Pal
0-2 cm	phosphate	11.2 ± 0.6	7.9 ± 0.4	13.1 ± 0.7	4.5 ± 0.7	2.9 ± 0.5	10.1 ± 1.0
2-4 cm	(µM PO_4)	8.5 ± 0.6	7.8 ± 0.1	8.5 ± 0.3	6.1 ± 0.2	4.6 ± 0.4	7.8 ± 0.2
4-6 cm		7.8 ± 0.7	7.6 ± 0.6	5.5 ± 0.6	4.6 ± 0.6	7.5 ± 0.5	9.3 ± 0.5
6-8 cm		5.7 ± 1.3	4.6 ± 0.3	5.1 ± 0.6	5.6 ± 0.3	8.2 ± 0.9	8.7 ± 0.8
8-10 cm		4.4 ± 0.9	4.8 ± 0.2	4.1 ± 0.3	6.0 ± 0.4	8.7 ± 0.6	7.7 ± 0.2
0-2 cm	ammonium	43.8 ± 6.9	65.9 ± 4.2	59.3 ± 7.1	56.9 ± 5.7	44.8 ± 2.7	22.0 ± 1.8
2-4 cm	(µM NH_4)	78.8 ± 5.6	52.3 ± 4.0	63.2 ± 4.3	81.6 ± 4.5	72.1 ± 6.7	27.3 ± 2.0
4-6 cm		98.2 ± 7.1	68.6 ± 6.8	48.1 ± 5.5	117.6 ± 2.9	88.4 ± 6.7	19.2 ± 4.1
6-8 cm		97.2 ± 6.7	80.4 ± 9.2	45.0 ± 1.9	105.1 ± 8.2	88.1 ± 2.8	24.4 ± 3.4
8-10 cm		93.0 ± 4.6	82.8 ± 1.5	38.8 ± 3.4	80.9 ± 7.9	86.3 ± 8.6	22.0 ± 3.6
0-2 cm	nitrate +	6.0 ± 1.2	1.6 ± 0.2	-	-	4.3 ± 1.1	-
2-4 cm	nitrite	4.1 ± 0.7	-	-	1.5 ± 0.3	2.9 ± 0.1	5.7 ± 1.8
4-6 cm	(µM NO_3+NO_2)	3.0 ± 0.3	0.1 ± 0.2	-	3.5 ± 0.6	3.0 ± 1.3	4.7 ± 0.5
6-8 cm		1.7 ± 0.5	0.8 ± 0.2	-	3.1 ± 0.4	2.3 ± 0.2	4.6 ± 1.4
8-10 cm		2.0 ± 1.3	2.5 ± 0.4	-	0.1 ± 0.1	3.3 ± 0.4	5.9 ± 2.4

from the coastal site Gusung Tallang consisted of sandy mud with 39% (dry wt) consisting of particles smaller than 63 microns. The sediment from the bay at Palanro was more sandy but still had 26% (dry wt) under 63 microns. Water content (expressed as a percentage of the wet weight) showed significantly lower values ($p < 0.05$) for the sand-dominated sediments at the coral islands (27-30%) and Palanro Bay (23%) than for the more muddy sediment at Gusung Tallang (46%).

Carbonate sediments had extremely low levels of organic carbon (all below 0.4%). Samples from terrigenous sediments were slightly richer in organic C (0.6-1.9%). The very high contents of $CaCO_3$ in the reef sediments accounted for the much higher values of total C (= inorganic C + organic C) at these localities if compared to terrigenous sites. Total P was four times higher in terrigenous sediments, but exchangeable P (P_2O_5) was considerably higher (2 to 5 times) in carbonate sediments, indicating a much higher availability of P to plant growth at these sites.

Chlorophyll-a concentrations in the sediments beneath the seagrasses ranged from 9.7 to 49.8 mg Chl-a m^{-2} with large differences between individual beds. The lowest value was recorded at Gusung Tallang (9.7 ± 2.5 mg Chl-a m^{-2}), the site which also had the greatest turbidity.

The concentration of dissolved nutrients in the interstitial water was much higher than in the water column (Table 2.3). Ammonium concentrations ranged from 39 to 118 µM in porewaters from carbonate sediments. A gradual decrease in the concentration of ammonium can be observed in the upper layers (0-4 cm) of the sediment in most of the results. A similar trend was found in the porewaters of Gusung Tallang (terrigenous sediment), where the ammonium concentration ranged from 45 to 88 µM. Porewater ammonium concentration was lower at the terrigenous site Palanro (average 23 µM), where no trend with sediment depth was found. The concentration of phosphate in all porewaters ranged from 3 to 13 µM. Most data from carbonate sediments showed a general decrease in concentration with increasing sediment depth. A similar but less obvious trend was found at Palanro, where the phosphate concentration ranged from 8 to 10 µM. At Gusung Tallang, the phosphate concentration ranged from 3 to 9 µM, showing an increase with sediment depth. No distinct trends were discovered in nitrate + nitrite concentrations in sediment porewaters. Concentrations were all below 6 µM, without major differences between carbonate and terrigenous sites.

With exception of porewater nutrient concentrations (which only differed in their behaviour in relation to depth between the two substrate types) and organic C (which was only significantly higher at GT), all sediment parameters differed significantly ($p < 0.05$) between terrigenous sites (both Gusung Tallang and Palanro) and carbonate sites (all four).

Table 2.4
Biomass data for each location, providing average values of n replicate samples and their standard deviation. (seagrass species: T.h. = Thalassia hemprichii; E.a. = Enhalus acoroides; H.o. = Halophila ovalis; H.u. = Halodule uninervis; C.r. = Cymodocea rotundata; C.s. = Cymodocea serrulata). Species with total biomass below 1 g AFDW.m-2 omitted.

Sampling station	Seagrass species	Above-ground biomass (a) (g AFDW m^{-2})	Below-ground biomass (b) (g AFDW m^{-2})	Total biomass (g AFDW m^{-2})	a:b ratio
Barang	T.h.	71 ± 23	427 ± 128	498 ± 149	0.17
Lompo	E.a.	15 ± 32	107 ± 212	122 ± 244	0.13
n=9	total:	86 ± 45	534 ± 240	620 ± 304	0.16
Bone	T.h.	41 ± 9	234 ± 128	275 ± 136	0.24
Tambung	E.a.	30 ± 40	139 ± 143	169 ± 182	0.15
n=3	H.o.	1 ± 1	2 ± 2	3 ± 3	0.39
	H.u.	25 ± 19	180 ± 166	205 ± 185	0.16
	total:	97 ± 47	556 ± 343	653 ± 383	0.25
Kudingareng					
Lompo	(mixed)				
n=3	total:	115 ± 72	391 ± 15	506 ± 87	0.29
Langkai	T.h.	40 ± 49	276 ± 363	316 ± 412	0.16
n=4	E.a.	27 ± 47	211 ± 366	239 ± 413	0.13
	H.u.	51 ± 26	165 ± 65	216 ± 90	0.30
	C.r.	27 ± 18	339 ± 226	366 ± 243	0.13
	total:	145 ± 67	991 ± 534	1137 ± 599	0.16
Gusung	E.a.	83 ± 66	157 ± 103	239 ± 167	0.53
Tallang	(=total)				
n=3					
Palanro	T.h.	32 ± 16	140 ± 66	171 ± 82	0.22
n=4	E.a.	2 ± 3	3 ± 5	5 ± 8	0.58
	H.o.	1 ± 1	1 ± 1	2 ± 2	1.47
	C.r.	1 ± 2	2 ± 3	3 ± 5	0.67
	C.s.	8 ± 5	26 ± 21	35 ± 26	0.42
	total:	44 ± 21	172 ± 83	217 ± 104	0.26

Species distribution and abundance

Seagrasses occurred in four different habitats: (1) reefflats (usually less than 2 m depth at HW) and (2) reefslopes (around 10-18 m depth) at coral islands, both dominated by carbonate sediment (varying from coral rubble to fine coral sands), (3) shallow bays dominated by black terrigenous sand (Palanro), and (4) intertidal coastal flats, dominated by soft terrigenous mud (Gusung Tallang).

Thalassia hemprichii and Enhalus acoroides were the dominant and constant species in the mixed beds on the reefflats of the four islands. Halodule uninervis and Cymodocea rotundata usually occurred as pioneering species occupying marginal areas near the beach and exposed sites close to the reef edge, where other species were absent. Their root and rhizome systems do not extend very deep (c. 3-4 cm) in the sediment. They are able to rapidly colonize barren strips, haloes and newly sedimented areas. Syringodium isoetifolium (absent from Barang Lompo), Halophila minor and H. ovalis occurred among the other species in low densities. On sand-dominated parts of reef slopes at depths of 10 to 35 m, H. ovalis and H. decipiens occurred. Occasionally, they formed extensive meadows at these depths, but due to the specific character and logistical problems, these meadows were not included in the rest of this study. H. uninervis was also found at considerable depths, but it never formed meadows. At Palanro mixed seagrass beds were found. These included T. hemprichii, E. acoroides, C. serrulata, C. rotundata, H. ovalis, H. minor, H. pinifolia, H. uninervis and S. isoetifolium. T. hemprichii, S. isoetifolium and C. serrulata were dominant, accounting for more than 75% of the total seagrass cover. H. uninervis, H. pinifolia, C. rotundata and occasionally H. minor occupied marginal areas along the shore and shallow pools on the beach. At Gusung Tallang monospecific beds of E. acoroides occurred. A few shoots of T. hemprichii and H. uninervis were also found, but these species were extremely rare (<1 %) at this site.

There was a striking absence of extensive and dense seagrass beds from some of the other islands in the area, such as Samalona, Barang Cadi and Kudingareng Keke, where T. hemprichii, E. acoroides and H. ovalis occurred only in low densities.

Shoot densities

Most seagrass beds showed a high degree of patchiness and at some parts of the reefflats of the coral islands extensive haloes occurred. Some species, especially pioneers, showed patterns of irregular coverage and their density usually decreased towards the centre of the meadow where other species (e.g. Thalassia hemprichii, Enhalus hemprichii) became dominant. Only some representative data were collected for Thalassia hemprichii and Enhalus acoroides, which showed a more consistent coverage. Thalassia hemprichii reached maximum densities of 3700

Table 2.5

Chemical nutrient tissue composition (% of dry weight) and atomic nutrient ratios for seagrasses from each site. Dominant seagrass species between brackets.

Location	Plant part	% C	% N	% P	C N P atomic ratio
Barang	leaves +				
Lompo	sheaths	35 58	2 66	0 22	418.27 1
(Thalassia)	rhizomes	36 36	0 60	0 09	1044 15 1
	roots	30 88	1 01	0 06	1329 37 1
Bone	leaves +				
Tambung	sheaths	34 39	0 47	0 16	555 6 1
(mixed)	rhizomes	34 66	1 68	0 05	1791 74 1
	roots	29 08	1 00	0 05	1502 44 1
Kudingareng	leaves +				
Lompo	sheaths	32 61	1 66	0 12	702 31.1
(Thalassia)	rhizomes	35 99	0 49	0 06	1549 18 1
	roots	30 01	1 20	0 08	830 39 1
Langkai	leaves +				
(mixed)	sheaths	37 63	0 56	0 14	694 9 1
	rhizomes	26 71	1 30	0 06	1150 48 1
	roots	30 54	0 96	0 07	1127 30 1
Gusung	leaves +				
Tallang	sheaths	31 63	2 71	0 34	240 18 1
(Enhalus)	rhizomes	38 70	1 46	0 16	624 20 1
	roots	31 68	1 11	0 13	629 19 1
Palanro	leaves +				
(mixed)	sheaths	34 19	1 50	0 16	552 21 1
	rhizomes	39 03	0 32	0 10	1008 7 1
	roots	30 07	0 91	0 11	706 18 1
	total	34 43	0 91	0 12	741 17 1

shoots m^{-2} at Barang Lompo (average 2414 ± 642), but only 500-700 shoots m^{-2} (average 641 ± 162) at Kudingareng Lompo. Enhalus acoroides reached average densities of 39 ± 6 shoots m^{-2} at Gusung Tallang, 24 ± 4 shoots m^{-2} at Barang Lompo, and 19 ± 4 shoots m^{-2} at Kudingareng Lompo.

Biomass

Biomass data (expressed only as ash-free dry weight) are summarized in Table 2.4. The patchiness of most of the seagrass beds and the occurrence of blow-outs and patterns of zonation (gradual or sometimes step-wise shift in dominance of different seagrass species with distance from beach) makes overal biomass estimations for the whole beds difficult. Most data presented in Table 2.4 were collected from relatively homogeneous and densily vegetated parts of the beds. Total seagrass biomass in these mixed beds may reach maximum values of 2140.7 g AFDW m^{-2} with average values of 576.8 g AFDW m^{-2}. Average total biomass of seagrasses was higher at carbonate sites (734 ± 447 g AFDW m^{-2}) than at terrigenous sites (231 ± 159 g AFDW m^{-2}), but this difference was not significant due to insufficient replicates (large SD). Below-ground biomass, however, was significantly lower ($p < 0.05$) at the two terrigenous sites than at the four carbonate sites.

At the four reef islands the above-ground : below-ground biomass ratio in mixed vegetations varied from 0.11 to 0.21 (all species taken together). At the sandy bay at Palanro this ratio ranged from 0.25 to 0.29 (all species taken together), whereas in monospecific Enhalus acoroides beds at Gusung Tallang it varied between 0.35 and 0.62. A comparison of different species, however, gave different results. Pioneering species usually show higher ratios (averages of 0.23 for Halodule uninervis, 0.62 for Cymodocea rotundata and 1.0 for Halophila ovalis) than climax species such as Thalassia hemprichii (average: 0.19). Another constant species, Enhalus acoroides, showed low ratio's when growing on carbonate sediments (average 0.13) but high ratio's when growing on terrigenous sands and muds (average 0.54).

Leaf morphology and leaf area index

The leaf morphology of seagrasses studied in samples haphazardly collected at three sites in the study area differed considerably between terrigenous and carbonate environments. Leaves were significantly longer ($p < 0.05$) at terrigenous sites (Palanro and Gusung Tallang) than at a carbonate site (Barang Lompo) for both Enhalus acoroides (Pal: mean 53.7 ± 26.2 cm; n=107; GT: mean 77.7 ± 43.0 cm; n=164; BL: mean 31.3 ± 14.8 cm; n=227) and Thalassia hemprichii (Pal: mean 9.6 ± 6.5; n=51; GT: mean 17.3 ± 6.0; n=97; BL: mean 7.4 ± 4.9; n=203). Leaf widths showed only minor variation among sites. In monospecific beds of Enhalus acoroides at Gusung Tallang, the leaf area index (calculated from leaf morphology data and shoot density data) ranged from 2.4 to 3.6. At Barang Lompo LAI reached 2.9 in a mixed vegetation (dominated by Thalassia hemprichii) and 2.6 in a monospecific area of Enhalus acoroides.

Total C-, N- and P-content of plant tissue

Data on total carbon, total nitrogen and total phosphorus content of different plant parts from different locations are presented in Table 2.5. All corresponding plant parts of different species within one sample of a site were taken together and considered as one sample. Average (± sd) concentrations of carbon, nitrogen and phosphorus in seagrass leaves (including sheaths) were 35.0 ± 2.1, 1.34 ± 1.03, and 0.16 ± 0.04 (% dry wt) for carbonate sites, and 32.9 ± 1.8, 2.10 ± 0.85, and 0.25 ± 0.13 (% dry wt) for terrigenous sites, respectively. It is noted that these data represent averages of leaf blades and sheath tissue, including both young and old leaves. The average atomic C:N:P ratio (leaf blade + sheath tissue only) was 565:18:1 for carbonate sites and 340:19:1 for terrigenous sites. This indicates a lower nutrient availability at carbonate sites. The C:N:P values found in this study are within the range of values reported for marine macrophytes in literature (Atkinson and Smith, 1983; Duarte, 1990).

Epiphytes

Although only limited data were collected, it appeared that epiphyte cover on seagrass leaves at carbonate sites was much poorer than at terrigenous sites. Epiphytes had heavily developed on the leaves of Enhalus acoroides at Gusung Tallang. They were dominated by filamentous green, red and blue-green micro-algae. Their biomass reached approximately 8 g AFDW m^{-2}, or 0.27 mg AFDW cm^{-2} (2.4 ± 0.6 µg Chl-a cm^{-2}) leaf surface (one side) at this station. Epiphyte cover was always low on young leaves and highest on old leaves. Epiphytes were poorly developed at the base of a leaf (< 0.4 µg Chl-a cm^{-2}) but became more abundant towards the top (at top: 2.6-3.2 µg Chl-a cm^{-2}). At carbonate sites, epiphytes on Enhalus leaves were dominated by coralline algae. Their biomass was usually low (often below detectable limits of the Chl-a determination), but at the terminal portions of the leaves their biomass was sometimes considerable (e.g. 1.5 ± 1.0 µg Chl-a cm^{-2} at BL). Diatoms were abundant on seagrass leaves at all sites (Sterrenburg et al., submitted), but poorly developed on the sediment, which is attributed to substrate instability (carbonate sites) or reduced insolation (Gusung Tallang).

Macroalgae

The biomass of the macroalgal component in the seagrass beds was usually low. Average macroalgal biomass reached 1.4 g AFDW m^{-2} at terrigenous sites and 3.6 g AFDW m^{-2} at carbonate sites. Recent data (personal observations, 1991) suggest that the macroalgal component at the coastal site Gusung Tallang is very dynamic in time, and shows only incidental peaks. Occasional blooming of certain species of macroalgae may occur at this location, during which their biomass may reach up to 207 g DW m^{-2} (April 1991: Hypnea sp. and Gracilaria spp.) or 257 g DW m^{-2} (September 1991: Ulva sp.).

DISCUSSION

Seagrass beds in the study area showed several distinct differences between carbonate and terrigenous sites. While the average biomass of seagrasses in terrigenous environments was lower than on carbonate sediments (though not significant), other primary producers in the ecosystem, such as associated epiphytes, macro-algae and phytoplankton, were often more pronounced and usually had much higher biomasses in the terrigenous environment. Seagrasses on carbonate sediments always had much more below-ground biomass relative to the biomass of above-ground plant parts than seagrasses in the terrigenous environment. Short (1987) also reported an unusually high root biomass for Syringodium filiforme beds on carbonate sediments in San Salvador, Bahamas. Nienhuis et al. (1989) found significant differences in the amount of below-ground biomass characteristic of the species of seagrass, with pioneering genera usually investing less biomass in below-ground plant parts than climax species. This is confirmed by data from the present study. This study, however, also showed a consistent difference between terrigenous and carbonate environments for individual species. Species that occurred in both environments always had invested more in below-ground biomass in the carbonate environment if compared to the terrigenous environment. The finding of high root biomass relative to leaf biomass in tropical seagrass beds in a low nutrient carbonate environment (< 2 µM porewater phosphate) in the Bahamas was suggested by Short et al. (1985) as a strategy of plant adaptation that increases nutrient absorptive root surface area. High root and rhizome biomass, however, may also be related to susceptibility of the substrate to waves and to their function in storage and repropagation, notably where the seagrasses experience full spring low-tide exposure or heavy grazing.

Leaves of seagrasses of the same species were found to be much longer when growing on terrigenous sediments than on carbonate sediment. This is attributed to a larger availability of nutrients in the terrigenous environment. Several authors have reported a consistent relationship between the size of the seagrass plants (notably the size and area of leaves) and sediment nutrient conditions (Short, 1983b, 1987; Duarte, 1991). The size of the leaf portion of eelgrass plants was reported by Short (1987) as the primary difference between eelgrass growth in high organic mud and that growing in low organic sand (mesocosm experiments). He concluded that leaf length and leaf area relate to sediment nutrient conditions.

Sediment chlorophyll-a (as a measure of microphytobenthos) did not show differences characteristic of the sediment type, but was lowest at the coastal site Gusung Tallang (9.7 mg m^{-2}), which is attributed to the high turbidity at this locality. Values at other localities varied considerably for individual beds and ranged from 13.6 to 49.8 mg m^{-2}. These values are within the range of those reported by Daehnick et al. (1992) for seagrass beds at Mississippi Sound near the Gulf of Mexico.

C:N:P ratios for above-ground tissues were within the range of those reported for seagrasses and other macrophytes from other areas (Atkinson and Smith, 1983; Duarte, 1990) but showed a significant difference between carbonate (565:18:1) and terrigenous sites (340:19:1). These data, together with the substantial load of phytoplankton and particulate organic material in the water column, the high biomass of epiphytes and macro-algae, the high ratio between above-ground and below-ground seagrass biomass and the increased size of leaves at terrigenous locations (notably Gusung Tallang) are all indicative of a nutrient-richer environment (Orth and van Montfrans, 1984; Birkeland, 1988; Sand-Jensen and Borum, 1991) if compared to the carbonate sites.

Statistical data analysis revealed that most sediment parameters were indeed significantly different between terrigenous and carbonate sites. Most of the water column parameters, however, were only significantly different at Gusung Tallang compared to any of the other localities. The water column environment at the other terrigenous locality, Palanro, was more comparable to the reef sites and indicated a much smaller influence from terrestrial run-off than at Gusung Tallang.

Measurements of the concentrations of dissolved nutrients (phosphate, ammonium and nitrate) in porewaters did not indicate significant differences between terrigenous and carbonate locations, except for the lower ammonium concentrations at Palanro. Some differences, however, were found in the trends of behaviour of porewater nutrients in relation to sediment depth. Phosphate concentration decreased significantly with increasing sediment depth in most carbonate sediments, whereas the terrigenous mud at Gusung Tallang showed a reverse trend. Recent data (Erftemeijer and Herman, submitted) indicate that these contrasting trends are consistent throughout the year. In addition, total phosphorus was much higher in terrigenous sediments, but the amount of exchangeable P was much larger in carbonate sediments. This may be attributed to differences in geochemical properties between the two sediment types. Adsorption of phosphate by calcium carbonate particles (DeKanel and Morse, 1978; Kitano et al., 1978) was suggested by Short (1987) as the key factor determining phosphorus limitation of seagrass growth on carbonate sediments. However, estuarine muds (i.e. terrigenous sediments) may also adsorb considerable amounts of phosphate, notably in fine-grained sediments (Jitts, 1959; Krom and Berner, 1980). Apparently, the particle size distribution of sediments plays a crucial role in nutrient adsorption-desorption processes. The carbonate porewater concentrations of phosphate found in this study (3-13 µM) are relatively high if compared to the value of 2 µM reported by Short et al. (1985, 1990) for carbonate silts in the Bahamas. Morse et al. (1985) found that phosphate was undetectable (< 0.5 µM) in porewaters from calcium carbonate-rich shallow water sediments in the Bahamas. They also attributed this to adsorption on carbonate mineral surfaces. They also reported significantly lower ammonium concentrations in these carbonate sediments than typically found in shallow water fine-grained terrigenous sediments. This is in contrast with the present study, where carbonate sediments had similarly high ammonium porewater concentrations if compared to the fine-grained terrigenous sediment at Gusung Tallang (no significant differences, $p > 0.05$), whereas the site with lowest porewater ammonium concentrations was a site with terrigenous sand (Palanro). Preliminary investigation of the primary elementary composition (low P) of calcareous epiphytes collected from seagrass leaves in the study area (data not shown), indicate that they probably do not contribute significantly to the availability of P in the sediments.

The present study provides a general quantitative overview of differences between seagrass communities on terrigenous and carbonate sediments from an area in the Indo-Pacific region. Data on porewater concentrations and sediment composition are very scarce in the literature on Indo-Pacific seagrass beds (Hattori et al., 1985). As long as a substantial data set with regard to nutrient levels is lacking, adequate testing of hypotheses on nutrient dynamics gained in E. Atlantic - Caribbean seagrass ecosystems cannot be achieved. It seems obvious, however, that geochemical properties and processes may play an important role in determining the availability of nutrients for seagrass growth, and that this may differ considerably between sediment types. Consequently, the response by the seagrass community will be ultimately linked in some way with these geochemical properties characteristic of the type of sediment on which they grow. Lapointe et al. (1992) recently reported on significant differences in nutrient availability to marine macroalgae and in their tissue chemical composition (C, N and P) between siliciclastic and carbonate-rich coastal waters in Florida, the Bahamas and the Caribbean. They concluded that the availability of N limits the productivity of macroalgae in temperate siliciclastic waters but that the availability of P may be of paramount importance in limiting primary production of macroalgae in carbonate-rich tropical waters.

A substantial amount of data gathered in this study indicates that seagrass communities on terrigenous sediments are characterized by an environment of richer nutrient supply (both N and P). This is no doubt related to the terrestrial run-off from the rivers which have deposited these terrigenous sediments there. The abiotic environment of some coastal seagrass beds (e.g. at Gusung Tallang) showed some estuarine characteristics with fluctuations in salinity and other water column parameters. Most seagrass beds on carbonate sediments are located too far from the coastline to experience any significant influence from the mainland in terms of nutrient supply. As such, several of the structural and functional differences between seagrass communities on terrigenous and carbonate sediments might be more directly related to this terrestrial input of nutrients rather than to the characteristics of the substrate itself. C:N:P ratios in plant tissues indicated that the availability of both nitrogen and phosphorus was higher in coastal areas than at reef sites, notably where the influence of river input was considerable.

Short (1987) stressed the importance of geochemical characteristics of the sediment in nutrient limitation of seagrass growth in the Caribbean. He concluded that P-limitation typically occurs in tropical carbonate sediments, due to the adsorption of phosphate onto carbonate mineral surfaces, and that N-limitation was more typical of terrigenous sediments depending on the rate of decomposition of organic matter. Data from the present study confirm the importance of geochemistry in the determination of nutrient availability to seagrass growth. It is suggested, however, that grain-size distribution of the sediment may play a crucial role in the adsorption-desorption processes which may overshadow the effects of the sediment's chemical composition. Porewater phosphate concentrations, P-contents in plant tissue and levels of exchangeable P in the sediment at carbonate sites in the study area were all considerably higher than those reported for the Caribbean/West Indies. Apparently, the relatively coarse composition of the carbonate sands in the Sulawesi study area limits the importance of phosphate adsorption, thus maintaining relatively high levels of available P. This is also in contrast with findings of Morse et al. (1987) in fine-grained sediments in the Bahamas, who stated that carbonate sediment porewater is unlikely to serve as a readily available phosphorus reservoir and unlikely to be a significant dissolved-molybdate-reactive phosphate pool.

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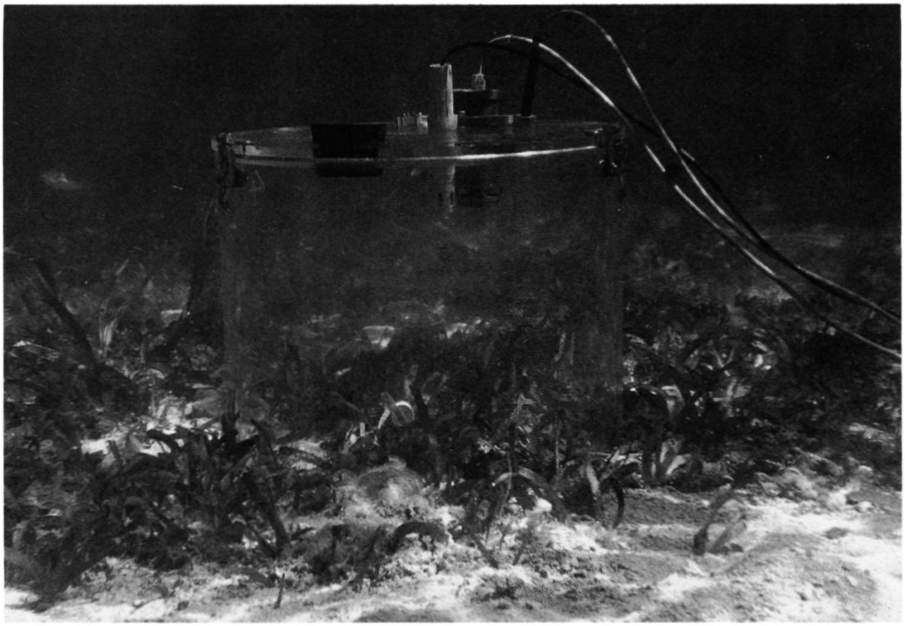
CHAPTER THREE

PRIMARY PRODUCTION OF SEAGRASS BEDS IN SOUTH SULAWESI (INDONESIA): A COMPARISON OF HABITATS, METHODS AND SPECIES.



Measuring seagrass primary production by monitoring
the oxygen concentration in transparant enclosures.

Erftemeijer, P.L.A., R. Osinga and A.E. Mars, 1993.
Aquatic Botany 46: 67-90.

PRIMARY PRODUCTION OF SEAGRASS BEDS IN SOUTH SULAWESI (INDONESIA): A COMPARISON OF HABITATS, METHODS AND SPECIES.

ABSTRACT

Primary production of tropical seagrass meadows was studied between April and August 1990 in South Sulawesi, Indonesia. Oxygen evolution studies in enclosures over seagrass vegetations revealed gross community production values between 900 and 4400 mg C m^{-2} d^{-1}. Assumed community respiration ranged from 800 to 1800 mg C m^{-2} d^{-1} in non-vegetated areas and from 1400 to 5100 mg C m^{-2} d^{-1} for areas with varying amounts of seagrass. Benthic community respiration varied considerably in response to diurnal fluctuations in the dissolved oxygen concentration in the water column. Net production was small (less than 500 mg C m^{-2} d^{-1}) and slightly negative on seven of 12 occasions. Light compensation points ranged from 50 to 340 µE m^{-2} s^{-1}. Bell jar measurements revealed no significant differences in seagrass production between coastal and reef island habitats. Leaf marking experiments with Enhalus acoroides (L.f.) Royle revealed significantly higher leaf growth in a coastal muddy area (3.1 ± 0.8 cm per shoot day^{-1}) than at an offshore sandy reef site (1.6 ± 0.5 cm per shoot day^{-1}), but relative growth rates were comparable between the two habitats (0.019 ± 0.005 and 0.012 ± 0.003 g g^{-1} AFDW day^{-1}, respectively). Leaf marking and plastochrone interval methods revealed similar results for net leaf production in a monospecific stand of Thalassia hemprichii (Ehrenb.) Aschers. at a reef site, which averaged 1.6 g C m^{-2} day^{-1}. Rhizome tagging experiments revealed net rhizome production values of 0.1-0.3 g C m^{-2} day^{-1} for Thalassia hemprichii at this reef site. Relative growth rate of leaves of Thalassia hemprichii (0.039 ± 0.010 g g^{-1} AFDW day^{-1}) at the reef site was significantly higher than that of Enhalus acoroides (0.012 ± 0.003 g g^{-1} AFDW day^{-1}). The pioneering seagrass species Halodule uninervis (Forssk.) Aschers. and Cymodocea rotundata Ehrenb. & Hempr. ex Aschers. had considerably higher horizontal apical rhizome growth rates (0.7-0.8 cm $apex^{-1}$ day^{-1}) than the constant species Thalassia hemprichii (0.1 cm apex day^{-1}). The suitability of different methods to measure seagrass productivity is evaluated.

INTRODUCTION

Seagrass beds are widely acknowledged to be important in stabilizing sediments, reducing coastal erosion and siltation of reefs, as well as by providing nursery and feeding areas for many fish and crustacean species (Phillips, 1978; Fonseca and Fisher, 1986; Bell and Pollard, 1989). Seagrass beds are amongst the most productive of submerged aquatic ecosystems (Zieman and Wetzel, 1980; Larkum and West, 1983; Hillman et al., 1989).

Studies and reviews on the effects of light (Beer and Waisel, 1982; Dennison, 1987), currents (Fonseca and Kenworthy, 1987), temperature (Bulthuis, 1987), nutrients (Hillman et al., 1989) and epiphytes (Sand-Jensen, 1977; Orth and Montfrans, 1984; Howard and Short, 1986; Mazella and Alberte, 1986; Silberstein et al., 1986; Borowitzka and Lethbridge, 1989) on seagrass photosynthesis have provided a basic understanding of the complexity of primary production in a seagrass meadow. Various components, such as seagrasses, benthic micro-algae and bacteria, epiphytic algae, macro-algae and phytoplankton, contribute to the total productivity of the seagrass ecosystem. In order to fully understand and estimate the total productivity of the system, all these autotrophic components must be measured (Den Hartog, 1979; 1983).

Several techniques have been developed to measure primary production of seagrasses and associated components. Methods vary from relatively simple biomass accumulation techniques (Westlake, 1963; Bellamy et al., 1973), leaf marking and plastochron interval techniques (Zieman, 1968,1974; Brouns, 1985a) and lepidochronological analyses (Pergent and Pergent-Martini, 1991), to complex metabolic techniques (oxygen evolution in open or closed systems) and carbon-14 tracer techniques (Nixon and Oviatt, 1972; McRoy, 1974; Bittaker and Iverson 1976; Lindeboom and De Bree, 1982; Lindeboom and Sandee, 1989). Each of these methods has shown specific advantages and shortcomings (Hillman et al., 1989; Kemp et al., 1990), but different techniques will provide differing kinds of information. The parallel use of more than one method has been suggested by Kemp et al. (1990).

Whereas most work on primary productivity of tropical seagrasses has been carried out in the Caribbean and Australia, few data are available for the Indo-Pacific region. Only recently, marking methods and oxygen evolution techniques have been used in Indonesia and Papua New Guinea, which revealed gross primary production rates of about 5 g C m^{-2} day^{-1} for an entire seagrass ecosystem (Lindeboom and Sandee, 1989) and maximum above ground production of 5.5 g AFDW m^{-2} day^{-1} for seagrass plants (Brouns and Heijs, 1986). The studies of Bittaker and Iverson (1976) on Thalassia testudinum Banks ex Koenig in the Gulf of Mexico and of Peduzzi and Vukovic (1990) in the Mediterranean Sea are among the few which compared productivity data obtained with different methods applied simultaneously in the same study area. No such data are available from the Indo-Pacific region.

The aims of the present study are:

(1) to compare productivity of entire seagrass communities in different habitats in South Sulawesi (Indonesia);
(2) to compare the net production of seagrass plants of the same species in two

contrasting habitats;

(3) to compare the growth and production of different seagrass species;

(4) to evaluate the suitability of marking techniques and a metabolic method for measuring seagrass primary production in a tropical environment.

METHODS AND MATERIALS

Study area

The present study was carried out between April and August 1990 in the Spermonde Archipelago and adjacent coastal areas in South Sulawesi, Indonesia (118°55'- 119°30'E, 4°30'- 5°40'S; Fig. 2.1). Monospecific and mixed-species seagrass beds cover extensive shallow areas along the coast, the reef flats of several of the coral reef islands and some deeper sandy areas. Productivity measurements of seagrass communities, using an oxygen evolution technique, concentrated on the reef flats of two coral islands, both covered by carbonate sediments (Barang Lompo and Bone Tambung), and two coastal areas dominated by terrigenous sediments (Palanro and Gusung Tallang). A comparison of measurement techniques (O_2 method and marking methods) was carried out simultaneously in a monospecific vegetation of Thalassia hemprichii (Ehrenb.) Aschers. on the reef flat of Barang Lompo (July 1990). Additional marking experiments were done at Langkai (coral island) and Gusung Tallang. Water levels at the localities varied from 50 cm below chart datum at Palanro and 12 cm below chart datum at Bone Tambung, to 30 cm above chart datum at Barang Lompo and 40 cm above chart datum at Gusung Tallang. Maximum tidal amplitude in the study area is 120 cm. A detailed description of water quality, sediment composition and plant characteristics of the study area will be presented elsewhere (Erftemeijer, in press).

Methods

Bell jar method

Cylindrical plexiglass enclosures (bell jars) were used according to Lindeboom and Sandee (1989) to study the uptake and release of oxygen by the seagrass community in relation to irradiance and biomass. Four bell jars, each with a surface area of 1520 cm^2 and a height of 34 cm, were used. The removable (transparent) lid of a bell jar was equipped with a YSI oxygen electrode (model 5739, Yellow Springs Instruments Inc., Ohio), a temperature sensor (DIHO, Yerseke) and a stirring mechanism (DIHO, Yerseke). Oxygen concentration and water temperature in the bell jars were monitored using a 12 channel Linseis LS 50 recorder (Selb, Germany). Winkler titrations were done to calibrate the oxygen electrodes (Bryan et al., 1976). Irradiance of photosynthetically active radiation (PAR) was measured under water with a Li-cor 185B Qrbp 1900-8501 quantum-meter (Lincoln, Nebraska, USA). The bell jars were placed over various amounts of seagrass. At each locality one bell jar incubation series was carried out over non-vegetated substrate to estimate the production and respiration by components of the community other than seagrass. Changes in oxygen concentration were monitored over periods of 20 to 120 minutes, after which the lids were temporarily removed to enable exchange with the surrounding water to prevent saturation or exhaustion of oxygen and excessive increase in water temperature inside the enclosures. Measurements were carried out in successive series of time intervals over a day. Respiration was measured in the early morning and late afternoon (when irradiance was 0 µE m^{-2} s^{-1}) or during daytime by temporarily covering the enclosures with black plastic sheets to create artificial darkness. All bell jar measurements were carried out under insolation conditions considered to be representative for the dry season (April-September). The temperature inside the bell jars never increased to more than 2 °C above the ambient water temperature, while ambient water temperature varied between 27 and 32 °C.

After the incubations the oxygen evolution in the bell jars was calculated as a function of the irradiance. It was thereby assumed that the respiration by the community during the night was the same as the respiration during the daylight period (Lindeboom and Sandee, 1989). The respiration was then calculated as the oxygen uptake over a 24 hour period. To determine possible diurnal fluctuations in the oxygen concentration of the water column, a series of triplicate samples was taken with hourly intervals during a full 24-hour cycle on the reef flat at Barang Lompo (16-17 November 1990) and oxygen analysed by Winkler titration (Bryan et al., 1976).

The daily production was calculated by plotting the oxygen evolution in the bell jars as a function of irradiance (P:I) by non-linear curve fitting (Peeters and Eilers, 1978) using the formula: $y = x/(ax^2+bx+c)$, in which y is the oxygen production/respiration in g O_2 m^{-2} h^{-1} and x is the irradiance under water in µE m^{-2} s^{-1}. Using the actual irradiance at the depth of incubation, the daily net oxygen production was subsequently calculated with the formula obtained from the curve fitting. Gross production was estimated by adding the assumed respiration during daylight to the measured net oxygen production.

For reasons of comparison, the oxygen data were converted to carbon equivalents using a factor of 0.30 (C/O_2) (Lindeboom and Sandee, 1989; Peduzzi and Vukovic, 1990). For calculation of production:biomass ratios, seagrass biomass data (in g AFDW m^{-2}) were transformed to carbon equivalents assuming organic carbon to be 46% of ash-free dry weight (Westlake, 1963, 1974; Zieman, 1974; Hillman et al., 1989).

After completion of the measurements, all above-ground seagrass material was collected from the bell jars. Epiphytes were carefully removed from the leaves by scraping. Leaf biomass (AFDW) was determined following Zieman and Wetzel (1980).

Microphytobenthos (expressed as mg Chl-a m^{-2}), present in the upper 1 cm of the sediment, was sampled according to Wolff (1987). Phytoplankton (expressed as mg Chl-a l^{-1}) was sampled by filtration of known volumes of surface water over 0.45 µm Whatman GF/C glass fiber filters. Epiphytes (expressed as mg Chl-a cm^{-2} leaf) were sampled by scraping known surface areas of seagrass leaves. Macroalgae and additional seagrass leaves were collected by hand for determination of the chlorophyll-a contents (expressed as mg Chl-a g^{-1} dry wt). Samples of microbenthic algae, phytoplankton, epiphytes, macroalgae and seagrass leaves were transported on ice and stored in a refrigerator at 4°C. Analysis of the chlorophyll-a content of these samples was done by standard acetone (90%) extraction followed by spectrophotometric readings according to Parsons et al. (1984), within 14 days of sampling. Seagrass leaves and macroalgae were ground in a mortar prior to the acetone treatment.

Marking methods

An adaptation of Zieman's (1968, 1974) leaf marking method was applied according to Kirkman and Reid (1979). In several random experimental plots (0.0625 m^2) a small hole was punched through all the leaves at the base of a shoot. This reference level was chosen close to the basic meristem of the shoot and was marked by the top of a small bamboo stick inserted into the sediment near the base of the shoot. The average number of shoots marked was 20 per plot, and these were randomly chosen within the plots. Four to six days after initial marking, the shoots were punched for a second time at the reference level and harvested. The new growth increments of the leaves (i.e. the leaf increment in between the initial hole and the hole punched at harvest) were cut out, dried and weighed. The remaining above-ground leaf material of the marked shoots was also dried and weighed (separately). These data were used to calculate relative growth rates (in g g^{-1} AFDW day^{-1}). Shoot densities were determined by counting those present in biomass samples or by field counts within frames (0.625 m^2 or 0.25 m^2) thrown randomly into the seagrass bed. Net above-ground production was calculated from data on average shoot production and shoot density or from data on standing crop and relative growth rates. Leaf growth was expressed as net areal productivity (mg C m^{-2} day^{-1}).

An adapted rhizome-tagging method (Bulthuis and Woelkerling, 1983; Dennison et al., 1987) was applied to measure below-ground growth of rhizomes. After removal of the superficial sediment from several random experimental plots (0.0625 m^2), rhizomes were tagged with plastic bird-rings before the last shoot on the rhizome prior to their apical meristem and the length from the tagged shoot to the apex of each rhizome was measured. The average number of rhizomes tagged was 10 per plot, which were randomly selected within each plot and marked with numbered bamboo sticks. After tagging, the rhizomes were covered again with a layer of sediment and the substrate was restored. Approximately 7-11 days after tagging, the length from tag to apex was measured again and the rhizomes were harvested. The new growth increments of the rhizomes were cut out and weighed. Rhizome production was calculated from data on rhizome apical density (m^{-2}), below-ground biomass, and from data on the weight of the newly grown rhizome increments in comparison to the weight of rhizomes initially present.

Table 3.1
Overview of growth and production measurements carried out in seagrass beds in South Sulawesi, with details on localities, methods and species. (E. = Enhalus; T. = Thalassia; C. = Cymodocea; H. = Halodule)

		locality	method	seagrass species
A.	Comparison of habitats (I)	Barang Lompo Bone Tambung Palanro Gusung Tallang	bell jars	integrated communities
B.	Comparison of habitats (II)	Barang Lompo Gusung Tallang	leaf marking	E. acoroides
C.	Comparison of methods	Barang Lompo	bell jars leaf marking rhizome-tagging plastochrone-interval (leaves)	T. hemprichii
D.	Comparison of species	Barang Lompo Langkai Gusung Tallang	leaf marking plastochrone-interval (leaves and shoots) rhizome-tagging	T. hemprichii E. acoroides C. rotundata H. uninervis

In addition, the plastochrone interval method (replacement technique) was applied according to Brouns (1985a). This technique is essentially a modification of Zieman's (1968, 1974) leaf marking method, and is based on the assumption that the output of new leaves is a continuous process, with an equal number of leaves emerging every day. The plastochrone interval (PI) of leaves is the time interval between the initiation of two successive leaves (Patriquin, 1973). A small hole was punched in the tip of the youngest leaf reaching a minimal reference level approximately 1 cm above the basic meristem (marked with the top of a bamboo stick) for each of a number of randomly selected shoots within random experimental plots (0.0625 m^2). The average number of marked shoots was again 20 plot^{-1}. After 10 to 16 days, all newly emerged leaves that had reached the reference level were counted. The plastochrone interval of leaves was calculated according to Jacobs (1979): $\boldsymbol{PI_{leaves} = (N \textit{ of shoots marked } x\ t)/N \textit{ of new leaves}}$, in which N = total number, and t = time interval between marking and harvesting (in days). Measurements of the average weight of fullgrown seagrass leaves and data on biomass and shoot density were used to calculate daily production.

In addition, some preliminary experiments were carried out by using a comparable technique to determine the plastochrone interval of shoots, i.e. the time interval between the initiation of two successive shoots on the rhizome. Rhizomes were tagged close to the apex before the first shoot longer than 1 cm. After approximately 20 days all new shoots (longer than 1 cm) that had developed between the tag and apex of a rhizome were counted. The plastochrone interval of shoots was calculated according to the formula: $\boldsymbol{PI_{shoots} = (N \textit{ of rhizomes tagged } x\ t)/N \textit{ of new shoots}}$, in which N = total number, and t = time interval between tagging and harvesting (in days). These data, together with data on average biomass of rhizome-increments in between the bases of two fullgrown shoots, shoot density and rhizome apical density, were used to calculate rhizome growth.

Table 3.1 provides an overview of the growth and production measurements that were carried out, with details on locality, method and species.

Data analysis

Comparisons between different localities, methods and species were statistically tested by Kruskall Wallis tests ($p < 0.05$). In the presence of statistically significant differences a notched box and whisker plot (Wilkinson, 1990) was used to demonstrate significant differences of medians of particular groups.

Table 3.2

Primary productivity of integrated seagrass communities in South Sulawesi, with details on daily gross production, assumed daily respiration and daily net production in relation to seagrass standing crop (g AFDW m^{-2} leaf material) at four different localities, as measured with the bell jar method (oxygen evolution). Locations: BL = Barang Lompo (29-30 May 1990); BT = Bone Tambung (7 June 1990); Pal = Palanro (14-15 June 1990); GT = Gusung Tallang (27-28 June 1990).

Loc.		standing crop (g AFDW m^{-2})	gross production (g C m^{-2} day^{-1})	assumed respiration (g C m^{-2} day^{-1})	net production (g C m^{-2} day^{-1})
BL	unvegetated	0	1.4	1.6	-0.2
	seagrass patch 1	23	2.5	2.3	0.2
	seagrass patch 2	100	3.0	3.1	-0.1
	seagrass patch 3	200	3.6	3.3	0.3
BT	unvegetated	0	1.0	0.8	0.2
	seagrass patch 1	35	2.8	2.4	0.4
	seagrass patch 2	104	4.4	4.2	0.2
	seagrass patch 3	148	4.3	5.1	-0.8
Pal	unvegetated	0	0.6	1.8	-1.2
	seagrass patch 1	14	1.9	2.4	-0.5
	seagrass patch 2	52	1.4	1.4	-0.1
	seagrass patch 3	71	3.1	2.4	0.7
GT	unvegetated	0	0.4	0.9	-0.5
	seagrass patch 1	22	0.9	1.7	-0.6
	seagrass patch 2	53	1.3	2.2	-0.8
	seagrass patch 3	174	2.0	3.6	-1.6

Table 3.3

Biomass (in mg Chl-a) of phototrophic components of the seagrass community in one volume of a bell jar (volume: 50 l; surface area: 0.15 m^2) and percentage (between brackets) of total Chlorophyll-a pool for each locality. Values presented are averages (± SD) for 3 vegetated bell jars. (Locations: see Table 2)

phototrophic component	BL		BT		Pal		GT	
seagrass	239 ± 25	(93.8)	339 ± 46	(95.4)	202 ± 82	(91.1)	339 ± 46	(94.2)
microphytobenthos	12.4 ± 6.4	(4.8)	13.0 ± 4.1	(3.6)	16.1 ± 8.7	(7.3)	10.2 ± 3.2	(2.9)
epiphytes	0.28 ± 0.09	(0.1)	0.20 ± 0.13	(0.1)	0.51 ± 0.24	(0.2)	7.2 ± 3.5	(2.0)
macroalgae	3 ± 1	(1.2)	3 ± 1	(0.8)	3 ± 1	(1.3)	3 ± 1	(0.8)
phytoplankton	0.04 ± 0.01	(0.1)	0.07 ± 0.02	(0.1)	0.05 ± 0.02	(0.1)	0.27 ± 0.09	(0.1)

RESULTS

Primary production of integrated seagrass communities: a comparison of habitats

Table 3.2 presents data on bell jar measurements of primary production for integrated seagrass communities (i.e. including organisms other than seagrass) at each of the four localities. Calculated daily gross production varied between 0.9 and 4.4 g C m^{-2} day^{-1} in vegetated areas of various seagrass cover. Assumed daily respiration of the entire seagrass community ranged from 1.5 to 5.1 g C m^{-2} day^{-1}. Daily net production values were all lower than 1 g C m^{-2} day^{-1} and slightly negative in 7 out of 12 occasions (vegetated areas). Our data do not indicate significant differences ($p > 0.05$) between coastal sites and reef localities. Unvegetated sediments had daily gross productions between 0.4 and 1.4 g C m^{-2} day^{-1}. Community respiration in these unvegetated areas ranged from 0.8 to 1.8 g C m^{-2} day^{-1} resulting in net production values from -1.2 to + 0.2 g C m^{-2} day^{-1}.

Table 3.3 presents data on the biomass (in Chl-a units) of the different autotrophic components and their relative contribution to the total amount of chlorophyll-a of the phototrophic community. Seagrasses represented over 91% of the total Chl-a pool at all localities, with other phototrophic components never contributing more than 9% to the total amount of Chl-a. Epiphytes had a larger biomass in coastal seagrass beds (significant ($p < 0.05$) at Gusung Tallang but not ($p > 0.05$) at Palanro) than at reef localities. The concentration of phytoplankton was significantly higher ($p < 0.05$) at Gusung Tallang in comparison to the other localities, and significantly lower ($p < 0.05$) at Barang Lompo than at the other localities.

Figure 3.1 gives an example of the relationship between productivity and irradiance for a monospecific patch of average seagrass cover and biomass on the reefflat at Barang Lompo. Other bell jars over seagrass at this locality gave comparable results. Productivity-irradiance relationships showed comparable curves for the seagrass communities from the other three localities. Table 3.4 gives an overview of the values of the constants a, b and c for the P:I-curves ($y = x/(ax^2+bx+c)$; see methods) of all bell jars at the different localities. Light compensation points (calculated from these formulas; i.e. the irradiance at which gross production equals respiration) for the different seagrass communities ranged from 50 to 340 µE m^{-2} s^{-1} (irradiance on sediment surface) with highest values at Gusung Tallang.

The relationship between leaf biomass (in g C m^{-2}) and gross production (in g C m^{-2} day^{-1}) for two localities is given in Figure 3.2. Seagrass beds at reef sites reached a maximum gross production of approximately 4.5 g C m^{-2} day^{-1} at biomass values above 50-70 g C m^{-2}. The seagrass bed at the coastal locality Gusung Tallang had

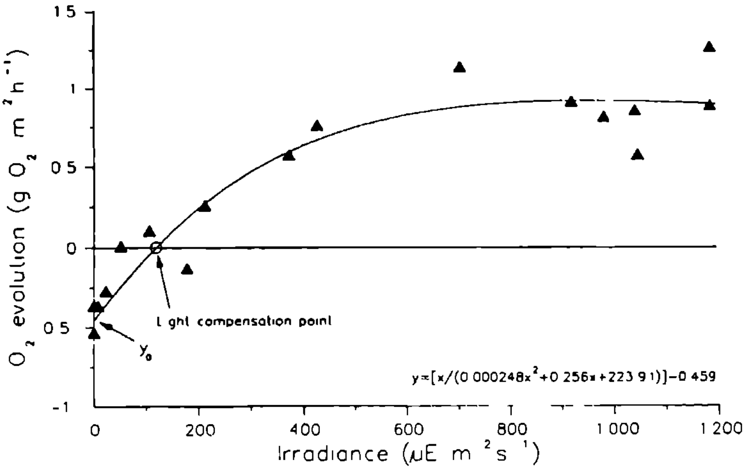


Fig. 3.1 Relationship between net community evolution (neg.= respiration; pos.= production) of oxygen (g O_2 m^{-2} h^{-1}) and irradiance (underwater on sediment surface, in µE m^{-2} s^{-1}) in a Thalassia hemprichii dominated meadow (standing crop 200 g AFDW m^{-2}) at Barang Lompo (29-30 May 1990) measured by bell jar incubation. The line was calculated by non-linear curve fitting of gross oxygen production versus irradiance using the formula $y = [x/(ax^2+bx+c)]$ and subsequently substracting the average community respiration (y_0) to yield a curve for net oxygen evolution.

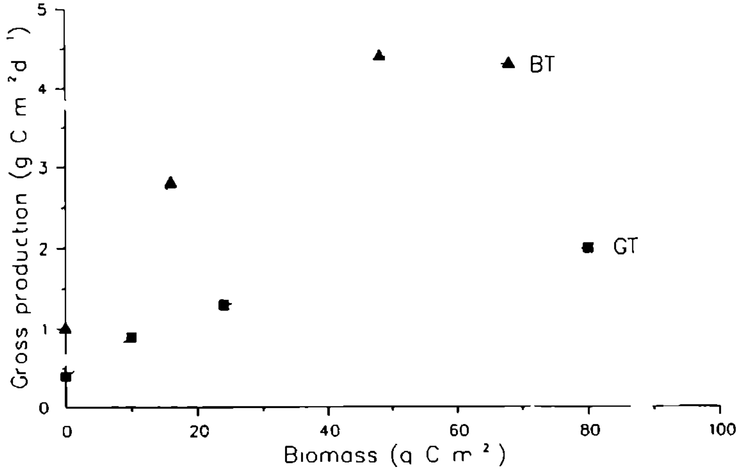


Fig. 3.2 Gross production (g C m^{-2} day^{-1}) as function of the leaf biomass (g C m^{-2}) of seagrass vegetation incubated under the bell jars at Bone Tambung (BT) and Gusung Tallang (GT).

a considerably lower gross production per unit of biomass than the meadows at the other localities, with a maximum value below 2 g C m^{-2} day^{-1}. This difference might be related to differences in turbidity, with sites of highest turbidity (GT) having the lowest production per unit of biomass.

Net production values measured at the same light intensity were usually higher in the morning than in the afternoon, which is attributed to differences in respiration rates between different times of the day. Our data indicate a peak of respiration in the late afternoon (after sunset) and early evening. Respiration was lowest in the early morning before sunrise. Figure 3.3 demonstrates the diurnal variation in the concentration of oxygen in the water column over the seagrass beds at Barang Lompo, measured at 16-17 November 1990. Comparable results were obtained at three similar 24-hour measurements during 1991 (data not shown).

Table 3.4

Average community respiration (in g O_2 m^{-2} h^{-1}) and values for constants (a, b, c) obtained by non-linear curve fitting of oxygen evolution data as a function of irradiance (P:I) for each bell jar at the four localities according to the formula $y = x/(ax^2+bx+c)$, in which y is the gross oxygen production in g O_2 m^{-2} h^{-1}, and x is the irradiance under water (on sediment surface) in µE m^{-2} s^{-1}. (Locations: see Table 2)

Loc.		Community respiration (g O_2 m^{-2} h^{-1})	a	b	c
BL	unvegetated	0.331	-0.001334	3.330	62.80
	seagrass patch 1	0.352	0.000029	0.888	258.05
	seagrass patch 2	0.526	-0.000145	1.010	81.53
	seagrass patch 3	0.459	0.000248	0.256	223.91
BT	unvegetated	0.108	0.001909	1.563	237.94
	seagrass patch 1	0.747	0.000434	0.874	27.12
	seagrass patch 2	0.714	0.000075	0.583	43.71
	seagrass patch 3	0.581	0.000251	0.444	52.49
Pal	unvegetated	0.256	0.007256	1.255	386.93
	seagrass patch 1	0.329	0.014788	-13.271	3406.63
	seagrass patch 2	0.212	-0.003035	3.453	95.20
	seagrass patch 3	0.321	-0.000521	1.239	22.57
GT	unvegetated	0.130	0.002318	4.186	920.37
	seagrass patch 1	0.235	0.005872	-2.860	1193.05
	seagrass patch 2	0.300	-0.006378	3.481	244.19
	seagrass patch 3	0.500	0.007168	-3.252	722.51

Average daily leaf growth per shoot (measured with leaf marking technique) for Enhalus acoroides (L.f.) Royle was 1.6 ± 0.5 cm day^{-1} at Barang Lompo and 3.1 ± 0.8 cm day^{-1} at Gusung Tallang (Table 3.5). Relative growth rates did not differ significantly ($p > 0.05$) between Gusung Tallang (0.019 ± 0.005 g g^{-1} AFDW day^{-1}) and Barang Lompo (0.012 ± 0.003 g g^{-1} AFDW day^{-1}). Areal production by Enhalus acoroides was significantly higher ($p < 0.05$) at Gusung Tallang (0.80 ± 0.15 mg AFDW m^{-2} day^{-1}) than at Barang Lompo (0.31 ± 0.07 mg AFDW m^{-2} day^{-1}), which is attributed to differences in shoot densities of this species between the two sites (average 39 ± 6 shoots m^{-2} at Gusung Tallang versus 24 ± 4 shoots m^{-2} at Barang Lompo). A major part of the seagrass meadow at Barang Lompo, however, consists of a mixture of Enhalus acoroides and Thalassia hemprichii, whereas the meadow at Gusung Tallang is monospecific. Therefore, total areal net production figures for Barang Lompo (3.7-3.9 g AFDW m^{-2} day^{-1}) are much higher than for Gusung Tallang (0.8 g AFDW m^{-2} day^{-1}).

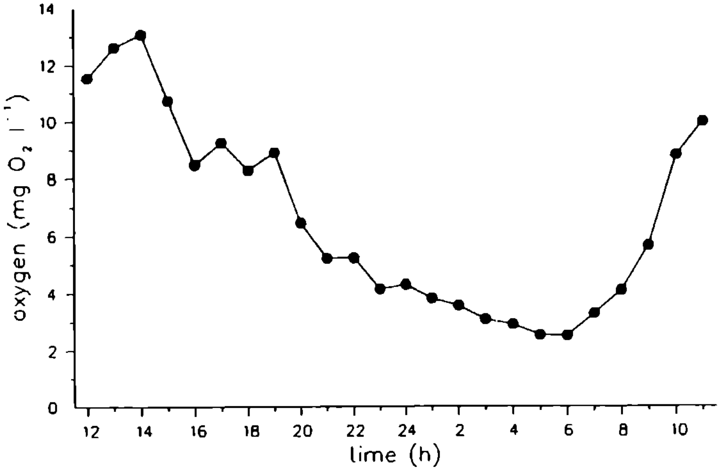


Fig. 3.3 Diurnal fluctuations in dissolved oxygen concentration (in mg O_2 l^{-1}) in the water column overlying the seagrass beds at Barang Lompo (16-17 November 1990). Values presented are averages of triplicate samples (SD never more than 10 % of average).

Primary production of Thalassia hemprichii: a field comparison of methods

The bell jar measurements (see also above) carried out at Barang Lompo in monospecific patches of Thalassia hemprichii revealed gross primary production rates between 2.5 and 3.6 g C m^{-2} day^{-1} (Table 3.2). Net community production data attained by this method were below 0.5 g C m^{-2} day^{-1}. By subtracting the respiration data obtained with bell jars over unvegetated sediments from those obtained with enclosures over seagrass-covered areas, the net production by the seagrasses (+epiphytes) can be estimated. Net production by the seagrass vegetations calculated as such, reached 1.5 to 1.9 g C m^{-2} day^{-1}.

Leaf marking experiments with Thalassia hemprichii at Barang Lompo revealed net daily areal production rates of 2.4 to 4.4 g AFDW m^{-2} day^{-1}, averaging 3.5 ± 0.6 g AFDW m-2 day^{-1} (Table 3.6), which is equivalent to 1.6 g C m^{-2} day^{-1}. The relative growth rate was 0.039 ± 0.010 g g^{-1} AFDW day^{-1}. Shoot density ranged from 1632 to 1952 shoots m^{-2} in these plots. The average growth rate of the leaves was 1.57 ± 0.21 cm per shoot day^{-1}.

Plastochrone interval measurements of leaves of Thalassia hemprichii at Barang Lompo revealed an average plastochrone interval 10.1 ± 1.6 days (n = 8). Net daily primary production estimates based on this method ranged from 1.6 to 4.8 g AFDW m^{-2}, with an average value of 3.1 ± 1.3 g AFDW m^{-2} (Table 3.7) which is equivalent to 1.5 g C m^{-2} day^{-1}. The relative growth rate of Thalassia hemprichii, as measured with this method, was 0.027 ± 0.005 g g^{-1} AFDW day^{-1}.

Rhizome tagging experiments revealed an average horizontal apical rhizome growth rate of 0.10 ± 0.02 cm $apex^{-1}$ day^{-1} (Table 3.8). Average density of rhizome apices was 254 ± 99 m^{-2} (n = 8). Average net daily production of rhizomes was 223 ± 137 mg AFDW m^{-2} day^{-1} (n = 14), which is equivalent to 0.1 g C m^{-2} day^{-1}. Rhizome production, as calculated from the plastochrone interval of shoots (limited data) reached an average value of 573 ± 238 mg AFDW m^{-2} day^{-1} (n = 2) which is equivalent to 0.3 g C m^{-2} day^{-1}. The average plastochrone interval of shoots for Thalassia hemprichii was 55 days at this location (n = 2).

Total net production of Thalassia hemprichii as measured with the different tagging and plastochrone interval techniques (calculated by adding below-ground production data to the above-ground production data) ranged from 3.2 to 4.3 g AFDW m^{-2} day^{-1}, equivalent to 1.7-2.2 g C m^{-2} day^{-1}.

Table 3.5
Average daily net primary production of leaves of the seagrass Enhalus acoroides at Barang Lompo (reef site) and Gusung Tallang (coastal area), with details on shoot growth (cm per shoot day^{-1}), relative growth rate (g g^{-1} AFDW day^{-1}), areal production (g AFDW m^{-2} day^{-1}), as measured with the leaf marking method (n = number of experimental plots). Locations: BL = Barang Lompo; GT = Gusung Tallang.

Loc.	shoot growth (cm per shoot day^{-1})	relative growth rate (g g^{-1} AFDW day^{-1})	areal production (g AFDW m^{-2} day^{-1})
BL (n=8)	1.6 ± 0.5	0.012 ± 0.003	0.31 ± 0.07
GT (n=8)	3.1 ± 0.8	0.019 ± 0.005	0.67 ± 0.12

Table 3.6
Average daily net primary production of leaves of the seagrass Thalassia hemprichii at Barang Lompo, with details on shoot growth (cm per shoot day^{-1}), relative growth rate (g g^{-1} AFDW day^{-1}), and areal production (g AFDW m^{-2} day^{-1}), as measured with the leaf marking method.

plots	shoot growth (cm per shoot day^{-1})	relative growth rate (g g^{-1} AFDW day^{-1})	areal production (g AFDW m^{-2} day^{-1})
n=9	1.57 ± 0.21	0.039 ± 0.010	3.46 ± 0.60

Table 3.7
Daily net primary production of leaves of Thalassia hemprichii at Barang Lompo with details on plastochrone interval (d), relative growth rate (g g^{-1} AFDW day^{-1}) and areal production (g AFDW m^{-2} day^{-1}), as measured with the plastochrone interval technique.

plots	plastochrone interval (days)	relative growth rate (g g^{-1} AFDW day^{-1})	areal production (g AFDW m^{-2} day^{-1})
n = 8	10.1 ± 1.6	0.027 ± 0.005	3.60 ± 1.64

Table 3.8
Daily net production of rhizomes of Thalassia hemprichii with details on daily horizontal growth per apex (cm apex^{-1} day^{-1}) and daily areal rhizome production (mg AFDW m^{-2} day^{-1}), as measured with the rhizome tagging technique.

plots	average growth rate (cm apex^{-1} day^{-1})	areal rhizome production (mg AFDW m^{-2} day^{-1})
n = 14	0.10 ± 0.02	223.5 ± 137.1

Primary production of tropical seagrasses: a comparison of species

Leaf marking experiments in beds of Thalassia hemprichii and Enhalus acoroides at Barang Lompo revealed considerable differences between the two species. Enhalus acoroides has a high average weight increase of shoots of 11.2 ± 2.5 mg AFDW per shoot day^{-1} but grows in relatively low shoot densities (18-28 sht m^{-2}), resulting in a relatively low average net production of 0.26 ± 0.06 g AFDW m^{-2} day^{-1}. The average daily weight increase of shoots of Thalassia hemprichii was relatively low (3.6 ± 0.5 mg AFDW per shoot day^{-1}) but this species grows in dense vegetations with high shoot densities (1632-3400 shoots m^{-2}), resulting in a relatively high net leaf production of 3.5 ± 0.6 g AFDW m^{-2} day^{-1}. Both species are considered climax species of stable environments (den Hartog, 1970).

Cymodocea rotundata Ehrenb. et Hempr. ex Aschers., a pioneering species (den Hartog, 1970), had an average above-ground daily net production of 2.6 ± 1.9 g AFDW m^{-2} day^{-1} (2 plots) in meadows at Langkai (leaf marking technique). Relative growth rates (0.030 and 0.043 g g^{-1} AFDW day^{-1}) were within the range of those found for Thalassia hemprichii at Barang Lompo. Below-ground horizontal apical rhizome growth rates were found to be significantly higher ($p < 0.05$) for pioneering species such as Cymodocea rotundata (0.71 ± 0.13 cm apex^{-1} day^{-1}; 2 plots) and Halodule uninervis (Forssk.) Aschers. (0.84 ± 0.02 cm apex^{-1} day^{-1}; 2 plots) than for constant species such as Thalassia hemprichii (0.10 ± 0.02 cm apex^{-1} day^{-1}). The term 'constant species' is used here for species that are considered to be permanently present in the climax vegetation. Rhizome growth of Enhalus acoroides was not measured. Some preliminary experiments with Halophila ovalis (R.Br.) Hook. f., also considered a pioneering species, at a depth of 11 m at Langkai island indicated a plastochrone interval of shoots of 4.4 days, with an average daily production of 2.36 mg AFDW per rhizome apex day^{-1} (total plant production).

DISCUSSION

Comparison of habitats

The biomass of epiphytes and phytoplankton was significantly higher ($p < 0.05$) at coastal areas (notably at Gusung Tallang which is located near the Tallo Estuary) than at reef sites. Macro-algae showed occasional blooming at Gusung Tallang (additional observations, 1991/92) but their effect on community production values was not assessed. These data do, however, indicate that the relative contribution to the total community production by phototrophic components other than seagrass may be considerably (up to 7 times) larger in coastal seagrass communities than in seagrass beds on offshore reef flats. The contribution of epiphytic algae to the total above-ground production of seagrass beds may be considerable and has been variously reported as 2-9% (Brouns and Heijs, 1986), 18% (Penhale, 1977), 25-33% (Jones, 1968), 35-44% (Heijs, 1985), 27-50% (Mazzella and Alberte, 1986), and 48-56% (Morgan and Kitting, 1984). Heffernan and Gibson (1983) indicated that the contribution of various photosynthetic components in seagrass beds at three stations in Florida may vary considerably between stations and from season to season. They suggested that the variation in epiphytic productivity may be a result of the incrustation of various epifauna. Jensen and Gibson (1986) suggested that the relative contributions by the different components of the photosynthetic community are affected by nutrient availability. Nutrient enrichment (such as occurs in coastal areas by terrigenous runoff and river inputs) may induce a shift in production from benthic plants to phytoplankton (Jensen and Gibson, 1986). Sand-Jensen and Borum (1991) formulated a similar relation between nutrient loading and the interaction among phytoplankton, periphyton and macrophytes in temperate waters and estuaries.

The bell jar measurements revealed gross production rates of 0.9 to 4.4 g C m^{-2} day^{-1} which are comparable to the range of values (1.2 to 4.7 g C m^{-2} day^{-1}) reported by Lindeboom and Sandee (1989) for seagrass beds in the Flores Sea (Indonesia). Daily net productions of integrated seagrass communities in the study area were all very small and even slightly negative on several occasions. Lindeboom and Sandee (1989) also reported a relatively low net production of 60 to 1060 mg C m^{-2} day^{-1}, but they did not find negative values. Assumed daily respiration values ranged from 1.4 to 5.1 g C m^{-2} day^{-1}. Lindeboom and Sandee (1989) reported respiration values between 0.9 and 3.9 g C m^{-2} day^{-1} for seagrass beds in the Flores Sea. Both our results and those obtained by Lindeboom and Sandee (1989) support the view that tropical seagrass beds are to a large extent energetically self-sustaining (Nienhuis et al., 1989). The major part of the gross primary production is used within the seagrass system for several consumption purposes (respiration, mineralisation). No significant differences ($p > 0.05$) in community production characteristics were found between seagrass beds in coastal areas and those at reef sites. Gross primary production by unvegetated sediments varied between 0.3 and 0.7 g C m^{-2} day^{-1}. In the bell jars containing seagrasses, the sediment will also show some production, but the contribution of benthic microalgae can only be significant at low seagrass biomasses (Lindeboom and Sandee, 1989). Daehnick et al. (1992) reported an annual production of 339 g C m^{-2} y^{-1} (which is equivalent to an average daily production of 0.93 g C m^{-2} day^{-1}) by sand microflora in relatively sparse beds of Halodule wrightii Aschers. measured by ^{14}C incorporation measurements. Since this figure is based on extrapolation of data obtained by relatively short incubations with low rates, this ^{14}C-based production is more likely to represent gross than net production (Kemp et al., 1990).

All bell jar measurements were carried out under comparable tidal circumstances, and as such do not allow interpretations of the effect of tides (neap versus spring tide) on production rates. Tidal waterlevel fluctuations may affect the amount of light received by the submerged seagrass leaves and as such their production, notably in shallow turbid waters. This effect may change during the year along with a shift in the hours of high and low water over the diurnal cycle. Exposure of extensive parts of seagrass beds to air and sunlight when fully emerged at spring low tides during daytime (e.g. Barang Lompo) is likely to have a considerable effect on production and growth rates of the seagrasses.

Leaf marking experiments with Enhalus acoroides at Gusung Tallang and Barang Lompo indicated that the relative growth rate of leaves does not differ significantly between a coastal environment and a reef environment. In another study, data on plant morphology, concentrations of chemical constituents in plant tissue, concentrations of phytoplankton and suspended particulate material, and the occurrence of algal blooms indicated a higher nutrient availability at coastal localities in the study area (Erftemeijer, in press). Without further experimental evidence, however, it would be unacceptable to conclude that increased nutrient availability does not affect growth rates of this species. Short (1987) demonstrated a significant relationship between nitrogen availability and eelgrass (Zostera marina L.) growth in mesocosm experiments.

The present study was carried out in the dry period (April-August 1990) and might, as such, not be representative for the whole year. Recent monthly leaf marking experiments at Barang Lompo and Gusung Tallang, as part of another (monitoring) study of seasonal dynamics in seagrass beds (Erftemeijer and Herman, submitted) indicated considerable seasonal dynamics in leaf production, with highest leaf production rates in the dry season.

Comparison of methods and species

Bell jar measurements revealed slightly negative net production values for integrated seagrass communities in 7 out of 12 occasions. We have noticed a considerable formation of air bubbles inside the bell jars during incubation on several occasions, notably around midday. This might be explained by the high oxygen concentration of the surrounding water at this time of the day (Fig. 3.3). With seawater temperature fluctuating between 27 and 32 °C and salinity ranging from 34 to 38 ‰S, oxygen solubility is roughly between 6.0 and 6.5 mg l^{-1}. At hours of maximum insolation, the oxygen concentration in the water column above the reef flat (open system) usually reaches values of 8 to 9 mg O_2 l^{-1} which is equivalent to 170-190 % saturation. Under these circumstances, incubations under enclosures might underestimate actual oxygen fluxes considerably, since the electrodes will not measure the oxygen that escapes in the form of gas bubbles. Analysis of these bubbles by gas chromatography revealed that they mainly consist of a mixture of gasses comparable to atmospheric air but with a slightly increased oxygen concentration (Lindeboom, pers. comm., 1993). Although incubation periods were kept at minimum length during these hours, formation of air bubbles could not be totally prevented. Besides, air bubbles were sometimes also formed in the surrounding environment outside the bell jars.

The seagrasses growing on shallow intertidal reef flats might have been subjected to photoinhibition, as suggested by Lindeboom and Sandee (1989) for seagrasses above a depth of 2 m. Under such a situation, production is lower at maximum light intensity than at lower light levels. Some of our data indeed indicate a slight decrease in production at maximum light levels, but the quantity of our observations is too limited to demonstrate significant differences ($p > 0.05$). The assumption that respiration during the day is the same as during the night might prove incorrect. Indications were found that respiration shows a clearly dynamic pattern during a 24-hour period, with peak respiration during the early evening and lowest respiration measured in the early morning before sunrise. Similar results were obtained in seagrass meadows in Mauritania (L. De Jong and P. Hofman, pers. comm., 1993). Respiration rates in shallow marine sediments depend for a major part on diffusion of oxygen from the overlying water (Hofman et al., 1991). The rate of this diffusion is likely to depend on the concentration of oxygen in the water column. Since the concentration of dissolved oxygen in the overlying water is considerably higher during midday and afternoon than during the night and early morning (see Fig. 3.3), respiration rates in the sediment are likely to vary accordingly. This might also explain the lower net production values by the community found at the same level of irradiance at different times of the day.

Leaf marking and plastochrone interval techniques gave comparable results for the net above-ground production of Thalassia hemprichii (1.6 and 1.5 g C m^{-2} day^{-1} respectively). Our data on shoot production, areal production and plastochrone interval for Thalassia hemprichii are well comparable with values reported by Brouns (1985b), who marked all shoots in small experimental plots in monospecific meadows of Thalassia hemprichii in Papua New Guinea. In our study, only 20 shoots were marked per experimental plot. To test if these shoots had been selected randomly, the average biomass of marked shoots in three experimental plots was compared with the average biomass of all shoots in these plots. Average biomass of marked shoots was significantly ($p < 0.05$) larger (79.5 ± 13.9 mg AFDW $shoot^{-1}$) than the average biomass of all shoots (39.3 ± 15.4 mg AFDW $shoot^{-1}$). Apparently, the marking of shoots was not done randomly but with unconscious preference for larger shoots. As a result, actual average production rates might have been overestimated, assuming that larger shoots have a higher production. Our results do, however, not differ markedly from those obtained by Brouns (1985b), which indicates that the effect on production figures of the apparent size-preference during marking is probably insignificant.

Below-ground production in Thalassia hemprichii meadows was relatively low (0.1-0.3 g C m^{-2} day^{-1}) in comparison to the above-ground production. Rhizome growth contributed 15 to 17 % to the total (leaf+rhizome) production. Brouns (1985b) found average net rhizome production values of 0.60, 0.14 and 0.14 g AFDW m^{-2} day^{-1} in three monospecific stands of Thalassia hemprichii in Papua New Guinea, which are equivalent to 0.28, 0.06 and 0.06 g C m^{-2} day^{-1}.

When comparing marking methods (leaf marking, rhizome tagging), plastochrone interval techniques (leaves, rhizomes), and bell jar incubations, each method appears to have its advantages and disadvantages (see also Kemp et al., 1990):

Bell jar methods provide a wide range of information on the gross and net production and respiration of the entire community, unvegetated sediments and seagrasses only, but involve a number of questionable assumptions and a wide range of practical and technical problems and they totally rely on a considerable amount of sensitive electronic equipment. The technical and practical complexity of this technique does not make it very suitable for large-scale application in tropical (developing) countries. In addition, the technique is unsuitable for tall seagrass species such as Enhalus acoroides, which may have leaves of up to 2 m long. The method, on the other hand, is very suitable for narrow-leaved species, such as Syringodium isoetifolium (Aschers.) Dandy or Halodule pinifolia (Miki) den Hartog, of which production is difficult to measure with the other techniques (see below).

Marking methods and plastochrone interval techniques are very simple and do not require any sophisticated equipment. This makes them very suitable for large-scale measurement programmes. The results obtained by these methods are very consistent and have a small standard error (SD) of the mean (especially with the leaf marking method). However, they only provide information on net production of leaves or rhizomes. Leaf marking methods and plastochrone interval techniques as applied in this study (hole-punching) inflict damage to the leaves and as such may have a deleterious effect on overall plant growth, although this effect is often considered insignificant (Dennison, 1990). Leaf marking methods are easy to apply in studies of seagrass species with broad leaves and a simple growth strategy from a basal meristem. They are, however, not suitable for narrow-leaved species (such as Syringodium isoetifolium and Halodule pinifolia) and require special alterations of the technique for species with deviating growth forms such as Thalassodendron ciliatum (Forssk.) den Hartog (Brouns, 1985c), Amphibolis antarctica (Labill.) Sonder et Aschers. (Walker, 1985) or Halophila species (Wahbeh, 1984; Brouns, 1987a; Kenworthy et al., 1989). In addition, grazing herbivores, exposure during spring low tides and heavy bioturbation may sometimes frustrate leaf marking experiments. These problems are largest with plastochrone interval methods because these require longer incubation periods than other marking techniques. Rhizome tagging techniques are impossible without disturbing the substrate, which might affect the growth of roots and rhizomes.

The principle of the plastochrone interval method may also be useful in studying the total net plant production in smaller species (i.e. Halophila ovalis) of which the rhizome-root systems do not penetrate too deep in the sediment. The plastochrone interval technique was not suitable for production measurements of leaves of Enhalus acoroides. The terminal portions of the full-grown leaves of this species usually disintegrate by decay or by physical damage, with hardly any intact full-grown leaves present throughout the meadows. As a result of this, application of the plastochrone interval technique to this species may lead to a considerable underestimation of the net leaf production in comparison with the leaf marking technique.

By adding data on above-ground and below-ground production, derived from leaf marking and rhizome tagging methods or from different plastochrone interval techniques, total net production of the seagrasses can be estimated. The methods that were applied for the measurement of below-ground production, however, did not include growth by roots. There are few data in the literature on the growth of seagrass roots. The relative contribution of below-ground plant parts to the overall plant production, however, seems small for constant species like Thalassia hemprichii or Enhalus acoroides. Even though the below-ground biomass of constant species can be very high, the production of their rhizome-root systems appears to be insignificant in comparison to the high growth rates of their leaves. Our data provide a preliminary indication that below-ground production can be considerable for pioneering species such as Halophila ovalis, Cymodocea rotundata, or Halodule uninervis, and might even equal that of above-ground plant parts.

It is evident that there are substantial differences between the methods in terms of what they can and cannot provide. Whereas gas-exchange methods (e.g. O_2-evolution) can only provide an integrated measurement of total community primary production, biomass accumulation techniques (plastochrone interval, leaf marking, rhizome marking) provide the simplest, least-costly measurements of seagrass production (Kemp et al., 1990). Selection of the most suitable method, which meets the objectives of a particular study, is essential. Investigators should carefully weigh the relative strengths and weaknesses of the methods for use in their own research programme. For large-scale monitoring studies of seasonal and year-to-year dynamics in particular, we recommend the use of leaf marking and rhizome marking methods. The applicability of bell jar techniques in tropical marine environments is limited due to the increased risk of frequent electronical and technical problems. If sufficient man-power is available, the parallel use of more than one method is strongly recommended.

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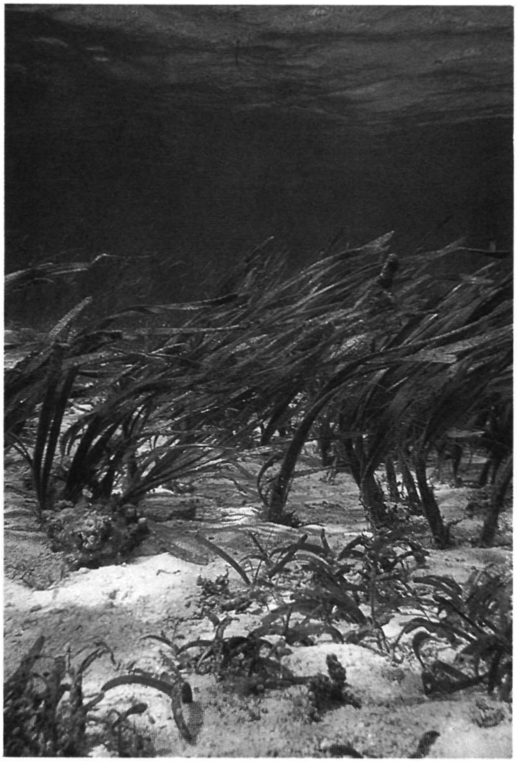
CHAPTER FOUR

SEDIMENT-NUTRIENT INTERACTIONS IN TROPICAL SEAGRASS BEDS: A COMPARISON BETWEEN A TERRIGENOUS AND A CARBONATE SEDIMENTARY ENVIRONMENT IN SOUTH SULAWESI (INDONESIA)



Thalassia hemprichii (short) and *Enhalus acoroides* (tall), the two dominant seagrass species in the study area.

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ABSTRACT

The relationship between porewater nutrient concentrations and sediment characteristics was studied in seagrass beds on two sediment types in South Sulawesi, Indonesia. Porewater nutrient concentration gradients with sediment depth and ratios between ammonium and phosphate porewater concentrations in a terrigenous muddy sedimentary environment could well be explained by modelling based on stoichiometric decomposition of organic material and molecular diffusion. Measured porewater phosphate concentrations at a carbonate sedimentary environment, however, were significantly higher (10 µM excess) in the upper few cm of the sediment than would be expected based on stoichiometry. This apparent phosphate enrichment is attributed to rapid regeneration of both N and P in the rhizosphere and subsequent rapid removal of ammonium by nitrification. Sampling artefacts and additional geochemical sources of dissolved P (reduction of hydrous ferric oxides, calcium carbonate dissolution) could be excluded as the cause of the enrichment. The capacity of carbonate sediments to adsorb phosphate was directly related to their grain-size composition. The coarse-grained carbonate sediment in the area maintained relatively high porewater phosphate concentrations as a result of its limited adsorption capacity, in contrast with extremely low porewater phosphate concentrations reported from fine-grained carbonate sediments in the Caribbean, where strong evidence for P-limitation of seagrass growth was found.

INTRODUCTION

Light and nutrients are among the primary requirements to seagrass growth, and their availability may limit seagrass productivity (Dennison et al., 1987; Short, 1987). Seagrasses are capable of taking up nutrients with both their leaves and root systems (Short and McRoy, 1984; Hemminga et al., 1991; Pérez-Lloréns et al., 1993). In tropical regions, dissolved nutrient concentrations in seawater are typically low (often below detectable limits), whereas porewater concentrations in the sediment are usually much higher. Nutrient uptake from the water column by tropical seagrass leaves is therefore considered to be insignificant relative to root uptake of nutrients from the sediments (Short, 1987), although this may depend on the ratio between leaf surface area and active sorptive root surface (Smith et al., 1979; Caffrey and Kemp, 1992).

Phosphorus in the sediment may be found in porewater (soluble reactive phosphorus, or PO_4), adsorbed to particles, bound to calcium (e.a. apatite), chemically adsorbed by ironoxyhydroxides and aluminiumoxides, in distinct iron compounds and contained in organics (Balzer, 1986). Nitrogen in the sediment may be found in porewater (NH_4, NO_3, NO_2 and dissolved organic nitrogen), adsorbed to particles (exchangeable NH_4), fixed in lattices of clay minerals, and contained in organics (Müller, 1977; Entsch et al., 1983; D'Elia and Wiebe, 1990). The availability of dissolved nutrients in sediment porewaters is a net result of the sources (regeneration) and sinks (removal) of these nutrients. Decomposition of organic material is the relevant process in which large quantities of nitrogen and phosphorus are regenerated. Sorption, precipitation, diffusion and uptake by organisms are the main removal processes. Sorption of both ammonium and phosphate occurs in all types of sediment, but the extent of adsorption and the balance between adsorption and desorption may vary considerably among sediments of different mineralogical composition. Calcium carbonate sediments are known to have a high capacity to adsorb phosphate (De Kanel and Morse, 1978; Kitano et al., 1978). Consequently, the concentration of dissolved inorganic phosphorus (here referred to as phosphate) in carbonate porewaters is often very low. Porewater nutrient availability may further be influenced by the redox potential, concentration of certain chemical constituents, pH, salinity and temperature of the porewater, and the rate of regeneration and biological consumption. Bioturbation, physical instability of the substrate and excretion of chemical substances by the seagrass roots may considerably affect balances in porewater chemistry in seagrass beds (Moriarty and Boon, 1989).

Short (1987) stressed the importance of geochemical characteristics of the sediment in the study of nutrient limitation of seagrass growth. He suggested an essential difference in nutrient cycling between terrigenous and carbonate sediments, owing to the phosphorus dynamics which are very different due to the binding (sorption) of phosphate ions to the carbonate matrix. On the basis of a literature review, Short (1987) concluded that seagrasses growing in terrigenous environments are often more typically nitrogen limited, whereas seagrasses occurring in tropical carbonate environments generally experience phosphorus limitation. Most work on this subject in the tropics has been carried out in the Caribbean, whereas data on nutrient concentrations and resources from the Indo-Pacific region are scarce.

The aim of this study is to test Short's (1987) hypothesis on phosphorus and nitrogen limitation in seagrass beds on two different sediment types in the Indo-Pacific region, and to evaluate the importance of the relationship between sediment grain-size and adsorptive capacity in the geochemical processes in controlling the availability of nutrients to seagrass growth.

MATERIALS AND METHODS

Study area

The study was conducted in the Spermonde Archipelago and adjacent coastal areas in South Sulawesi, Indonesia, during 1991. Two contrasting field sites were selected for this study: the shallow-water reef flat of Barang Lompo (5°03'S, 119°20'E), a coral island situated about 14 km from the coast, and Gusung Tallang (5°04'S, 119°27'E), an intertidal mudflat along the coast, located approximately 0.5 km north of the mouth of the Tallo River (Fig. 2.1). Both sites are characterized by extensive well-developed seagrass meadows dominated by Enhalus acoroides at Gusung Tallang, and by a mixture of Thalassia hemprichii and Enhalus acoroides at Barang Lompo. The reef flat at Barang Lompo is covered by at least 30 cm of carbonate sand, mainly derived from erosion material of the reef. This sand was bioturbated with some relief (about 10 cm) resulting from numerous shrimp mounds. At Gusung Tallang, the substrate is dominated by sandy terrigenous mud, which is protected from waves and currents by a long and narrow sandbar in the north, running perpendicular to the coast. These two sites are considered representative of reef-associated and coastal seagrass beds in the area (Erftemeijer, in press).

Methods

Monthly sediment samples were collected randomly in the seagrass beds at both sites during a 12-month period (February 1991-January 1992) with small hand corers (d = 6 cm) to a depth of 10 cm. To study porewater nutrient behaviour in deeper layers, the cores in September 1991 (Gusung Tallang) and October 1991 (Barang Lompo) were taken to an additional depth of 30 cm. Each core was separated into 2 cm sections. The coinciding sections of 12 successive cores were combined to reduce spatial heterogeneity and treated as one sample. These samples were transported on ice in sealed plastic bags for further treatment in the laboratory. Plant parts, large living benthic animals and large stones were removed prior to further treatment. Within at most 4 h after sampling, porewaters were extracted by filtration of the samples over Schleicher & Schüll membrane filters (0.45 µm) under low pressure (1-3 bar) using nitrogen gas, following a slightly modified technique of Kelderman (1985). Porewater samples were subsequently filtered over 0.2 µm filters and phosphate and ammonium were analysed spectrophotometrically on the same day according to methods described by Strickland and Parsons (1972). The remainder of these sediment samples was dried for 48 h at 80°C and stored for analysis of pH, which was determined in a KCl suspension. Grain-size distribution of the different depth fractions of the sandy sediment from Barang Lompo was determined by dry-sieving analysis, from which the median grain-size for each representative depth was calculated.

Separate bulk samples of the top 10 cm sediment layer were taken to determine porosity (calculated from water contents = weight loss after drying for 48 h at 80 °C), $CaCO_3$ content (by gasvolumetry according to Hulsemann (1966)), total average grain-size distribution (by dry-sieving of sandy sediments (Barang Lompo) or by using a Malvern Particle Sizer 3600 Ec for muddy sediments (Gusung Tallang)), total carbon, organic carbon, total nitrogen, total phosphorus, exchangeable phosphorus and exchangeable ammonium. Organic carbon was analysed by applying an adapted methodology (Nieuwenhuize et al., 1993): 10 replicate sediment splits (20 mg) were treated with several drops of 25% HCl (2 times 20 µl) in small silver (Ag) containers to remove all inorganic C (from $CaCO_3$), and then heated (60-100°C) to vaporize remaining HCl. Organic carbon (after treatment with HCl drops), total carbon (without such previous treatment) and total nitrogen (no treatment) were determined on a Carlo-Erba NA 1500 CN-analyser. Total phosphorus and exchangeable phosphorus (i.e. the fraction of P in the sediment that is most readily exchangeable with the dissolved P in the porewater) were analysed using a standard colorimetric determination of phosphate following digestion by strong oxidizing (hydrochloric acid + nitric acid + perchloric acid) and weak oxidizing reagents (lactic acid + acetic acid + ammonia) respectively (Allen, 1974).

Table 4.1
Overview of sediment data (± SD) from the two study sites (upper 10 cm of the sediment).

	n	Barang Lompo	Gusung Tallang
particle-size (mm) (% dry):	10		
< 0.075		4.7 ± 1.3	48.2 ± 3.6
0.075-0.105		2.5 ± 0.7	25.5 ± 3.1
0.105-0.15		11.5 ± 1.5	13.9 ± 1.1
0.15-0.21		14.9 ± 1.6	7.4 ± 2.1
0.21-0.3		13.1 ± 0.8	2.5 ± 1.6
0.3-0.42		8.7 ± 0.6	1.7 ± 0.9
0.42-0.60		8.4 ± 0.7	0.8 ± 0.4
0.60-1.0		13.1 ± 0.7	0
> 1.0		23.1 ± 4.6	0
$CaCO_3$ (%)	10	98 ± 5	10.8 ± 3.7
Total C (%)	10	12.05 ± 0.06	6.72 ± 0.06
Organic C (%)	10	0.30 ± 0.05	1.89 ± 0.06
water contents (% wet)	4	27 ± 2	47 ± 2
porosity	4	0.53 ± 0.04	0.72 ± 0.02
KCl-pH	20	8.96 ± 0.08	7.87 ± 0.08
Total P (ppm)	10	275 ± 17	1009 ± 22
Exchangeable P (ppm)	10	87.8 ± 3.9	26.6 ± 5.2
Total N (ppm)	10	40 ± 10	80 ± 30
Exchangeable N (ppm)	10	5.54 ± 0.47	11.65 ± 0.52

Exchangeable ammonium was determined by a 1-step potassium chloride extraction, shaking dried sediment and 2M KCl for 2 h at sediment:KCl proportions of 1:20 (w:v) followed by a standard spectrophotometric ammonium determination (Patriquin, 1972; Rosenfeld, 1979). Total P and Fe were determined in a selection of dried sediment sections (i.e. 0-2, 2-4, 4-6, 6-8 and 15-18 cm for total P, and 0-0.5, 0.5-1, 1-2, 4-6, 8-10 cm for Fe). Fe was determined by atomic spectroscopy following a microwave dissolution, according to Nieuwenhuize et al. (1991).

The relationship between grain-size and adsorption capacity of phosphate was studied using carbonate sediments collected from the field site (Barang Lompo seagrass beds). Dried samples from the sediment were sieved in a sieving machine to yield seperate sediment fractions, of which five different particle size categories were used in the experiment (>1 mm, 0.6-1 mm, 0.3-0.42 mm, 0.15-0.21 mm and <0.075 mm). Adsorbed phosphate was removed from the sediment by multiple seawater extraction in a rotation machine until no further PO_4 was retrieved in the supernatant. This procedure was also effective in equilibrating the sediments with the experimental solution. Duplicate flasks (glass) containing 12 g of sediment for each particle size category were soaked in 400 ml of artificial seawater enriched at a concentration of 72 µM phosphate, and thoroughly mixed in a rotation machine. Blank flasks (containing phosphate-enriched seawater without sediment) were used to determine flask wall adsorption. After 3 h, the seawater was filtered and analysed for change in phosphate concentration. Sorption time was chosen to achieve optimal adsorption and to minimize effects of sorption on vessel walls and disaggregation of the sediment material.

RESULTS

Description of the sediment

Basic data on the composition of the sediment from the two sites are summarized in Table 4.1. The sediment at the reef site (Barang Lompo) has a very high calcium carbonate content (nearly 100%), is very poor in organic material (organic C: 0.29 ± 0.05%) and has a relatively coarse grain-size distribution (medium to coarse sand). Macroscopic identification (Milliman, 1974) of the coarser fraction of the sediment (> 1 mm) with the use of a binocular microscope revealed a dominance of scleractinian corals, foraminifera and fragmented molluscs with smaller amounts of calcified green algae (e.g. Halimeda), serpunculid polychaetes and fragments of crustaceans, echinoderms and fish bones. The sediment at the coastal site (Gusung Tallang) is composed of terrigenous sandy mud. It has a $CaCO_3$ content of 10.8 ± 3.7% (mainly shell fragments) and contains some more organic material (organic C: 1.89 ± 0.05 %). A major proportion of this sediment consists of weathered alimunosilicates and volcanoclastics, dominated by augite and some basic hornblende. The sediment from the Enhalus acoroides beds at

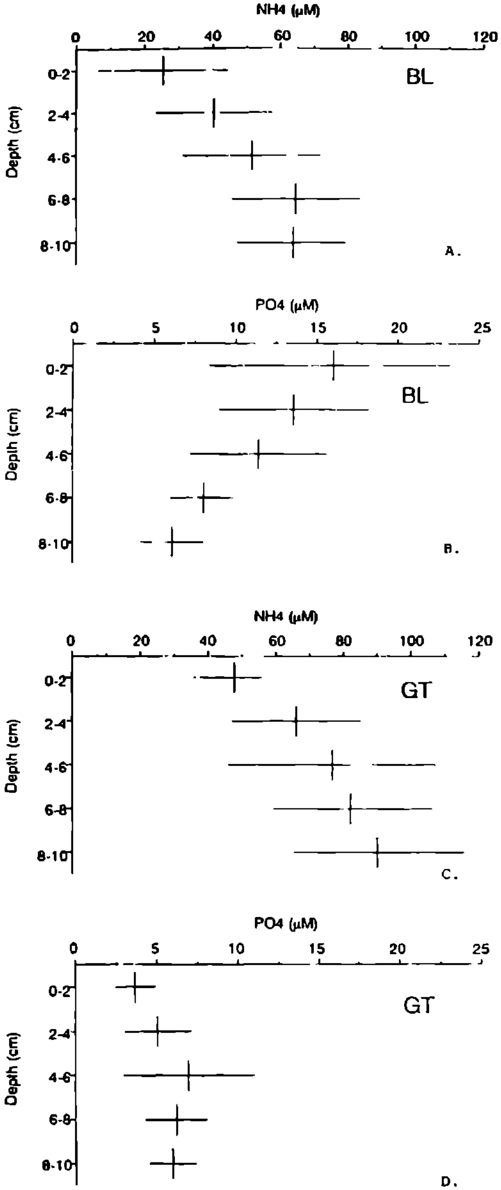

Figure 4.1 Average and standard deviation of porewater nutrient concentrations in the upper 10 cm of the sediment of 12 monthly duplicate sampling series from Barang Lompo (BL, carbonate) and Gusung Tallang (GT, terrigenous) seagrass beds: (a) ammonium, BL; (b) phosphate, BL; (c) ammonium, GT; (d) phosphate, GT. (n = 24)

Gusung Tallang exhibits little variation with respect to grain-size characteristics and consists predominantly of fine sand-sized (63-129 µm) and silt- and clay-sized (< 63 µm) particles. Coarser sand-sized (> 0.2 mm) particles constituted less than 5% of the dry weight. The sediment from the mixed seagrass beds at Barang Lompo consists of a largely heterogenous mixture of coarse, medium and fine sand, with 58-72% of the particles larger than 0.2 mm.

Porosity (n = 4) of the carbonate sand (0.53 ± 0.04) was found to be smaller than that of the terrigenous sandy mud (0.72 ± 0.02), with sediment water contents of 27 ± 2% at Barang Lompo and 47 ± 2% at Gusung Tallang. Sediment pH (KCl extraction) was 8.96 ± 0.08 in the carbonate sand and 7.87 ± 0.08 in the terrigenous mud and did not show significant variation with depth (both localities). Additional punch-in pH measurements (electrode) made in fresh cores from the mud at Gusung Tallang in 1992 revealed pH values between 7.4 (40 cm depth) and 7.8 (surficial sediment) with a gradual decrease of pH with depth.

Total P (n = 4) in the terrigenous mud (1009 ± 22 ppm) is nearly four times higher than in the carbonate sand (275 ± 17 ppm). In contrast, exchangeable phosphate (n = 10), is almost four times higher in the carbonate sediment (87.8 ± 3.9 ppm) than in the coastal mud (26.6 ± 5.2 ppm). Total N (n = 10) in the coastal mud (80 ± 30 ppm) is twice as high as in the reef sediment (40 ± 10 ppm). KCl-extractable ammonium (n = 4) is about two times lower in the carbonate sediment (5.54 ± 0.47 ppm) than in the coastal mud (11.65 ± 0.52 ppm).

Porewater phosphate and ammonium

Data from 12 months of repetitive sampling and analysis of porewater nutrients (upper 10 cm) from Barang Lompo and Gusung Tallang were averaged and plotted (Fig. 4.1). Although there was a relatively large variation in porewater nutrient concentrations, the measurements revealed significant trends with depth that were consistent throughout the year. Porewater ammonium concentrations increased with sediment depth in both types of sediment. Analyses of samples to depths of 30 cm (September 1991: Gusung Tallang; October 1991: Barang Lompo) showed that ammonium concentrations increased with sediment depth until reaching a constant level at about 8 cm (carbonate sand) or 12 cm depth (coastal mud) after which the concentration remained roughly unchanged with further depth at both sites (Fig. 4.2). The median ammonium concentrations were 60.1 µM for the carbonate site and 106.8 µM for the terrigenous site. Porewater phosphate concentrations at the coastal site Gusung Tallang showed a gradual increase with sediment depth in the upper 6 cm, reached a relatively constant level (of approximately 6 µM) between 6 and 10 cm depth (Fig. 4.1 and 4.2), but increased again at greater depth (Fig. 4.2). The overall impression is that of an increasing trend with depth, which is consistent throughout the year (Fig. 4.1). In the carbonate sediment porewaters collected from Barang Lompo, phosphate showed maximum

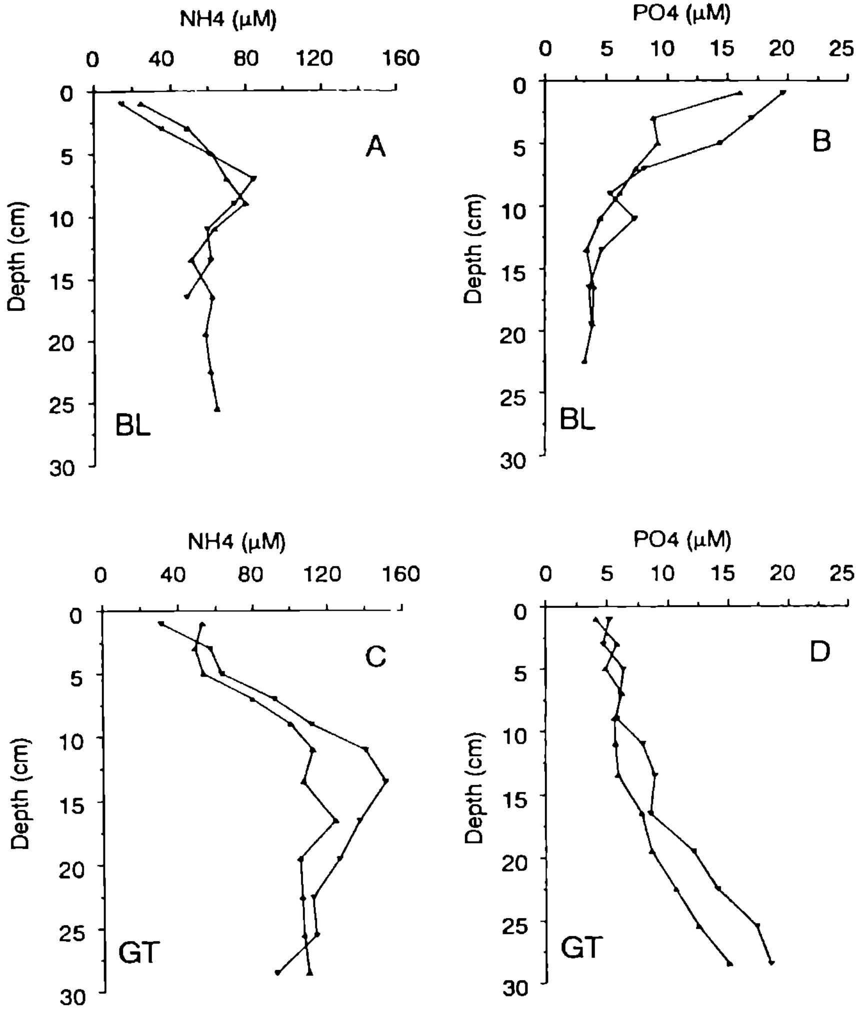

Figure 4.2 Porewater nutrient (NH_4 and PO_4) concentrations in duplicate sampling series from carbonate (Barang Lompo) and terrigenous (Gusung Tallang) sediments of seagrass beds in South Sulawesi: (a) ammonium, Barang Lompo; (b) phosphate, Barang Lompo; (c) ammonium, Gusung Tallang; (d) phosphate, Gusung Tallang.

concentrations of 15 to 20 µM PO_4 at a depth of about 2 cm, and then decreased to relatively low levels (< 5 µM) in deeper layers of the sediment (> 10 cm). Again, this trend was found to be consistent throughout the year (Fig. 4.1) and persisted at greater depths to 30 cm (Fig. 4.2). Median porewater phosphate concentrations were comparable at the two sites, 7.8 and 6.1 µM at Gusung Tallang and Barang Lompo, respectively. The samples to a depth of 30 cm are considered to provide porewater nutrient depth profiles representative of the two localities and are used as such for further discussion in this paper.

Table 4.2
Primary elemental constituents (in % of dry weight) and atomic N:P ratios of seagrass plant tissue from the study sites. (n = 6)

Location seagrass species	Plant part	%N	%P	N:P atomic ratio
1. Barang Lompo				
Enhalus	leaf blades	0.96 ± 0.02	0.11 ± 0.07	19:1
acoroides	sheaths	0.86 ± 0.14	0.19 ± 0.03	10:1
	rhizomes	0.40 ± 0.08	0.09 ± 0.02	10:1
	roots	0.36 ± 0.09	0.05 ± 0.01	16:1
Thalassia	leaf blades	1.90 ± 0.42	0.14 ± 0.02	30:1
hemprichii	sheaths	0.83 ± 0.39	0.12 ± 0.01	15:1
	rhizomes	0.48 ± 0.04	0.07 ± 0.01	15:1
	roots	0.98 ± 0.27	0.06 ± 0.01	36:1
2. Gusung Tallang				
Enhalus	leaf blades+			
acoroides	sheaths	2.71 ± 0.14	0.34 ± 0.09	18:1
	rhizomes	0.88 ± 0.20	0.10 ± 0.02	19:1
	roots	1.31 ± 0.73	0.13 ± 0.03	22:1

From the porewater nutrient depth profiles (Fig. 4.2) we calculated the rate of diffusion of nutrients across the sediment-water interface. The simple diffusive flux (ionic and molecular diffusion) of a nutrient across the sediment-water interface is equal to the product of the porosity, the apparent diffusion coefficient of this nutrient and the concentration gradient between porewater and water column (Li and Gregory, 1974; McCaffrey et al., 1980). Apparent diffusion coefficients in deionized water (D_o), taken from Li and Gregory (1974) for a water temperature of 25°C, were corrected for tortuosity using porosity data from Table 1 and porosity-tortuosity relationships reported by Sweerts et al. (1991). The apparent dissusion coefficients for the flux across the sediment-water interface

(D_s) thus calculated for NH_4 are 376.2 cm^2 y^{-1} for Barang Lompo and 397.6 cm^2 y^{-1}) for Gusung Tallang. For PO_4 these are 152.0 cm^2 y^{-1} for Barang Lompo and 160.6 cm^2 y^{-1}) for Gusung Tallang. Water column concentrations roughly averaged 1 μM for PO_4 and NH_4 at both sites (Erftemeijer, in press). Vertical diffusion between sediment and water column was calculated from Fick's first law of diffusion: J_s = -øD_s(dc/dx), where J_s is the flux in μmol cm^{-2} y^{-1}, ø the porosity of the sediment, D_s the sediment molecular diffusion coefficient for the diffusing substance in cm^2 y^{-1}, dc/dx the initial concentration gradient in the sediment in μmol cm^{-3}, and x the sedimentary depth (in cm). As such, we estimated a NH_4 flux of 3.79 μmol cm^{-2} y^{-1} and 11.16 μmol cm^{-2} y^{-1} for Barang Lompo and Gusung Tallang respectively, and a PO_4 flux of 1.37 μmol cm^{-2} y^{-1} and 0.46 μmol cm^{-2} y^{-1} for Barang Lompo and Gusung Tallang respectively.

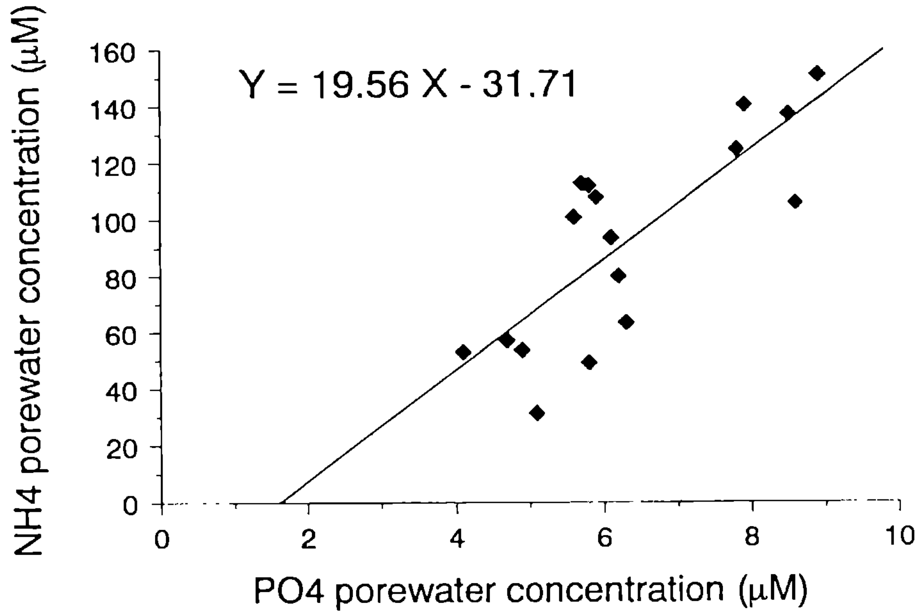

Figure 4.3 Stoichiometric modelling of porewater nutrient concentrations from Gusung Tallang by linear regression of ammonium and phosphate concentrations from coinciding sediment sections (according to $[NH_4] = 19.56 * [PO_4] - 31.71$) ($r^2$ = 0.62)

The N:P ratio of the (decomposing) organic material can be used to predict the resulting ammonia and phosphate concentrations in interstitial waters of nearshore marine sediments and vice versa (Sholkovitz, 1973; Martens et al., 1978). By plotting corresponding porewater NH_4 and PO_4 enrichments from the mud at Gusung Tallang, a linear stoichiometric relationship was found from which a N:P ratio of 19.6 was derived (Fig. 4.3). This estimated N:P ratio of decomposing organic matter corresponds well with an average N:P ratio of 19.7 ± 2.1 found in living seagrass material (leaf blades + sheaths + rhizomes + roots) from the same study site (Table 4.2). The average N:P ratio in living seagrass material at Barang Lompo was 19 (± 9). Hence it is fair to assume that the expected porewater phosphate concentration at Barang Lompo can be calculated using observed NH_4 concentrations and a N:P ratio of 19. No corrections were made to this N:P ratio to account for differences in diffusion rates and adsorption affinities between ammonium and phosphate. When calculated and observed porewater phosphate profiles are compared, a remarkable deviation occurs in the upper sediment layer (Fig. 4.4).

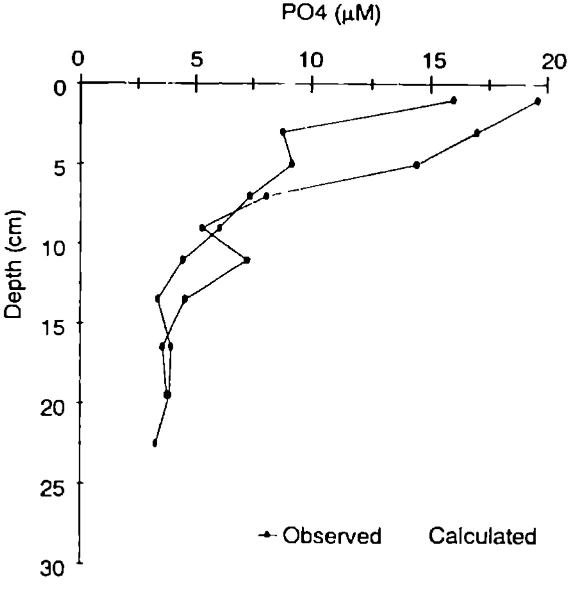

Figure 4.4 Relationship between observed porewater phosphate concentrations in the carbonate sediments from seagrass beds at Barang Lompo and the expected porewater phosphate profile calculated from the observed ammonium profile using an N:P ratio of 19.

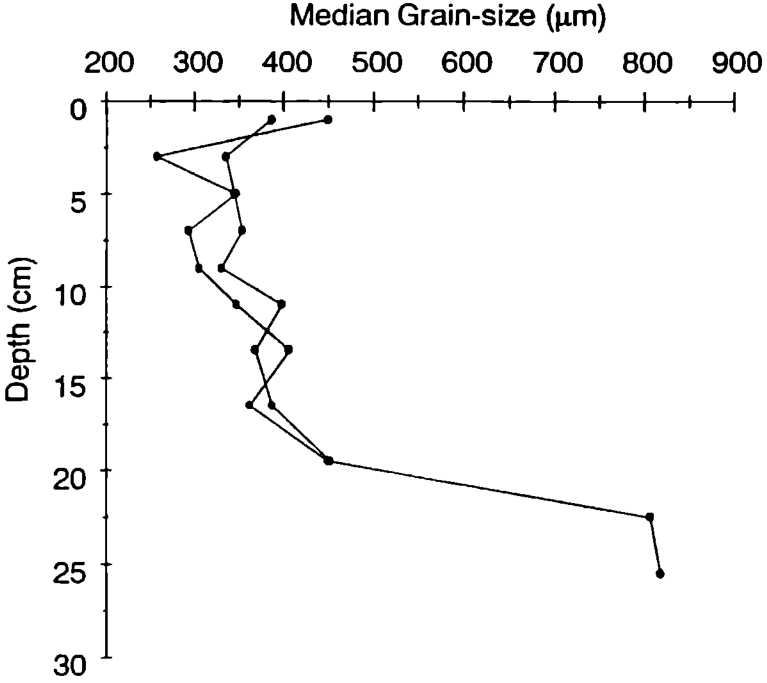

Figure 4.5 Relationship between median sediment grain-size (µm) and sediment depth of carbonate sediments in seagrass beds at Barang Lompo (n = 2).

Adsorption capacity

The carbonate sediments at Barang Lompo had a relatively coarse particle-size composition (Table 4.1). Analysis of median particle size along a sediment depth gradient in samples from Barang Lompo indicated an even coarser sediment composition in deeper layers (Fig. 4.5). To study the relationship between particle-size and adsorption capacity, we carried out an adsorption experiment (see methods). This experiment indicated that fine-grained sediment fractions adsorbed more phosphate than coarser fractions (Fig. 4.6). This might explain why fine-grained carbonate sediments often maintain lower dissolved phosphate concentrations in the porewater than coarse-grained sediments.

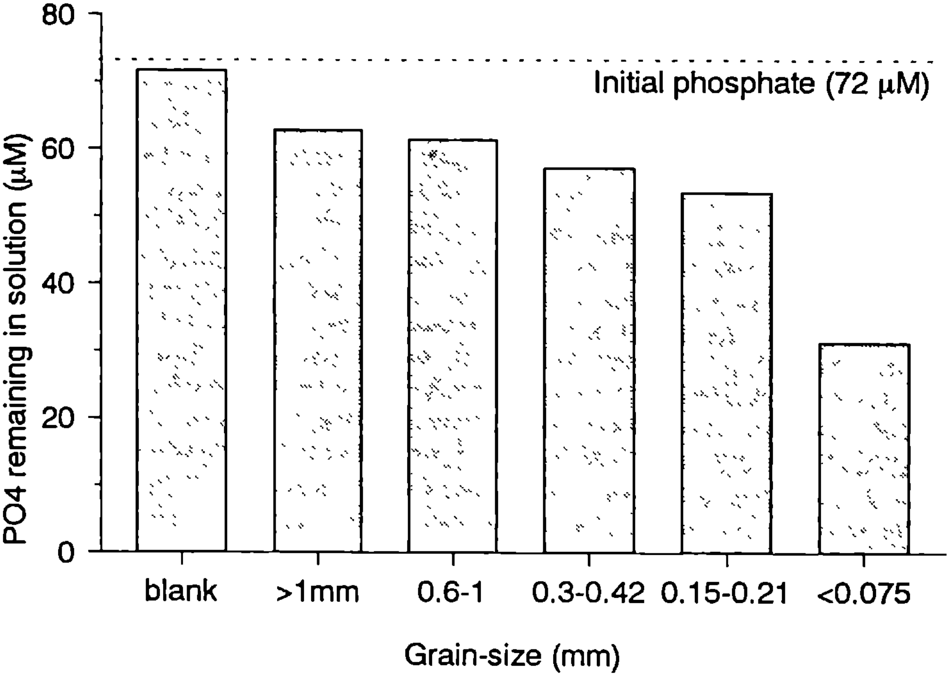

Figure 4.6 Phosphate adsorption by calcium carbonate sediment (Barang Lompo) of different grain-size categories after 3 h incubation in an initial PO_4 solution of 72 μM (experimental procedure: see text). (maximum SD < 1 μM)

DISCUSSION

The two sedimentary environments investigated in this study showed considerable differences with respect to sediment composition and nutrient availability. Total P and N were significantly higher in the coastal muddy sediment in comparison to the carbonate sand from Barang Lompo, due to an increased terrestrial input of organic matter by the Tallo River. Exchangeable P, however, was considerably higher in the carbonate sediment which is attributed to the stronger adsorption affinity of the carbonate matrix to phosphate in comparison to the alimunosilicate and volcanoclastic sediment particles. Exchangeable N was significantly lower in the carbonate sand than in the terrigenous mud. Rosenfeld (1979) also found that less ammonium was extractable from carbonate than from terrigenous sediments of comparable dissolved ammonium concentrations and that the adsorbed ammonium in carbonate sediments was predominantly associated with organic matter.

Porewater nutrient concentration gradients with sediment depth and ratios between ammonium and phosphate porewater concentrations in the terrigenous mud at Gusung Tallang could well be explained for by stoichiometric modelling based on decomposition of organic material, and molecular diffusion. Theoretically expected porewater phosphate concentrations at Barang Lompo, calculated from the observed porewater ammonium profiles and the average N:P ratio in plant material at this site, were significantly lower than the PO_4 concentrations that were actually measured in the upper layers of the sediment. In these calculations, no corrections were made for differences in diffusion rates and adsorption affinities between ammonium and phosphate. In carbonate sediments, however, these two processes generally outweigh each other for these two nutrients (e.g. Middelburg, 1991).

This discrepancy between observed and calculated phosphate concentrations requires some detailed discussion on additional sources and sinks. Additional dissolved P may arise from dissolution of calcium carbonate or from reduction of hydrous ferric oxides (Van Cappellen and Berner, 1988).

In the upper millimetres of the sediment, carbon dioxide and acids are produced as a result of aerobic decomposition of organic material and oxidation of reduced sulphur compounds (Froelich et al., 1979). These acids may cause dissolution of calcium carbonate at the sediment-water interface. Consequently, the phosphate adsorbed on and incorporated in these carbonate particles will also dissolve and as such result in a net enrichment of porewater phosphate. On the basis of 275 ppm P in $CaCO_3$ (Table 4.1) we estimate that the observed porewater enrichment of 10 µM phosphate corresponds with a porewater enrichment of about 11 mM Ca. This estimate is based on stoichiometric dissolution or desorption and equal diffusivities of Ca^{2+} and PO_4^{3-}. The estimated porewater enrichment of Ca (11 mM) due to $CaCO_3$ dissolution is almost five-fold the maximum enrichments due to $CaCO_3$

dissolution that have been reported in literature (e.g. Walter and Burton, 1990). Accordingly, it seems that the maximum enrichment of phosphate which can be attributed to $CaCO_3$ dissolution is in the order of 2 µM PO_4 only.

The reduction of hydrous ferric oxides constitutes another potential source of dissolved phosphate in porewaters of sediments overlain by aerated bottom waters (Berner, 1974; Van Cappellen and Berner, 1988). These hydrous ferric oxides have a very high specific surface area and are known to strongly adsorp phosphate from seawater under oxic conditions (Stumm and Leckie, 1970; Berner, 1973). Under reducing conditions in the sediment, ferric-oxide reduction releases both soluble ferrous ions and phosphate into solution (Van Cappellen and Berner, 1988). This release of reactive P is likely to mimic closely the changes in redox conditions (Van Cappellen and Berner, 1988). Although oxygenated micro-zones may occur around seagrass roots and the holes of burrowing organisms, the sediments in the study area are considered to be largely anoxic, with the exception of the upper few millimetres or perhaps 1 or 2 centimetres at the sediment-water interface. Sediments in the area smelled of hydrogen sulphide, indicating reducing anoxic conditions. Anoxia within centimetres of the sediment surface in tropical carbonate sediments was also reported by Hines and Lyons (1982), Tribble (1988) and Walter and Burton (1990).

Table 4.3
Total iron (n = 3) and total phosphorus (n = 2) contents (± SD) in carbonate sediment samples from Barang Lompo.

depth (cm)	P total (ppm)		depth (cm)	Fe ($mg\ g^{-1}$)	
0-2	262.1	± 26.2	0-0.5	0.29	± 0.06
2-4	266.5	± 26.2	0.5-1	0.33	± 0.10
4-6	209.7	± 34.9	1-2	0.35	± 0.10
6-8	209.7	± 26.2	4-6	0.38	± 0.08
15-18	244.7	± 8.7	8-10	0.38	± 0.12

Some Fe enrichment might be received from terrigenous inputs, given the fact that the carbonate study site is located at approximately 14 km from the mainland of Sulawesi, which is primarily volcanic in origin (De Klerk, 1982). We analysed the concentration of total iron and total phosphorus in a number of samples from different depths in the sediment. The results (Table 4.3) indicate a slight enrichment of total P (209.7-266.5 ppm) in the upper layer of the sediment and no significant enrichment of Fe (0.29-0.38 $mg\ g^{-1}$). Assuming a quantitative transfer of this slight excess solid-phase P (52.4 ppm) to solution, and no diffusive losses, a maximum dissolved porewater phosphate enrichment of about 4 µM can be estimated using data on porosity (0.53) and density (2.7 for $CaCO_3$) (Table 4.1 and 4.3). The effects of this process should be more pronounced at the coastal locality Gusung Tallang, but at this site, however, no phosphate enrichment of upper sediment layers was detected.

Since geochemical processes can be excluded as the cause of the phosphate enrichment with respect to ammonium in the upper few cm at Barang Lompo, the problem still persists. Alternative explanations or responsible processes are more likely of biological or microbiological nature. McRoy and Barsdate (1970) experimentally demonstrated that eelgrass Zostera marina can take up phosphate with both its leaves and roots. A portion of labelled (^{32}P) phosphate absorbed by the roots was subsequently released into the water surrounding the leaves. The isotope data indicated that the reverse process also occurred, but the intensity of the former was much greater. Pérez-Lloréns et al. (1993) reported on ^{32}P root-uptake experiments with Zostera noltii. They found that up to 70% in the light and 33% in the dark of the total amount of P taken up by the root-rhizomes was translocated to the leaves (mainly to young leaves). Patriquin (1972) suggested that the sediments may temporarily buffer the supply of phosphate for Thalassia testudinum by storing seawater phosphate, taken up by the leaves of Thalassia testudinum during periods of high supply, into the sediments by root excretion. It is, however, unlikely that such a pathway would contribute significantly to the phosphate pool in the sediments under investigation, because it would have to occur against the ambient concentration gradient.

There is, however, considerable difference in the root layer between Enhalus acoroides and Thalassia hemprichii. The thick rhizomes of Enhalus acoroides bear several coarse, soft, unbranched roots without root hairs, while Thalassia hemprichii bears one or more roots at each node with numerous root hairs (Kuo and McComb, 1989). At Barang Lompo, the rhizosphere is dominated by Thalassia hemprichii (which occurs in high shoot densities of 2400 ± 640 sht m^{-2} average (Erftemeijer, in press)), from which the rhizomes, roots and root hairs form an entangled network in the upper 6 to 8 cm of the sediment, with roots or rhizomes rarely penetrating deeper into the sediment. At Gusung Tallang, the rhizosphere is entirely dominated by Enhalus acoroides (which occurs at relatively low shoot densities of 39 ± 6 sht m^{-2} average), of which the rhizomes and long unbranched roots penetrate much deeper into the sediment (at least up to 25 cm in the soft mud at this site) and do not form such a compact network in the upper sediment layer.

When the majority of organic matter (detritus) in the seagrass bed at Barang Lompo is trapped in the upper layer of the sediment by the entangled rhizosphere of Thalassia hemprichii and decomposed there, this would lead to a considerable enrichment of both N and P in the upper few cm of the sediment in comparison to deeper layers. Several investigators have reported concentrations of soluble reactive phosphorus to be higher in the root zone of seagrass beds than in deeper zones or in nearby unvegetated areas (McRoy et al., 1972; Montgomery et al. 1979; Pulich, 1982; Boon, 1986) as observed at Barang Lompo. We did not, however, observe a peak in porewater ammonium concentrations at this site which might imply significant ammonium sinks in the upper few cm of the sediment. Assimilatory uptake by seagrass roots is likely to be an important sink for both ammonium and phosphate in the rhizospere, but would also result in lower phosphate levels. Diffusion of ammonium is significantly faster than that of phosphate, but might be compensated for by sediment adsorption, which is stronger for phosphate. Nitrification might account for a considerable removal of ammonium in the oxic upper layer of the sediment and in oxic zones around seagrass roots (Iizumi et al., 1980; Moriarty and Boon, 1989). Preliminary measurements of nitrate+nitrite concentrations in porewaters (data not shown) from Barang Lompo did not indicate significantly higher levels in the upper few cms and were usually below 5 µM. Recently, Capone et al. (1992) reported significantly lower porewater NH_4 concentrations in coarse-grained carbonate sediments in comparison to fine-grained and muddy carbonate sediments of three reefs in the central area of the Great Barrier Reef. They suggested that shallow carbonate sands are very active sites of bacterial nitrogen transformations with turn-over times of less than 1 day. Accordingly, the apparent phosphate enrichment (based on stoichiometry) observed at Barang Lompo is related to rapid generation of both phosphate and ammonium and subsequently rapid removal of ammonium by nitrification. Ammonium removal rates may be high due to tight coupling of microbial nitrogen transformations, known to be characteristic of the rhizosphere of aquatic plants (Reddy et al., 1989).

Leaving the high phosphate concentrations in the upper few centimetres of the sediment out of discussion, the porewater phosphate concentrations below 5 cm depth are still relatively high in comparison to similar carbonate-rich sediments in other geographical areas. Several studies in carbonate sediments in the tropical Caribbean and Florida have reported extremely low phosphate concentrations, usually below 2 µM (Patriquin, 1972; Short et al., 1985; Short et al., 1990; Fourqurean et al., 1992a), which are generally attributed to adsorption of phosphate onto the carbonate matrix. These findings have resulted in the hypothesis that seagrass growth on carbonate sediments is phosphorus limited. Most of these studies were, however, carried out in predominantly fine-grained sediments (fine sand, muddy carbonate or even carbonate silt). Reports on carbonate porewater phosphate concentrations that are higher than 2 µM often appear to arise from coarse-grained sediments (Gaudette and Lyons, 1980; Boon, 1986; Alongi, 1989; McGlathery et al., 1992). This indicates that the observed differences might represent different sorptive capacities of the carbonate sediments between the locations, such as was recently suggested by McGlathery et al. (1992). The sorption capacity of carbonates is directly related to the number of surface sites available, hence the reactive surface area (Comans and Middelburg, 1987; Stumm, 1992). The reactive surface area, in turn, depends on the grain size of the substrate, the smaller the grain-size, the larger the surface area (Morse and MacKenzie, 1990). Direct experimental evidence for grain-size dependent sorption on calcite has been presented by McBride (1979, 1980) and in this study (Fig. 4.6).

However, part of the differences reported in the literature might also be accounted for by differences in methodologies applied to collect porewaters, with sippers or comparable in situ suction devices generally yielding lower concentrations than core squeezing or centrifugation techniques (Patriquin, 1972; Rosenfeld, 1979; Gaudette and Lyons, 1980; Entsch et al, 1983; Short et al., 1985; Morse et al., 1987; Alongi, 1989; Short et al., 1990; Powell et al., 1991; Fourqurean et al., 1992a; McGlathery et al., 1992). Porewater sampling artefacts of squeezing methods have been evaluated recently by De Lange et al. (1992). Oxidation during sample treatment may result in the formation of ferric hydroxides which strongly adsorb phosphate ions. As such, oxidation artefacts - if they do occur - will result in lower, rather than higher porewater phosphate concentrations. The squeezing of root fluids when squeezing with very high pressures (150-350 bar) may result in some increase of dissolved nutrient concentrations in the porewater (Bolliger et al., 1992), but is not likely to occur when using a very low pressure (such as 1-3 bar used in our study). Moreover, it does not seem logical why this would be specifically the case for phosphorus (high PO_4 enrichment) and not for nitrogen (no NH_4 enrichment) and would only occur in carbonate sediments. It is therefore concluded, that the increased phosphate concentration in the upper sediment at Barang Lompo is not a sampling artefact caused by the squeezing technique applied.

The relatively high availability of phosphate in porewaters from coarse-grained carbonate sediments in seagrass beds in the study area is in contrast to the general assumption that seagrass growth on carbonate sediment is phosphorus-limited (Short, 1987). Nutrient enrichment experiments in seagrass beds on carbonate sediments by Short et al. (1985), Short et al. (1989) and Fourqurean et al. (1992a) have found clear evidence of phosphorus limitation, but they were all working in fine-grained sedimentary environments (carbonate mud and silt). In their study on nutrient limitation of the rhizophytic macroalga Penicillus capitatus, associated with subtropical seagrass meadows on carbonate sediments in Bermuda, McGlathery et al. (1992) found evidence of nitrogen-limitation. They observed that P. capitatus may acquire nutrients directly from sediment sources via rhizoid holdfasts. They suggested that the limited adsorptive capacity of the relatively coarse carbonate sediment in the area resulted in relatively high porewater phosphorus concentrations.

Apparently not all carbonate-rich tropical sediments induce phosphorus limitation of benthic macrophytes. This study has shown that the grain-size of the sediment is one of the primary factors determining the availability of phosphate in a tropical carbonate sedimentary environment. In addition, it is speculated that the quality of the root zone (depth penetration, root density, presence or absence of root hairs) and the rate of microbial nitrogen transformation processes may be of considerable importance in regulating the availability of nutrients in a seagrass meadow.

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CHAPTER FIVE

THE LIMITED EFFECT OF IN SITU PHOSPHORUS AND NITROGEN ADDITIONS TO SEAGRASS BEDS ON CARBONATE AND TERRIGENOUS SEDIMENTS IN SOUTH SULAWESI, INDONESIA

The author, studying the seagrass vegetation at Kudingareng Lompo in response to experimental fertilization.

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THE LIMITED EFFECT OF IN SITU PHOSPHORUS AND NITROGEN ADDITIONS TO SEAGRASS BEDS ON CARBONATE AND TERRIGENOUS SEDIMENTS IN SOUTH SULAWESI, INDONESIA

ABSTRACT

Seagrass response to in situ sediment nutrient enrichment with slow-release fertilizers was studied (4 to 5 months after fertilization) in three tropical seagrass beds in South Sulawesi, Indonesia. N addition and P addition had no significant effects on seagrass biomass, shoot density, and leaf production in mixed seagrass beds in a terrigenous sandy bay and a carbonate sedimentary reef flat environment, simultaneously fertilized in 1990. An additional experiment using a slightly adapted methodology (1991) at another carbonate site, characterized by a more homogeneously vegetated, and largely monospecific seagrass meadow of Thalassia hemprichii, again showed no significant response of seagrass growth, biomass, and shoot density to fertilization. C and N contents of plant tissue, however, had increased significantly ($p < 0.05$) to 12-25% above the controls in response to N-addition at this locality. The relatively high ambient porewater nutrient concentrations (about 10 µM PO_4, about 100 µM NH_4) and rather low C:N:P ratios (565:18:1) in seagrass tissue, indicate that nutrient supply meets seagrass demand and provide an explanation for the lack of response to the manipulations. The relatively high porewater phosphate concentrations in carbonate sediments are attributed to the relatively coarse particle-size distribution of these sediments in the study area, which limits their adsorption capacity and prevents P-limitation of seagrass growth, which is generally considered to be characteristic of tropical carbonate-rich environments.

INTRODUCTION

Primary production in macrophyte-dominated marine ecosystems is often limited by nutrient availability, particularly when irradiance and temperature are not critical (Smith, 1984; Howarth, 1988). Nitrogen (N) and phosphorus (P) are considered to be the primary limiting nutrients to seagrass growth (Hillman et al., 1989), and their availability appears to be primarily dependent on biogeochemical processes (Short, 1987).

Several authors have addressed the issue of nutrient limitation in seagrass beds and have come to contradictionary results (e.g. Raymont, 1947; Orth, 1977; Bulthuis & Woelkerling, 1981; Harlin & Thorne-Miller, 1981; Roberts et al., 1984; Pulich, 1985; Short et al., 1985; Dennison et al., 1987; Powell et al., 1989; Short et al., 1990; Perez et al., 1991; Tomasko & Lapointe, 1991; Bulthuis et al., 1992; Burkholder et al., 1992; Fourqurean et al., 1992b). In his well-known review on the matter, Short (1987) has tried to draw some general conclusions from the various reports. He suggested that seagrasses growing in northern temperate climates (and) in habitats with terrigenous sediments typically experience nitrogen-limitation, while having ample phosphorus, whereas seagrasses occurring in tropical environments (and) on carbonate sediments appear to experience phosphorus limitation due to sorption of phosphate to the sediments.

Phosphorus limitation of seagrass growth on carbonate sediments has recently been supported by additional evidence from in situ sediment fertilization experiments (Powell et al., 1989; Short et al., 1990) and by evidence from tissue nitrogen and phosphorus composition (Fourqurean et al., 1992b). Perez et al. (1991) and Murray et al. (1992a), however, found evidence for P-limited growth of seagrasses on terrigenous sediments in the temperate region indicating that controversy still exists.

In contrast to the situation in the tropical Caribbean, where much work on this subject has been carried out, there are no data on the effects of in situ fertilization on seagrass growth in the Indo-Pacific region. The aims of the present study are: (1) to provide data on the effects of in situ fertilization on seagrass growth in South Sulawesi, (2) to test the nutrient limitation hypothesis (Short, 1987) in an area in the tropical Indo-Pacific, and (3) to compare the response of seagrasses on different substrates (carbonate and terrigenous) to N and P fertilization. By following exactly the methodology as used by Short et al. (1990, and pers. comm., 1990) who found clear evidence for P-limitation of seagrass growth on carbonate sediments in the Caribbean, it was possible to compare the results between the two geographically different areas and sedimentary distinct characteristics.

MATERIALS AND METHODS

Experimental stations

The study was carried out from August-December 1990 and from July-December 1991 at three stations in the Spermonde Archipelago in South Sulawesi, Indonesia (118°55'-119°30'E, 4°30'-5°40'S; Fig. 2.1). Two stations, Kudingareng Lompo and Palanro, were selected for in situ fertilization experiments in seagrass beds in 1990. In 1991, an additional fertilization experiment was carried out in a seagrass bed at Barang Lompo (Fig. 2.1). Two of these localities (Kudingareng Lompo and Barang Lompo) are coral reef islands, both located at approximately 14 km from the coast and considered to be beyond significant terrigenous influences and inputs. The other locality (Palanro) is a shallow bay dominated by terrigenous sand, and is considered to be under moderate influence of terrigenous inputs (Erftemeijer, in press). The two localities, simultaneously fertilized in 1990 (Kudingareng Lompo and Palanro), had extensive shallow-water mixed-species seagrass meadows, dominated by Thalassia hemprichii (Ehrenb.) Aschers. and Cymodocea rotundata Ehrenb. & Hempr. ex Aschers. at Kudingareng Lompo, and by Thalassia hemprichii, Syringodium isoetifolium (Aschers.) Dandy and Cymodocea serrulata (R.Brown) Aschers. & Magnus at Palanro. Other species that occurred, included Halophila ovalis (R.Brown) Hooker f. and Enhalus acoroides (L.f.) Royle, but their contribution to the standing crop of the experimental plots was relatively insignificant. The third locality (Barang Lompo) has extensive mixed stands of Thalassia hemprichii and Enhalus acoroides, but the experiments were carried out in largely monospecific vegetations of Thalassia hemprichii. Some basic characteristics of the three sites are summarized in Table 5.1. Average ambient nutrient concentrations (PO_4 and NH_4) in the water column at these sites were generally below 2 µM (Erftemeijer, in press).

Table 5.1
Characteristics of the three experimental stations in South Sulawesi, Indonesia, during the experimental period in which the effects of in situ sediment fertilization was monitored in seagrass beds (1990 and 1991). Data are averages for these sites derived from Erftemeijer (in press).

	Palanro	Kudingareng Lompo	Barang Lompo
type of locality	coastal site	coral island	coral island
sediment type	terrigenous	carbonate	carbonate
$CaCO_3$ (%)	7.5	100	98
particle size range (%):			
< 63 µm	26	14	11
> 312 µm	8	42	46
cm +/- chart datum (ELWS)	- 60	+ 20	+ 30
secchi depth (m)	8.8	21.4	18.2
salinity (‰S)	33	35	34

Enrichment

The experimental set-up followed exactly that of Short et al. (1990). Triplicate plots in dense, relatively homogeneously vegetated areas in the seagrass bed were enriched with various additions of inorganic slow-release N (ureaform 38%) and P (osmocote 41%) fertilizer (release time: six months). The fertilizer was placed in the sediment at a depth of 10 to 15 cm below plugs of seagrass, which were temporarily removed with a core sampler (0.00283 m^2). The size of the experimental plots was 0.25 m^2 at Palanro and Kudingareng Lompo and 0.125 m^2 at Barang Lompo. For the control plots, treatments 0N and 0P, no fertilizer was placed below the seagrass plugs. Four levels of P treatment (0P, 50P, 200P, and 2000P) and three levels of N treatment (0N, 10N, 100N) were established in a complete factorial design. These levels were established in order to elevate porewater nutrients above ambient concentrations (ambient [NH_4^+] = 100 µM and ambient [PO_4^{3-}] = 10 µM; Erftemeijer, in press); [example (Barang Lompo): A plot was considered as a box of 25 x 25 x 25 cm, thus having a total volume of 15.625 l. The sediment porosity at Barang Lompo was 0.55, thus a box contained 8.6 l porewater. To yield 100 N (i.e. 100 times the ambient porewater NH_4 concentration of 100 µM), 3.2 g fertilizer (containing 38% total N, i.e. 86 mmol N) was added to the total box volume at a depth of approximately 12 cm. The addition of 86 mmol to a total porewater volume of 8.6 l, resulted in a potential concentration of 10 mM N]. It is noted that this is the treatment level; due to various removal processes (e.g. diffusion, adsorption, uptake by other organisms) the actual porewater concentrations that become available to the plants are considered to be much lower. To study actual porewater nutrient enrichment levels, two additional series of duplicate plots were enriched with maximum treatment levels (100N and 2000P) at the 1991 experimental site (Barang Lompo). Porewater concentrations in these enriched plots were compared with (ambient) porewater concentrations in two control plots after 1 month.

Data collection

Fertilizer was added to seagrass sediments in August 1990 (Kudingareng Lompo and Palanro) and July 1991 (Barang Lompo), and plant response and nutrient dynamics assessed after 4 (1990) or 5 (1991) months.

Leaf growth in the experimental plots was studied (after the 4 or 5 months incubation period) by using the plastochrone interval method (1990 experiments) according to Brouns (1985a), or using the leaf marking method (1991 experiment) according to Kirkman & Reid (1979). An average of 10 (plastochrone interval) or 20 (leaf marking) randomly selected plants were marked within each plot. Leaf growth was assessed after 6 days (leaf marking) or 12 to 15 days (plastochrone interval).

Seagrass biomass (g dry wt m^{-2}) was measured by collecting quantitative samples (0.0625 m^2) from all plots, using a 25 x 25 cm iron frame and a spade. These samples were taken after completion of the leaf growth experiments. The dry weights of marked shoots harvested for the leaf marking experiment were included in the total biomass of each plot. Shoot densities (m^{-2}) were calculated from counts of the number of plants present in the biomass samples.

Seagrass tissue C, N and P content of dried (24 h at 80 °C), powdered plant tissue was measured on a Carlo-Erba NA 1500 C-/N- Analyzer (for C and N) or by a strong oxidizing acid digestion (hydrochloric acid + nitric acid + perchloric acid) followed by a standard colorimetric phosphate determination of the digest solution (for P) (Allen, 1974). Data are presented as the average of samples from the 3 replicate treatments (± SD). Calcareous epiphytes were removed from seagrass leaves in samples from Barang Lompo, by rinsing with a solution of approximately 5% phosphoric acid, as suggested by Dawes and Kenworthy (1990) and others. This treatment did, however, result in significant increases of the P-contents of the leaf material to values far above acceptable range, and as such, data on P-contents of leaf material from this locality are not presented. Epiphytes in samples from Palanro and Kudingareng Lompo were removed by scraping without additional acidification. Samples of root material from Kudingareng Lompo contained to much carbonate sediment (difficult to remove when dry) to produce reliable results in the analysis of elemental constituents.

The effects of enrichment were statistically tested for levels of significance ($p < 0.05$) using multiple analyses of variance (MANOVA). In the MANOVA, variables were divided in two main groups of variables (biomass variables including shoot density, versus tissue nutrient content variables) which were tested separately. Production data (not collected with the same methodology at each of the three sites) were tested separately for the three localities by means of one-way analyses of variance (ANOVA). Differences in seagrass response to N and P additions between the two reef localities versus the coastal locality were tested for variables that proved significant in the overall MANOVA and ANOVA tests (i.e. C, N and P contents). This was done by a single degree of freedom comparison of the linear component of the interaction terms (P addition respectively N addition) with location.

Porewater nutrient concentrations were analysed in samples from the additionally enriched plots (maximum treatment levels only) and two control plots (no treatment). One month after fertilization, series of 6 sediment cores were collected from each plot using small hand corers ($d = 6$ cm) to a depth of 10 cm. Each core was separated into 2 cm sections. The coinciding sections of every 6 successive cores were combined to reduce spatial heterogeneity and treated as one sample. These samples were transported on ice in sealed plastic bags for further treatment in the laboratory. Plant parts, large living benthic animals and stones were removed prior to further treatment. Within 3 h after sampling, porewaters were extracted by filtration of the samples over Schleighel & Schull membrane filters (0.45 µm) under low pressure (1-3 bar) using nitrogen gas, following a slightly modified technique of Kelderman (1985). Porewater samples were subsequently filtered over 0.2 µm filters and phosphate (control plots and P-enriched plots) and ammonium (control plots and N-enriched plots) were analysed spectrophotometrically on the same day according to methods reported by Strickland & Parsons (1972). Differences in porewater concentrations between enriched and control plots were tested for significance by two-way ANOVA.

The relationship between sediment grain-size and adsorption capacity of

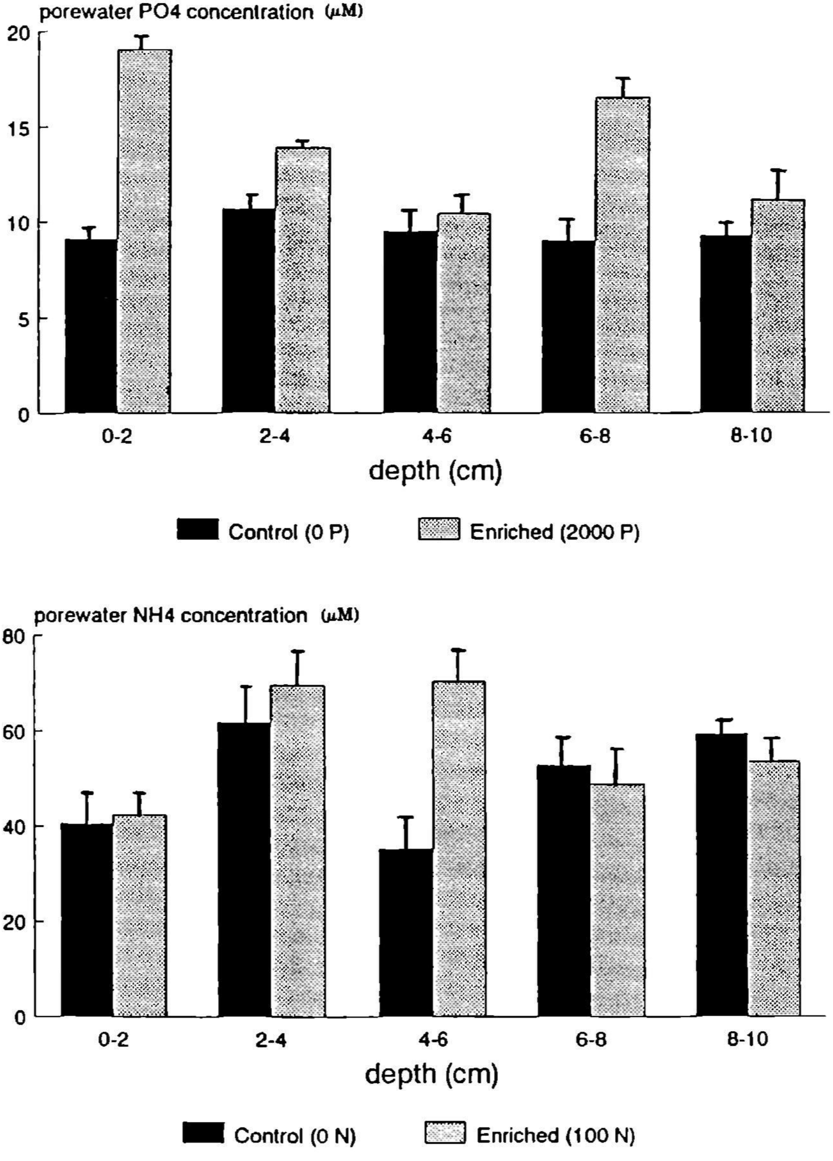

Figure 5.1 The effect of fertilization on mean (± SD) porewater nutrient concentrations in carbonate sediment at Barang Lompo (1 mo postfertilization). A: phosphate (2000 P enriched versus control), B: ammonium (100 N enriched versus control).

phosphate by $CaCO_3$ sediments was studied using carbonate sediment collected from the field (Chapter 4). Sediment samples of five different particle size categories (>1 mm, 0.6-1 mm, 0.3-0.42 mm, 0.15-0.21 mm, and <0.075 mm) were shaken with a 71.6 µM enriched phosphate seawater solution. After 3 h, the seawater was filtered and analysed for change in phosphate concentration (see Chapter 4 for detailed description of methodology).

RESULTS

Effects of enrichment on porewater nutrient concentrations

Porewater phosphate concentrations in the plots separately enriched with P (2000 P) had increased significantly ($p < 0.05$) after 1 month to an average of 1.7 times above ambient porewater levels in control plots (Fig. 5.1). Ammonium concentrations in the N-enriched plots (100 N) were significantly higher ($p < 0.05$) than in the unfertilized plots in the upper 6 cm (1 month after fertilization) but the overall increase was small. Both the effects of N and P enrichment on porewater concentrations (of PO_4 and NH_4) showed a significant interaction with sediment depth. Apparently porewaters are not equally enriched with depth, depending on the depth of application of the fertilizer.

Seagrass response

Shoot density

Shoot density (all species taken together) varied considerably among the different plots at Palanro and Kudingareng Lompo (ranging from 597 to 1579 sht m^{-2} at Kudingareng Lompo, and from 1035 to 2640 sht m^{-2} at Palanro), but no significant relationship was found between shoot density and fertilization ($p > 0.05$) (Table 5.2). It is therefore concluded that the experimental plots at these localities apparently were rather heterogeneously vegetated. The experimental plots at Barang Lompo were more homogeneously vegetated (shoot density ranging from 2219 to 3003 sht m^{-2}), but again shoot density showed no significant response to fertilization ($p > 0.05$) (Table 5.2).

Biomass

MANOVA testing of biomass data (all localities taken together) revealed practically no overall significant effects ($p > 0.05$) of N or P addition to seagrass biomass. There were no significant differences in the total seagrass biomass (in g AFDW m^{-2}) between control plots and enriched plots at Palanro and Barang Lompo (Table 5.3). Some statistically significant ($p < 0.05$) differences occurred at Kudingareng Lompo, but the differences that occurred had no significant correlation with the type of treatment. Standard deviations of means were large at this locality, probably due to the degree of patchyness of the vegetation and (in part) to

Table 5.2 Shoot densities of seagrass plants in enriched and control plots for the various treatment levels at the three experimental sites. Data are average values (± SD) of triplicate plots for each treatment level. All seagrass species are taken together in the counts.

Treatment level	SHOOT DENSITY (sht m^{-2}) Palanro	Kudingareng Lompo	Barang Lompo
Blank	1808 ± 416	1019 ± 140	2529 ± 99
50 P	1035 ± 160	1397 ± 276	2608 ± 283
200 P	1806 ± 452	1296 ± 144	3003 ± 570
2000 P	2496 ± 115	1147 ± 296	2459 ± 20
10 N	1632 ± 248	1579 ± 282	2597 ± 417
100 N	1771 ± 145	1563 ± 222	2219 ± 67
50 P/10 N	1621 ± 154	944 ± 209	2629 ± 117
50 P/100 N	1333 ± 157	768 ± 184	2411 ± 118
200 P/10 N	2315 ± 191	597 ± 88	2565 ± 345
200 P/100 N	2640 ± 504	869 ± 270	2491 ± 326
2000 P/10 N	1109 ± 172	1088 ± 327	2528 ± 73
2000 P/100 N	1812 ± 373	699 ± 197	2784 ± 151

Table 5.3 Biomass (g AFDW m^{-2}) of seagrasses in enriched and control plots for the various treatment levels at the three experimental sites. Data are average values (± SD) of total seagrass biomass (including above-ground and below-ground plant parts of all species together) of triplicate plots for each treatment level.

Treatment level	BIOMASS (g AFDW m^{-2}) Palanro	Kudingareng Lompo	Barang Lompo
Blank	766 ± 83	713 ± 70	818 ± 56
50 P	694 ± 50	1228 ± 415	767 ± 44
200 P	705 ± 161	939 ± 178	868 ± 99
2000 P	728 ± 59	933 ± 126	705 ± 36
10 N	716 ± 81	1316 ± 215	763 ± 37
100 N	794 ± 65	1124 ± 153	730 ± 43
50 P/10 N	836 ± 94	749 ± 166	764 ± 70
50 P/100 N	756 ± 114	689 ± 217	746 ± 19
200 P/10 N	787 ± 106	593 ± 28	775 ± 99
200 P/100 N	870 ± 55	637 ± 191	819 ± 77
2000 P/10 N	686 ± 55	809 ± 343	735 ± 90
2000 P/100 N	761 ± 29	999 ± 229	816 ± 56

variability in the degree to which sediment was removed from root fractions during sample treatment. Comparison of biomass of particular plant parts (leaf blades, sheaths, roots, and rhizomes) between control plots and enriched plots revealed no consistent pattern of significant differences that could be related to the type and level of treatment at any of the localities (data not shown). Standard deviations of mean values were relatively large (in the range of 10-40 % of the mean), which might have masked true differences in seagrass biomass.

Leaf growth

Marking experiments (plastochrone interval and leaf marking) revealed no significant differences in leaf productivity of the dominant seagrasses (Thalassia hemprichii and Cymodocea spp.) between control plots and enriched plots in the ANOVA ($p > 0.05$) at any of the three localities (Table 5.4). Average plastochrone interval of leaves was 10.4 ± 1.5 days at Palanro and 10.1 ± 1.9 days at Kudingareng Lompo. Average leaf growth was 5.3 ± 0.9 g AFDW m^{-2} d^{-1} at Barang Lompo.

Table 5.4 Seagrass productivity measured as plastochrone interval of leaves (= PI; at Palanro and Kudingareng Lompo; in days) or as leaf growth (by leaf marking; at Barang Lompo; in g AFDW m^{-2} d^{-1}) in enriched and control plots for the various treatment levels. Data are average values (± SD) of triplicate plots for each treatment level.

		PRODUCTIVITY	
Treatment level	Palanro PI (days)	Kudingareng Lompo PI (days)	Barang Lompo Leaf growth (g AFDW m^{-2} d^{-1})
blank	10.2 ± 1.0	13.0 ± 1.9	4.27 ± 0.50
50 P	9.3 ± 0.9	12.4 ± 1.1	5.55 ± 2.29
200 P	10.7 ± 1.2	11.0 ± 0.9	5.52 ± 1.17
2000 P	9.3 ± 0.8	11.6 ± 1.3	4.94 ± 0.69
10 N	10.7 ± 1.1	7.9 ± 0.9	4.21 ± 0.47
100 N	10.0 ± 1.0	7.6 ± 1.0	4.30 ± 1.60
50 P/10 N	12.0 ± 1.3	8.8 ± 0.9	5.84 ± 2.18
50 P/100 N	11.6 ± 1.1	11.9 ± 1.4	5.95 ± 1.04
200 P/10 N	6.9 ± 0.9	7.6 ± 0.8	5.33 ± 0.36
200 P/100 N	9.6 ± 1.0	9.1 ± 1.0	5.21 ± 1.32
2000 P/10 N	12.5 ± 1.4	10.1 ± 1.1	5.21 ± 1.39
2000 P/100 N	12.0 ± 1.2	9.3 ± 0.9	7.71 ± 0.78

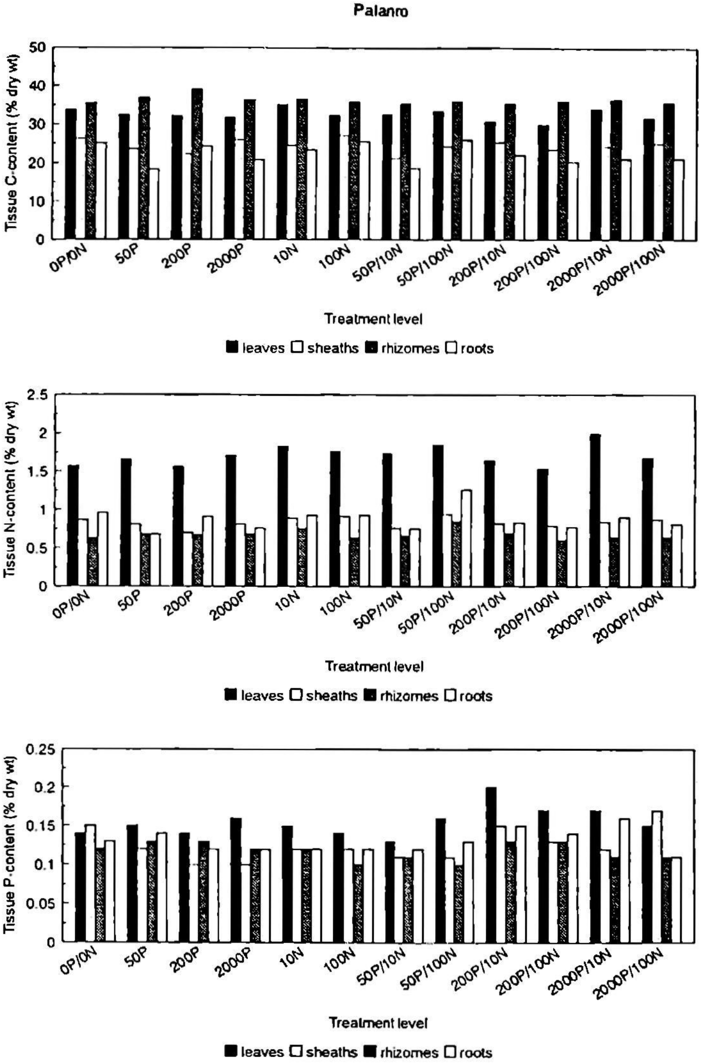

Figure 5.2 Carbon (above), nitrogen (middle) and phosphorus (below) contents of seagrass tissue from different plant parts (leaf blades, sheaths, rhizomes and roots) in enriched and control plots for the various treatment levels at Palanro. Data are average values of triplicate plots for each treatment level (SD ranged from 4 to 8 % of mean).

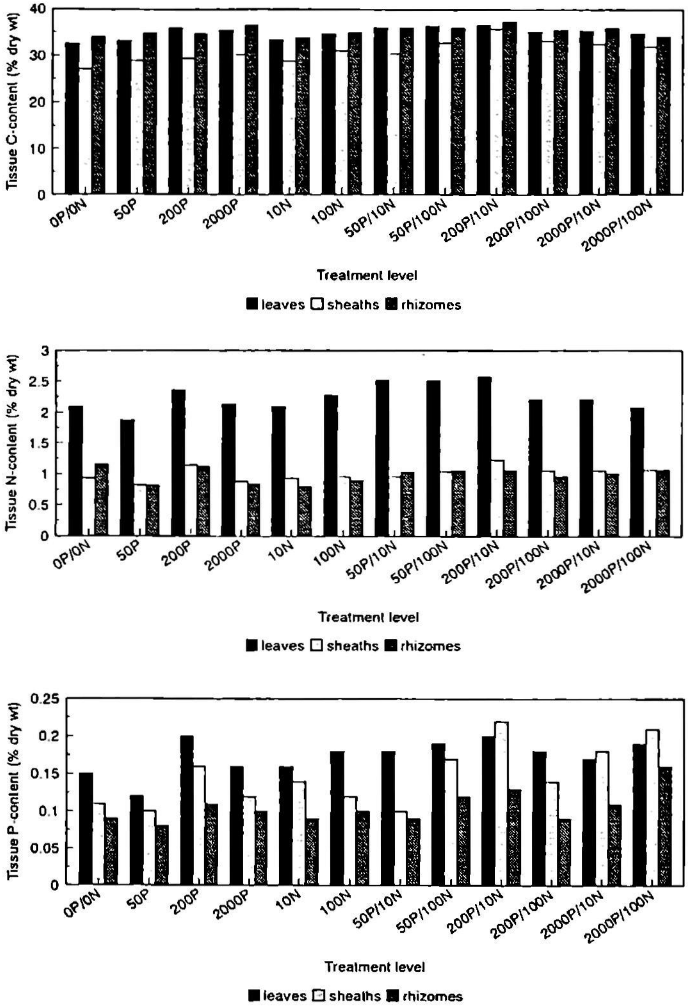

Figure 5.3 Carbon (above), nitrogen (middle) and phosphorus (below) contents of seagrass tissue from different plant parts (leaf blades, sheaths, rhizomes and roots) in enriched and control plots for the various treatment levels at Kudingareng Lompo. Data are average values of triplicate plots for each treatment level (SD ranged from 4 to 8 % of mean).

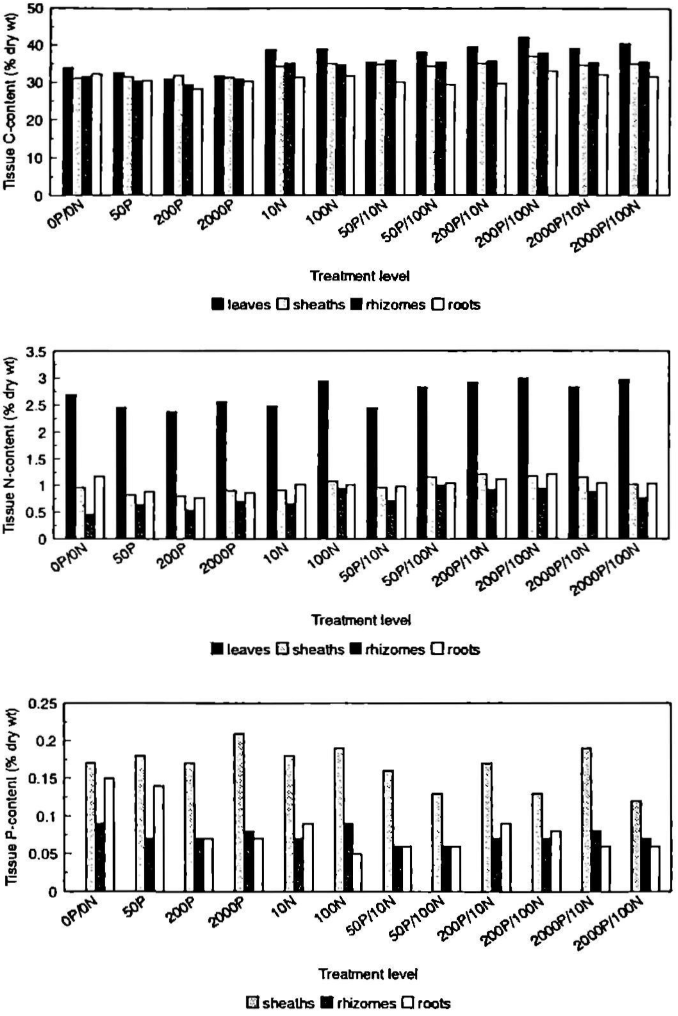

Figure 5.4 Carbon (above), nitrogen (middle) and phosphorus (below) contents of seagrass tissue from different plant parts (leaf blades, sheaths, rhizomes and roots) in enriched and control plots for the various treatment levels at Barang Lompo. Data are average values of triplicate plots for each treatment level (SD ranged from 4 to 8 % of mean).

Plant tissue nutrient contents

The effects of nitrogen and phosphorus additions on the N and P contents of seagrass tissues were significant in the 1991 experiment but were inconsistent with the type and level of fertilization in the experiments at Kudingareng Lompo and Palanro in 1990 (Fig. 5.2 and 5.3). Enrichment had no significant effects on the atomic C:N, C:P and N:P ratios in seagrass tissue at these stations. In the 1991 experiments at Barang Lompo, total C and N contents in tissue of most plant parts had increased significantly ($p < 0.05$) in response to N-addition in comparison to the control plots (Fig. 5.4). However, maximum increases were only in the order of 12-25% above the controls (except for N contents in rhizomes which nearly doubled in response to 100 N and 50 P/100N addition). P-addition had no significant effects on tissue elementary composition at Barang Lompo. C:P and N:P atomic ratios of plant tissue from enriched plots at Barang Lompo were not significantly different ($p > 0.05$) from the control plots. The C:N atomic ratio in shoot and rhizome tissue decreased significantly ($p < 0.05$) with N-addition, but not in leaf and root tissue. Average C-N-P contents (in % dry wt) of seagrass tissue in control plots were 30-1.0-0.13, 31-1.4-0.12, and 32-1.3-0.14 at Palanro, Kudingareng Lompo, and Barang Lompo respectively. The MANOVA of C-, N- and P-data from all three localities indicated an overall significant effect of N-only and P-only treatments, but not of the combined N+P treatments (Table 5.5). MANOVA testing of the effects of N and P additions on C, N and P contents at carbonate sites (Barang Lompo and Kudingareng Lompo) versus those obtained at the coastal site (Palanro), revealed significant differences for the effects of P-addition ($p < 0.05$) between reef sites versus the coastal site, whereas the responses to N addition were significantly different between all three localities.

Table 5.5

Multivariate analysis of variance (MANOVA) for effects of P, N, N+P additions and locality on C-, N- and P-contents on seagrass leaf, sheath, rhizome and root tissue.

MANOVA Wilks' Lamba	Value	F	Degrees freedom Num	Denom.	p
N-addition	0.305	7.592	16	150	0.000
P-addition	0.608	1.702	24	218	0.026
N+P-addition	0.450	1.369	48	373	0.059
Locality	0.002	227.201	16	150	0.000
N-add x Loc	0.140	6.121	32	278	0.000
P-add x Loc	0.236	2.647	48	373	0.000

Adsorption capacity of carbonate sediments

Experimental shaking of different particle-sized sediment samples with known (enriched) seawater concentrations of phosphate demonstrated that fine-grained carbonate sediment fractions adsorbed more phosphate than coarser fractions (see Chapter 4; Fig. 4.6). Given the fact that the carbonate sediments in the study area are characterized by a relatively coarse particle-size composition with generally less than 15% of the particles smaller than 63 µm (Table 5.1), it is likely that these sediments have a relatively low adsorption capacity for phosphate in comparison with fine-grained carbonate sediments.

DISCUSSION

The results of the present study revealed that nutrient levels are likely to meet plant growth requirements and that both nitrogen and phosphorus are not likely to be limiting in the study area in both terrigenous and carbonate sedimentary environments. An explanation for the absence of obvious evidence for phosphorus limitation at the two carbonate sites under investigation here might be found in the particle-size distribution of these sediments in the study area. The coarse grain-size of the carbonate sediments (>80% larger than 63 µm, of which usually >40% larger than 312 µm) in seagrass beds on many of the reef platforms in the Spermonde Archipelago was found to be responsible for a limited adsorption capacity of phosphate onto the carbonate mineral surfaces, thus maintaining relatively high porewater phosphate concentrations (Erftemeijer & Middelburg, submitted).

The limited response of seagrass growth, shoot density and biomass to fertilization might, however, in part be related to the inevitably overlapping influences of environmental factors in the natural environment (see Short, 1987) and to the degree of heterogeneity of the vegetation in the experimental plots. Furthermore, different seagrass species might show a differing response to fertilization. This could have resulted in a shift in the relative dominance of the various species in a mixed meadow, while the total biomass and productivity of the meadow remained unchanged. There were, however, no indications of a marked change in the relative abundance of the different seagrass species during the course of the present study, and of significant differences between enriched and control plots. True differences in seagrass biomass among treatments might have been partly masked by the small sample size, high variance, and reduced maintenance of treatments as time progressed. Standard error of mean roughly ranged from 10 to 25 % of the average biomass. Fertilizer, albeit time-released, was added in the beginning of the experiment only (see also Williams, 1990).

Although the wide diversity of methods used to investigate submersed plant nutrition contributes to the variabilities in results and interpretations, several broad patterns of N and P regulation of plant growth are emerging (Murray et al., 1992a). The lack of dramatic plant response to fertilization in the present study indicates that plant growth in the study area might not be limited by either N or P. One can argue about methodologies and in what way they may affect the results of the experiments, but in the present study the applied methodology was largely copied from Short et al. (1990), who found a dramatic increase in seagrass growth, biomass and tissue phosphorus composition 7 months after P-enrichment in seagrass meadows of Syringodium filiforme Kütz. in the Bahamas. The average concentrations of reactive phosphate in carbonate sediment porewaters (average 10 µM) found in the present study were considerably higher than those normally reported for some fine-grained carbonate sediments in the tropical Caribbean (e.g. < 2 µM in carbonate silt in the Bahamas: Short et al., 1990). The average atomic C:N:P ratio (565:18:1) of seagrass tissue from carbonate sites in the present study area (Erftemeijer, in press) also differed markedly from the ratio (1390:47:1) reported from the Bahamas (Short et al., 1985).

The ratio of carbon relative to nitrogen and phosphorus in aquatic angiosperm tissue is regarded as providing an index of element availability in the aquatic environment from which the plants were collected (Gerloff & Krombholz, 1966; Atkinson & Smith, 1983; Duarte, 1990), similar to what has been demonstrated for phytoplankton (Redfield et al., 1963). Duarte (1990) reviewed available literature and suggested that seagrass plants with nutrient levels in leaves below the median levels of all those reported for seagrasses (i.e. < 1.8% N and < 0.20% P as % dry wt) are strongly nutrient-limited, and that, in contrast, seagrass plants with nutrient levels similar or higher than these critical values are likely to show a minor or statistically non-significant response to nutrient enrichment. The N contents (2.0-2.5%) and P contents (0.15-0.20%) in seagrass leaf tissue from carbonate sites (P not analysed for Barang Lompo) in the present study (Fig. 4 and 5) are near (P) or above (N) these critical levels and suggest that ambient nutrient supply (both N and P) meets the plants' demands. As such, the lack of significant plant response to fertilization and these leaf tissue N and P contents support the suggestion of Duarte (1990) that these median values may be used to derive predictions on the likelihood of nutrient limitation of seagrass stands upon examination of their nutrient content.

The addition of 2000 P (or 100 N) did not lead to a conspicuous increase of the ambient phosphate (or ammonium) concentration in porewaters of control plots. The presence of slow-release fertilizer in the sediment might not necessarily increase actual porewater levels of dissolved P and N, but rather increase rates at which their concentrations are being replenished after removal by plant uptake, diffusion or adsorption. Actual porewater enrichment was not studied by Short et al. (1990). Fertilization of carbonate sediments by bird excrements caused a significant increase in porewater phosphate and ammonium concentrations in the upper 20 cm of the sediment in comparison to control plots in seagrass beds in Florida (Powell et al., 1989). This indicates that porewater enrichment might depend on the methodology of fertilization and type of fertilizer that is applied. Kenworthy and Fonseca (1992) used balanced fertilizer granules containing N and P within the same coating. They observed competition among ammonium and phosphate molecules for release through pores in the coating, which resulted in a relatively faster release of the smaller ammonium molecules. It is suggested to address further geochemical parameters in future studies in order to fully understand what the actual effects of the application of fertilizer granula (slow-release osmocote and ureaform) are on the sediment fertility status and nutrient availability to seagrass growth (e.g. adsorbed or exchangeable N and P versus dissolved inorganic N and P in porewaters, nitrification-denitrification rates, nitrogen fixation).

In addition, heavy bioturbation and a high degree of sediment instability may have a considerable influence on the success of fertilization experiments, and we suggest that these and other geochemical factors be taken into account in future enrichment bioassays. Bulthuis et al. (1992) found little or no response to fertilization at a site with heavy bioturbation, where many of the osmocote fertilizer granules were found lying on the sediment surface 1 month after treatment. In the present study, however, only very few granules were found on the sediment surface at the end of the experiment, whereas appreciable amounts of fertilizer granules were retrieved in the sediment between roots in the samples dug out for seagrass biomass determination, which rules out the possibility that substantial amounts of fertilizer were removed from the plots as a result of bioturbation and subsequent transport by water currents.

Whereas nutrient enrichment of the water column normally leads to increased development of epiphytes and blooming of macroalgae and phytoplankton and may eventually lead to a decline of seagrasses (Short & Short, 1984; Silberstein et al., 1986; Tomasko & Lapointe, 1991; Burkholder et al., 1992), sediment enrichment apparently has no dramatic effects on phototrophic organisms other than seagrasses. No obvious differences were noticed (visual observations) in epiphyte cover of the seagrass blades in response to the various fertilizations, nor in macroalgal or phytoplankton biomass. Williams (1990) found that the microalgal mat on the sediment surface was more pronounced in most fertilized plots for a few weeks after fertilization, but such was not observed in the present study. Seagrasses are the only phototrophic organisms capable of utilizing the nutrient pool in the sediment porewater (Short and McRoy, 1984) although the microalgal mat and some rhizophytic macroalgae may utilize porewater nutrients that diffuse from of the sediment. Williams (1990) found that sediment nutrients are incorporated primarily by the below-ground biomass, which accumulates slowly, and that the above-ground biomass lags in response to increased sediment nutrients. Williams (1987) found clear evidence of competition for sediment nutrients between Syringodium filiforme and Thalassia testudinum in a Caribbean lagoon.

Finally, one might speculate that the results of several enrichment experiments that showed no significant plant response to fertilization have never been published. As such, only studies which did show effects have entered the literature and led to the general assumption that seagrass growth is usually limited by N or P. The present study clearly demonstrates that even in tropical carbonate sediments nutrient availability may meet plant requirements for growth. Internal resorption of nutrients from old plant parts during decay might be involved as an important additional mechanism of nutrient supply to the highly productive seagrass plants, notably in nutrient-poor environments as suggested by Hemminga et al. (1991). In contrast to seagrass growth in fine-grained carbonate sediments in the Caribbean, which was found to be strongly P-limited, the coarse grain-size of the carbonate sands in the present study area limits their adsorptive capacity of phosphate, resulting in a relatively high availability of dissolved P to plant growth.

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CHAPTER SIX

SEASONAL CHANGES IN ENVIRONMENTAL VARIABLES, BIOMASS, PRODUCTION AND NUTRIENT CONTENTS IN TWO CONTRASTING TROPICAL INTERTIDAL SEAGRASS BEDS IN SOUTH SULAWESI (INDONESIA).

Daylight exposure of seagrass beds during extreme low tides may cause a significant loss of above-ground plant biomass due to desiccation and burning of the leaves.

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SEASONAL CHANGES IN ENVIRONMENTAL VARIABLES, BIOMASS, PRODUCTION AND NUTRIENT CONTENTS IN TWO CONTRASTING TROPICAL INTERTIDAL SEAGRASS BEDS IN SOUTH SULAWESI (INDONESIA).

ABSTRACT

Seasonal dynamics were studied by monthly monitoring of biological and environmental variables in permanent quadrats (PQ) in two contrasting intertidal seagrass communities in South Sulawesi, Indonesia, from February 1991 to January 1992. Datasets were analysed with Canonical Correlation Analysis for correlations between environmental and biological variables. Considerable variation in biomass, production and plant tissue nutrient contents in a monospecific seagrass bed of Enhalus acoroides, growing on a coastal terrigenous mudbank (Gusung Tallang), although likely to be related to riverine influences of the nearby Tallo River, could not be significantly correlated to seasonal patterns in rainfall, salinity, tides, nutrient availability, water motion or turbidity. A seasonal cycle in biomass, production and nutrient contents in a mixed seagrass bed of Thalassia hemprichii and Enhalus acoroides growing on carbonate sand on the reef flat of an offshore coral island (Barang Lompo) was found to be largely determined by tidal exposure and water motion. Exposure of the intertidal seagrass bed on hours of low water during spring tides showed a gradual shift from exposure during the night (January-June) to exposure during daylight (July-December). Daylight exposure resulted in a significant loss of above-ground plant biomass through desiccation and 'burning' of leaves. The observed seasonal dynamics in the seagrass bed on reef sediment are in contrast with reports from the Caribbean, where the effect of tidal exposure on comparable shallow-water seagrass communities is relatively insignificant due to a small tidal amplitude.

INTRODUCTION

The important ecological and economic functions of seagrass beds have been widely acknowledged, notably their importance to fisheries (Bell and Pollard, 1989) and their role in preventing coastal erosion and siltation of coral reefs (Scoffin, 1979; Fonseca and Fisher, 1986; Fonseca, 1989). Nevertheless, human-induced declines of seagrasses are being increasingly reported from various parts of the world (Kemp et al., 1983; Orth and Moore, 1983; Cambridge and McComb, 1984; Cambridge et al., 1986; Shepherd et al., 1989; Walker and McComb, 1992).

Detailed ecological information on seagrasses from the tropical Indo-Pacific region is scarce and lags considerably behind that from the temperate region and the tropical Caribbean. Only recently, various structural and functional aspects of

Indo-Pacific seagrass beds have been studied (Brouns and Heijs, 1986; Lindeboom and Sandee, 1989; Nienhuis et al., 1989). However, the study of structural and functional components of the seagrass system alone does not provide information on dynamics, whereas most seagrass communities are liable to change (den Hartog, 1979). Particularly with regard to conservation, it is important to document changes with time in the composition, biomass and productivity of seagrass communities, and to study what environmental variables are responsible for the observed dynamics.

The aims of the present study were (1) to collect detailed information with respect to seasonal changes in biological variables in seagrass communities (including seagrass density, biomass, production and tissue nutrient contents) from an area in the tropical Indo-Pacific region, (2) to study to what extent these changes are a response of the seagrasses to seasonal fluctuations in environmental variables (including availability of nutrients and light, water movements, salinity and tide) and (3) to compare the seasonal variations in environmental variables and seagrass response between a coastal muddy environment under direct influence of a river and an offshore reef environment under oceanic conditions.

MATERIALS AND METHODS

Study area

The study was carried out in two contrasting field sites in South Sulawesi, Indonesia: (1) the reef flat of Barang Lompo, a coral island situated 14 km from the coast, and (2) Gusung Tallang, a coastal mudflat located 500 m north of the mouth of the river Tallo (Fig. 2.1). Both sites are characterized by extensive, well-developed seagrass meadows. The sediment at Gusung Tallang consists of sandy terrigenous mud which is protected from waves and currents by a long and narrow sandbar in the north, running perpendicular to the coast. The seagrass vegetation at this site consists of a monospecific meadow of Enhalus acoroides and covers an estimated 20 ha. The reef flat at Barang Lompo is covered by a layer of at least 30 cm of relatively coarse carbonate sand, mainly derived from erosion material of the reef. A dense mixed-species seagrass vegetation dominated by Enhalus acoroides and Thalassia hemprichii covers approximately 50 ha of this reef flat.

Monthly monitoring

Biological and environmental variables were monitored monthly (from February 1991 to January 1992) within a permanent quadrat (PQ) of 100 m^2 at each site. Both PQ's were situated in areas of representative seagrass cover (based on preliminary surveys). Biological variables included shoot density, biomass, leaf production, tissue nutrient contents (C, N, P) and ash contents of the seagrasses.

Environmental variables included water motion, salinity, turbidity, tide, rainfall and nutrient concentrations in water column and sediment porewater (PO_4, NH_4 and NO_3+NO_2).

Shoot density of Enhalus acoroides, which occurred at both sites, was determined monthly by 50 counts within an iron frame (50 x 50 cm) thrown randomly in the seagrass bed. Three replicate samples consisting of 6 to 8 shoots of Enhalus acoroides (including their below-ground parts) were collected randomly within the PQ each month using a spade. Biomass data of these shoots were converted to data per m^2 using the average shoot density counted for that particular month. Biomass samples (three per month) of Thalassia hemprichii, which only occurred at Barang Lompo, were collected randomly in the PQ using an aluminium frame (25 x 25 cm) and a spade. Shoot densities of this species were determined by counting the shoots present in the biomass samples. Biomass samples of the seagrasses were rinsed with freshwater and divided into leaf blades, sheaths, rhizomes and roots. Epiphytes were removed from leaves by careful scraping. To remove calcareous epiphytes, some leaf samples were treated by soaking in a solution of approximately 5 % phosphoric acid as suggested by Dawes and Kenworthy (1990), but this resulted in unacceptable data on total P-contents in leaf tissue, which were therefore discarded. Macroalgal biomass was sampled during periods of blooming and was treated similar to the seagrass samples.

The plant parts were dried at 60-80 °C to constant dry weight and stored for the determination of primary elemental constituents (C, N and P) and ash contents. Carbon and nitrogen content of powdered plant tissue was measured using a Carlo-Erba NA 1500 CN Analyser. Phosphorus content was measured by a strong oxidizing acid digestion (hydrochloric acid + nitric acid + perchloric acid) followed by a standard colorimetric phosphate determination of the digest solution (Allen, 1974). Ash contents were analysed by determining the weight loss after ashing for 1 hour at 550 °C.

Leaf production was studied in random plots within the PQ's using the leaf marking method according to Kirkman and Reid (1979). This method was recommended as most suitable for large-scale monitoring studies of seagrass primary production in tropical environments (Erftemeijer et al., 1993). An average of 10 plants in four plots (Enhalus acoroides) or 20 plants in three plots (Thalassia hemprichii) were arbitrarily selected and marked each month. Leaf growth was assessed after 6 days and expressed as relative growth rate (g g^{-1} d^{-1}).

The exposure of the seagrass plants to water motion was studied by means of the clod card technique according to Doty (1971). We used blocks of Plaster of Paris with an average weight of approximately 60 g which were prepared from a mixture of 1.67 kg plaster per litre water. The blocks were glued to numbered plastic cards. Each month 9 blocks (mounted on bricks) were placed at c. 10 cm above the sediment surface. Their weight loss after 24 h was regarded as a relative (cumulative) measure of the rate of exposure to (irregular) multi-directional water movements. The accuracy of this method was recently evaluated by Jokiel and Morissey (1993), who found a linear correlation between the weight loss of clod cards and the flow velocity of seawater in experimental tanks at the laboratory. To facilitate comparison with results from other studies, the results are expressed as 'diffusion factor' (DF), which is defined as the ratio of the weight loss in experimental blocks (field) to the weight loss in calm water (blanks). Blanks were held for 24 h in a calibration chamber ($v = 15$ l) filled with calm seawater with a salinity of 32‰ S and a water temperature of 30 °C. Average weight loss of blanks was 1.96 ± 0.65 g 24 h^{-1}. The DF concept is potentially valuable as a dimensionless index of water motion (Jokiel and Morissey, 1993).

Salinity of the seawater overlying the seagrass beds was measured monthly in an average of 5 replicate samples collected on different visits to each site with the use of a refractometer. Accuracy of this method proved to be within 0.5‰ S of the results obtained by titration with $AgNO_3$. Turbidity was determined by measurements of the irradiance of photosynthetically active radiation (PAR) with a Li-cor 185B Qrbp 1900-8501 quantum-meter. Underwater measurements of PAR just below the water surface and at depth (D) in the seagrass beds at both sites were used to calculate attenuation coefficients (k) according to the Lambert-Beer equation (Jerlov, 1970). Data on rainfall, sunshine and predicted tides were derived from the local meteorological and oceanographic institutes (Balai Meteorologi dan Geofisika, Ujung Pandang, and Dinas Hidro-Oseanografi TNI-AL, Jakarta).

Monthly replicate samples of surface water (usually six replicates on a visit) were collected at each site, filtered in the field over 0.2 µm Minisart NML disposable syringe filters and transported on ice. At the laboratory, these samples were directly analysed spectrophotometrically, using a Nanocolor 100D-MN filter photometer, for phosphate, ammonium and nitrate+nitrite according to Strickland and Parsons (1972).

Sediment samples were taken randomly in the PQ's (once a month) with small hand corers ($d = 6$ cm) to a depth of 10 cm while snorkling. Each core was separated into 2 cm sections in the field. The coinciding sections of every 12 successive cores were combined and treated as one sample to reduce spatial heterogeneity. These samples were transported on ice in sealed plastic bags for further treatment in the laboratory. Plant parts, large living benthic animals and stones were removed prior to further treatment. Within a maximum of 4 h after sampling, porewaters were extracted by filtration of the samples over Schleicher & Schuell membrane filters (0.45 µm) under low pressure (1-3 Bar) using nitrogen gas, following a slightly modified technique of Kelderman (1985). Porewater samples were subsequently filtered over 0.2 µm filters and phosphate, ammonium and nitrate+nitrite were analysed spectrophotometrically. Data on porewater nutrients are presented as the median (as well as minimum and maximum) of values found for monthly duplicate series of the different sediment depth sections. Data on depth profiles of porewater nutrient concentrations are given elsewhere (Erftemeijer and Middelburg, submitted).

Data analysis

The relationship between seasonal changes in biological variables and fluctuations in environmental variables was tested by applying a canonical correlation analysis. This analysis is a multivariate correlation analysis which performs an ordination of the data sets of biological and environmental variables in such a way that an optimal correlation is achieved (Gittins, 1980). In the analysis, the multidimensional coordinate frames of the sample spaces are rotated to a new position in which some feature or property of the data is emphasized. The data are regarded as two separate sample spaces, of dimensions corresponding to biological and environmental sets of variables respectively. Rotation of these two separate coordinate frames is performed simultaneously until an optimal correlation between the two is achieved. The rotations are equivalent to finding linear transformations of each set of variables such that the correlation of the transformed variables is maximized. The covariation of the various measurement domains is tested for significance by Chi-square statistical analysis.

The canonical correlation analysis provides two types of results: canonical coefficients and canonical loadings. Canonical coefficients are interpretable as multiple correlation coefficients between a particular canonical variate of one domain and the complete set of variables of the other (in other words they provide a quantitative indication of the individual contribution of a particular variable to the covariation, when all other variables are considered as constants). Canonical loadings (or weights) represent a sort of compromise between maximizing between-set covariation while disentangling within-set covariation (i.e. allowing other variables to covary).

In the present study, combined sets of data from Barang Lompo and Gusung Tallang were subjected to the canonical correlation analysis. Total biomass of Thalassia and Enhalus were added and expressed as total seagrass biomass. Shoot density was not included because of a strong correlation with total biomass. Standing stocks of nutrients in plant tissue (proportional sum of all plant parts of Thalassia and Enhalus) were expressed as C:N ratio and C:P ratio. Relative growth rates (RGR) of Thalassia and Enhalus at Barang Lompo were averaged proportionally to their leaf biomass. Missing values in the data matrix were linearly interpolated. In addition to the overall correlation analysis, the datasets of the two localities were also tested separately (using a selection of variables) to exclude possible interference effects of data from one locality to those from the

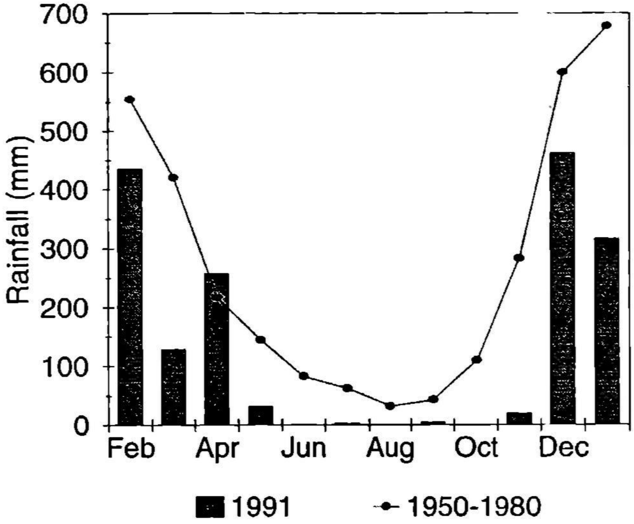


Fig. 6.1 Monthly rainfall (mm) in 1991 and average rainfall during 1950-1980, measured at Paotere harbour, Ujung Pandang, South Sulawesi. (source: Balai Metereologi dan Geofisika, Ujung Pandang).

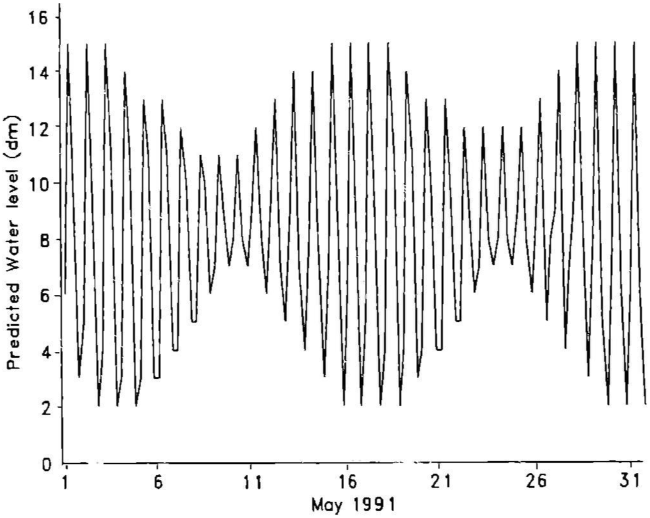


Fig. 6.2 Predicted tidal oscillation curve for Ujung Pandang harbour during May 1991 (source: Dinas Hidro-Oseanografi TNI-AL, Jakarta).

other.

RESULTS

Rainfall and sunshine

The study area is governed by a tropical climate. The mean air temperature in the area is 27 °C and shows only minor seasonal variation. Rainfall is subject to large seasonal variations with a distinct dry and wet period (Fig. 6.1). During the months May to October, when south-easterly winds prevail, average monthly rainfall normally does not exceed 100 mm. From November to April north-westerly winds dominate and bring considerable quantities of rain (usually more than 70% of the total annual precipitation) with monthly rainfall frequently exceeding 300 mm. Total annual rainfall in 1991 (2186 mm) lagged behind considerably in comparison to the average for 1950-1980, with a prolonged dry season with hardly any rainfall from May until the end of November, which is attributed to the effect of the 1991-1992 El Niño Southern Oscillation event (Murray et al., 1992b; Kessler and McPhaden, 1992). Monthly total hours of sunshine in 1991 were lower during the months February 1991, December 1991 and January 1992 (100-150 h per month) than during the rest of the year (200-250 h per month).

Tides

The west coast of South Sulawesi is subject to a mixed, predominantly semi-diurnal tidal regime with a maximum tidal amplitude (at spring tide) of 150 cm (130 cm in 1991) and a minimum tidal amplitude (at neap tide) of less than 20 cm. An example of the tidal oscillation in the study area (May 1991) is given in Figure 6.2. To determine the situation of the seagrass beds relative to chart datum (ELWS), measured (field) and predicted (tide table) water levels were compared. It was calculated that the PQ at Barang Lompo was situated at 19 ± 10 cm above ELWS (n = 60) and the PQ at Gusung Tallang at 30 ± 16 cm above ELWS (n = 74). At Gusung Tallang, the mean difference between measured and predicted water level was significantly lower in the rainy period (19 ± 15 cm) than during the dry period (37 ± 10 cm), which is attributed to wind stress from the (mainly) northwestern monsoonal winds which may propel the nearshore water levels up to higher levels than during other months. From the second half of February until the beginning of July low waters of spring tides occur during the hours of darkness (between 18.00 pm and 06.00 am). From the second half of July until early February, however, the spring ebb tides occur during the daylight period (Fig. 6.3). This predicted 'seasonality' in the tidal regime was consistent in 5 successive years (1988-1992).

When a low-water of spring tide occurs at mid-day, seagrass beds that are located above ELWS are exposed to sunshine and air, and may suffer from desiccation or 'burning' of their leaves. At Barang Lompo, this was observed regularly during the

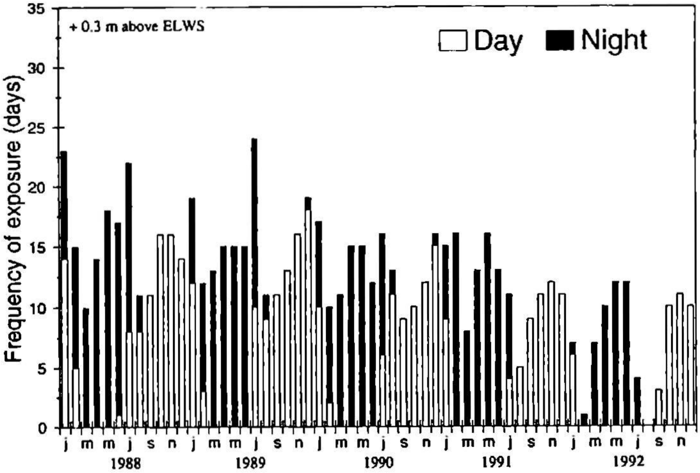


Fig. 6.3 Predicted frequency of spring low tide exposure (in days per month) during daylight (white bars) and at night (black bars) for stations situated +0.3 m above chart datum in the study area during 1988-1992 (source: predicted tide tables, Dinas Hidro-Oseanografi TNI-AL, Jakarta).

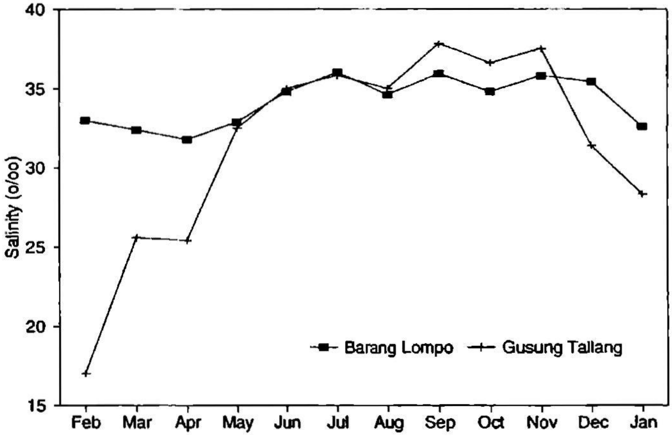


Fig. 6.4 Monthly variation in salinity of surface water (‰ S) above seagrass beds in the PQ's at Barang Lompo and Gusung Tallang during 1991 and January 1992 (SD < 2‰).

months August-December (a couple of consecutive days, twice a month). The seagrass bed at Gusung Tallang, however, although situated between 19 (wet season) and 37 cm (dry season) above ELWS, was rarely exposed entirely to air at these low waters. At this locality, it was observed that a lens of water (10 to 15 cm deep) was retained over the seagrass-covered mudbank at low tides, preventing the seagrass plants from becoming fully emerged. Since topographic transects over the mudbank at Gusung Tallang revealed no berm that could retain the water on the bank, this lens-retention is attributed to flow reduction by the seagrass canopy, a phenomenon which appears to occur particularly in broad shallow meadows subject to relatively slow currents (Fonseca et al., 1983; Fonseca and Fisher, 1986). Apparently, faster currents (see also the results of the clod card technique) and differences in general topography do not permit such a lens retention at Barang Lompo.

Salinity

Salinity of the seawater remained more or less unchanged throughout the year at Barang Lompo (mean 34.1 ± 3.9 ‰ S; n = 65), with minimum values of 31‰ and 32‰ recorded in February, March and April 1991 and in January 1992 (Fig. 6.4). At Gusung Tallang, however, seasonal changes in salinity occurred with comparable values as at Barang Lompo during the months May-November (mean: 35.8 ± 1.7‰ S; n = 38), but much lower salinities during the rainy period (December-April), with lowest recordings of 17‰ S in February 1991 and 15‰ S in January 1992.

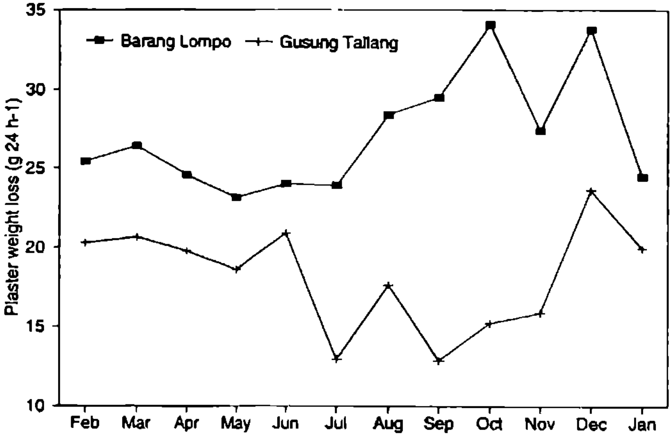
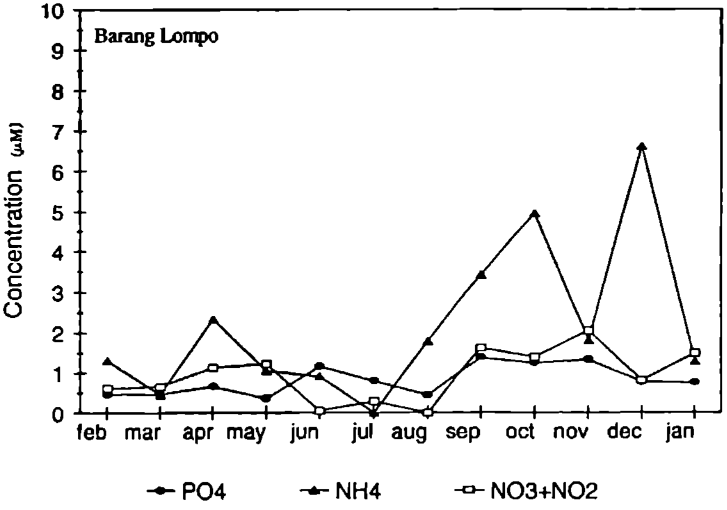


Fig. 6.5 Seasonal variation in clod card weight loss (in g 24 h^{-1}) as a measure of exposure to water movements in the PQ's at Barang Lompo and Gusung Tallang during 1991 and January 1992. (SD < 1.9 g)



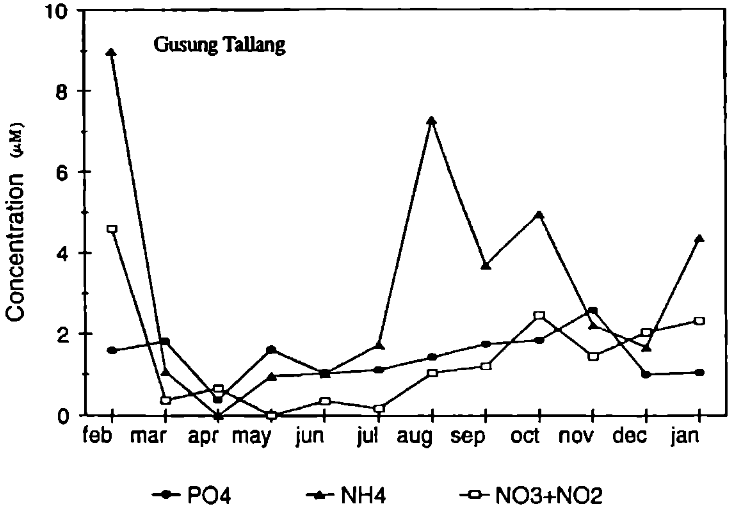


Fig. 6.6 Seasonal variation in the concentrations of phosphate, ammonium and nitrate+nitrite (monthly means) in the water column above the seagrass beds (PQ's) at Barang Lompo and Gusung Tallang during 1991 and January 1992 (SD < 0.5 (PO_4 and NO_3+NO_2); SD < 2.0 (NH_4)).

Exposure to water movement

At Barang Lompo, the weight loss of clod cards was highest in the months August-December, and lower and relatively stable during the other months (Fig. 6.5). At Gusung Tallang, weight loss was lower from July-November than during the rest of the year. Throughout the year, the PQ at Gusung Tallang was characterized by substantially lower exposure to water movements than the PQ at Barang Lompo. The average diffusion factor (DF) was 14.9 ± 2.0 for Barang Lompo and 10.3 ± 1.9 for Gusung Tallang which is within the range of values reported for reef environments (Jokiel and Morissey, 1993).

Nutrient concentrations

Month-to-month variation in the concentrations of dissolved nutrients in the water column was conspicuously larger at Gusung Tallang than at Barang Lompo and was most conspicuous for ammonium (Fig. 6.6). The annual averages of phosphate, ammonium and nitrate+nitrite concentrations in the water column (in µM) were 0.8 ± 0.4, 2.2 ± 1.9 and 0.9 ± 0.6 for Barang Lompo and 1.4 ± 0.6, 3.2 ± 2.8 and 1.4 ± 1.3 for Gusung Tallang respectively. Increased water column nutrient concentrations at Barang Lompo in the months August-January coincided with the period of low-tide exposure during daylight. Increased nutrient concentrations in the water column at Gusung Tallang did not coincide with periods of peak rainfall. Median, minimum and maximum porewater nutrient concentrations (in the upper 10 cm of the sediment) showed a comparable range of monthly variation at both sites, except for phosphate, which showed considerably larger fluctuations at Barang Lompo (Fig. 6.7). Maximum concentrations did not coincide among the different nutrients and among the two sites. The annual average porewater concentrations for phosphate, ammonium and nitrate+nitrite (in µM) were 10.9 ± 3.9, 49.7 ± 16.8 and 3.4 ± 1.6 for Barang Lompo and 5.5 ± 1.0, 68.7 ± 13.3 and 2.6 ± 2.0 for Gusung Tallang respectively. As such, porewater nutrient concentrations were in the order of 2-4 (NO_3+NO_2), 4-14 (PO_4) and 21-22 (NH_4) times higher than in the water column.

Turbidity

Light availability to the seagrass plants is dependent on the turbidity of the water. Li-cor measurements in the shallow water above the seagrass vegetation at Barang Lompo revealed an average attenuation coefficient of 0.34 ± 0.13 m^{-1} with only minor variation during the year (Fig. 6.8). Turbidity levels at Gusung Tallang were much higher (mean $k = 1.59 \pm 0.75$ m^{-1}) and fluctuated considerably, with maximum light attenuation measured in February, October and November ($k > 2.5$ m^{-1}).

Seagrass shoot density

Shoot density of Thalassia hemprichii at Barang Lompo increased from 2064 ± 127 m^{-2} in February to 3733 ± 605 m^{-2} in July, but subsequently dropped to 1856 ± 617 m^{-2} in August and remained low (around 2000 m^{-2}) during the rest of the year (Fig.

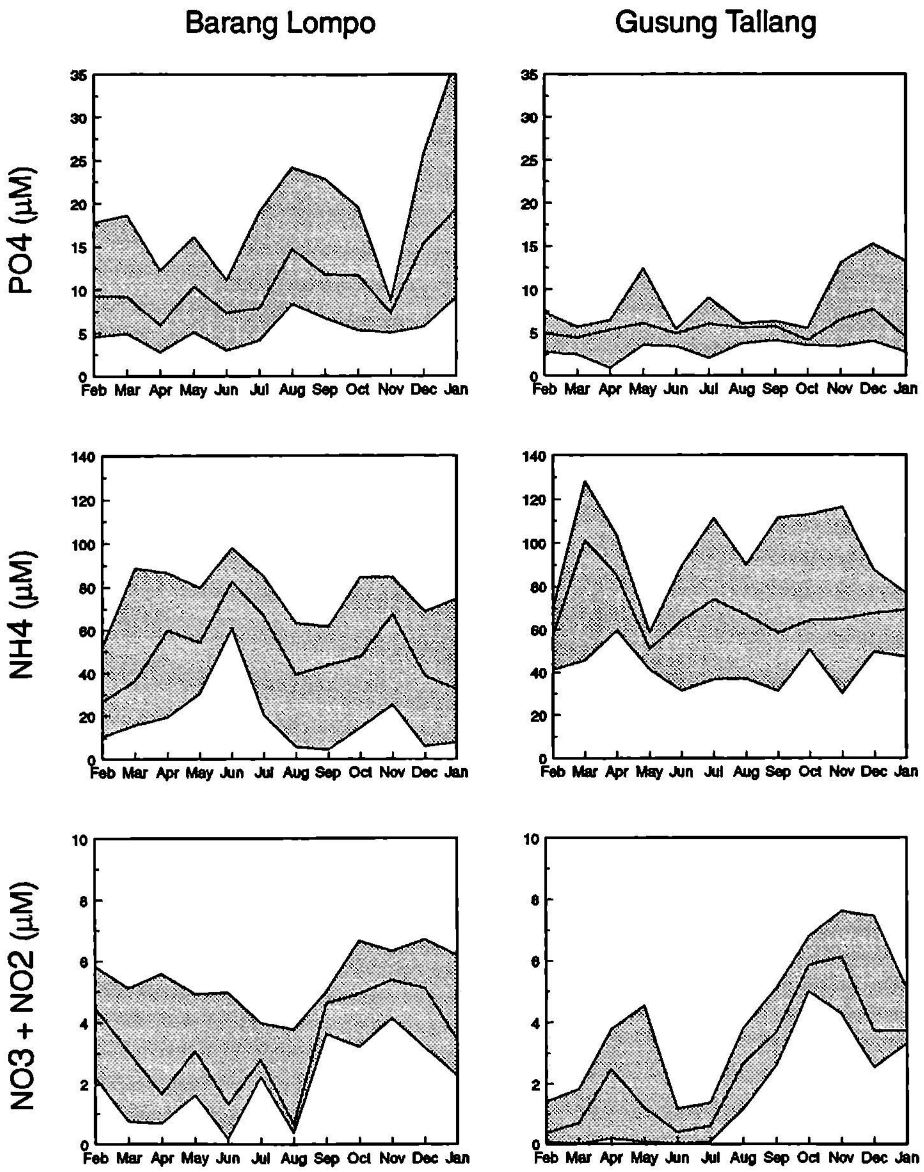


Fig. 6.7 Seasonal variation in the concentrations of sediment porewater nutrients (phosphate, ammonium and nitrate+nitrite) in the seagrass beds (PQ's) at Barang Lompo and Gusung Tallang during 1991. Plots show median, minimum and maximum values for each month recorded within the upper 10 cm of the sediment.

6.9). The relatively low shoot densities of this species during August-January coincide with the period of spring low tide exposure during daylight. The remaining months (when spring low tides occur at night) seem to represent the recovery period, in which *Thalassia* can gradually build up higher shoot densities. Shoot density of *Enhalus acoroides* at Barang Lompo ranged from 18 to 28 m^{-2} with only minor fluctuations which occurred in the period August-November (Fig. 6.9). At Gusung Tallang, shoot density increased from 27 m^{-2} in February to 50 m^{-2} in May, then dropped to 40 m^{-2} a number roughly maintained during the rest of the year (Fig. 6.9). Throughout the year, shoot density of *Enhalus acoroides* was significantly lower at Barang Lompo than at Gusung Tallang. Annual mean shoot densities were 2380 ± 624 m^{-2} for *Thalassia hemprichii* and 24 ± 3 m^{-2} for *Enhalus acoroides* at Barang Lompo, and 39 ± 5 m^{-2} for *Enhalus acoroides* at Gusung Tallang.

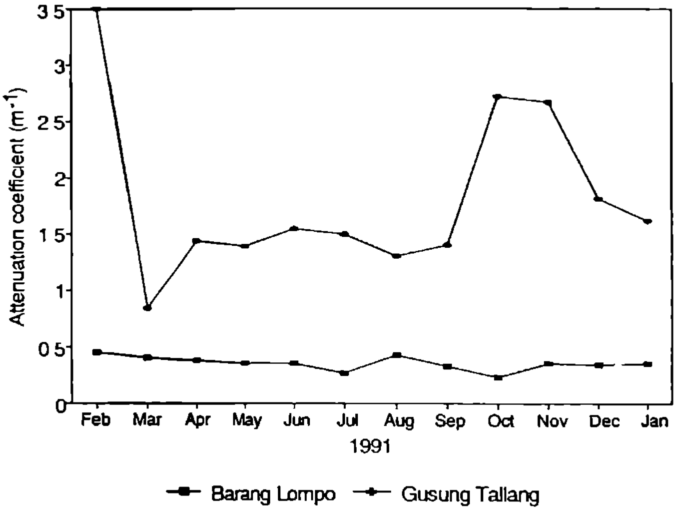


Fig. 6.8 Seasonal changes in turbidity (expressed as attenuation coefficient (k) in m^{-1}) of the water column (monthly averages) at Barang Lompo and Gusung Tallang during 1991. (n = 3-5; SD: Barang Lompo < 0.1; Gusung Tallang < 0.4).

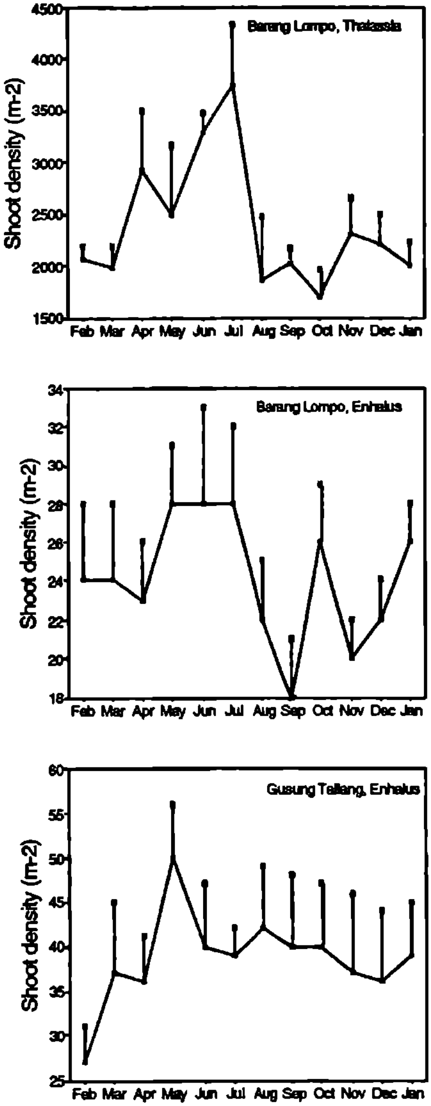


Fig. 6.9 Seasonal changes in shoot density of Thalassia hemprichii (n=3) and Enhalus acoroides (n=50) in the PQ's at Barang Lompo and Gusung Tallang during 1991 (monthly means +SD).

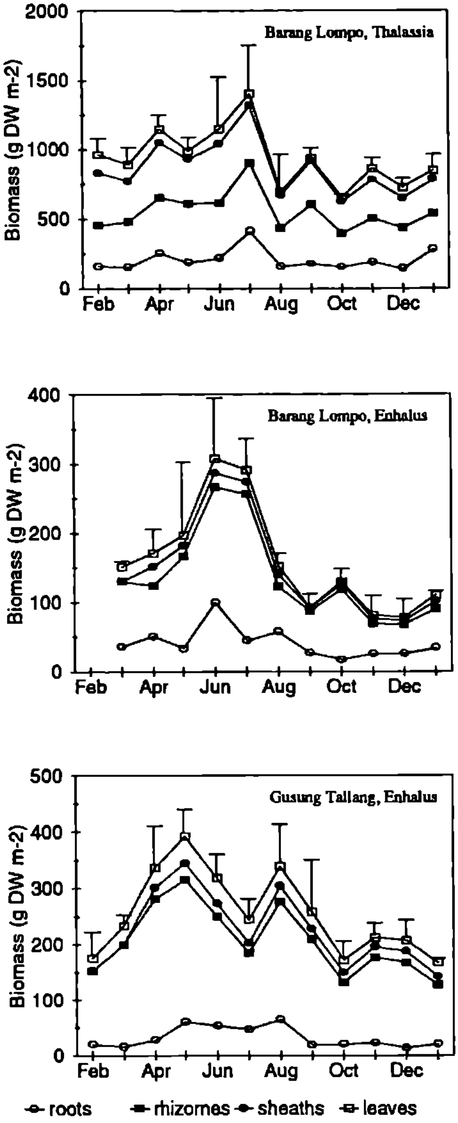


Fig. 6.10 Seasonal changes in seagrass biomass (in g dry wt m^{-2}) of Thalassia hemprichii and Enhalus acoroides (in PQ's) at Barang Lompo and Gusung Tallang during 1991. Data are presented as cumulative weights of the monthly means of the biomass of different plant parts (roots, rhizomes, sheaths and leaves). (SD values of total biomass are given on top of the cumulative graphs).

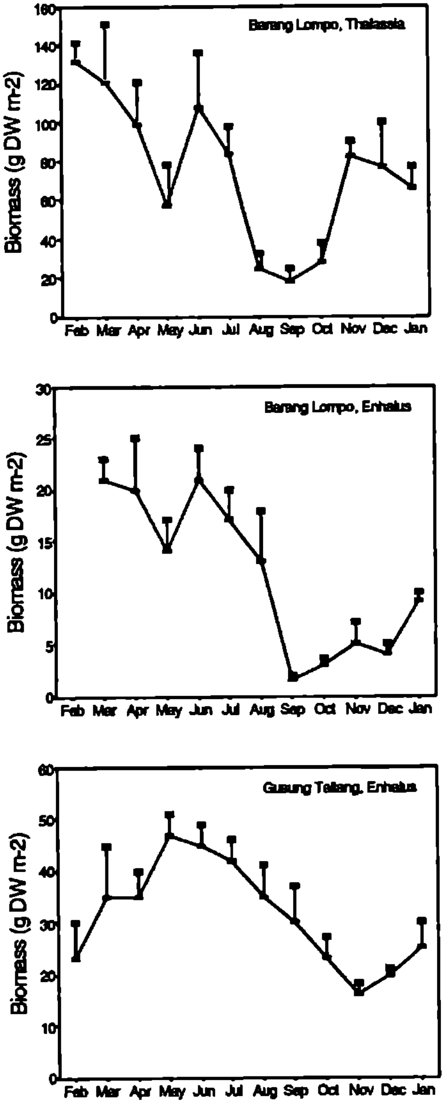


Fig. 6.11 Seasonal changes in leaf blade biomass (in g dry wt m^{-2}) of Thalassia hemprichii and Enhalus acoroides (in PQ's) at Barang Lompo and Gusung Tallang during 1991 (monthly means + SD).

Seagrass biomass

Total biomass of seagrasses at Barang Lompo showed a gradual increase to a maximum during June-July (Thalassia hemprichii 1144-1401 g DW m^{-2}, Enhalus acoroides 292-308 g DW m^{-2}). Subsequently, their biomass decreased considerably in August and remained low at levels around 800 g DW m^{-2} (Thalassia) and 100 g DW m^{-2} (Enhalus) until the end of the year (Fig. 6.10). The general picture for Enhalus at Gusung Tallang is similar. Leaf blade biomass of Thalassia hemprichii at Barang Lompo dropped considerably during August, September and October to levels below 30 g DW m^{-2} (Fig. 6.11). Sampling in these months took place shortly after several days of spring low tide exposure (during daylight), when the major part of the above-ground biomass had suffered from desiccation and 'burning'. Standing crop showed a rapid regeneration within approximately ten days after spring tide (field observations). A massive die-off of above-ground plant material and subsequent rapid regeneration also occurred in July, November and December, but in these months biomass samples were taken after the leaf biomass had recovered. Leaf biomass of Enhalus acoroides at Barang Lompo followed a similar pattern as that of Thalassia hemprichii, except that the steep drop in leaf biomass of Enhalus did not appear until September and that regeneration was slower (Fig. 6.11). Leaf biomass of Enhalus acoroides at Gusung Tallang showed a gradual increase in the first half of the year to a maximum of nearly 100 g DW m^{-2} in July, followed by a general decrease in the remaining months of the year to values around 25 g DW m^{-2} (Fig. 6.11).

Leaf production

Relative growth rates (RGR in g g^{-1} day^{-1}) ranged from 0.022-0.056 for Thalassia hemprichii (Barang Lompo) and from 0.018-0.037 (Barang Lompo) and 0.012-0.024 (Gusung Tallang) for Enhalus acoroides. Highest relative growth rates were observed in July-August-September (Barang Lompo, both species) and July-August (Gusung Tallang) (Fig. 6.12). The annual average RGR for Enhalus acoroides was significantly higher ($p < 0.05$) at Barang Lompo (0.028 ± 0.007 g g^{-1} d^{-1}) than at Gusung Tallang (0.019 ± 0.005 g g^{-1} d^{-1}). Leaf production per m^{2} (calculated from RGR values and monthly standing crop data) ranged from 1.02-5.08 g DW m^{-2} d^{-1} (mean: 2.98 ± 1.29) for Thalassia hemprichii (Barang Lompo) and from 0.09-0.57 g DW m^{-2} d^{-1} (mean: 0.33 ± 0.16) at Barang Lompo and 0.24-2.35 g DW m^{-2} d^{-1} (mean 0.63 ± 0.54) at Gusung Tallang for Enhalus acoroides. Variation in leaf production per m^{2} for Thalassia hemprichii was considerably larger than for Enhalus acoroides, due to greater changes in standing crop. Total annual leaf production of Thalassia hemprichii at Barang Lompo amounted to approximately 1 kg dry wt m^{-2} year^{-1}, which is equivalent to 390 g C m^{-2} year^{-1}. Total annual leaf production of Enhalus acoroides ranged from c. 100 g dry wt m^{-2} year^{-1} at Barang Lompo to c. 200 g dry wt m^{-2} year^{-1} at Gusung Tallang.

Primary elemental constituents

Annual mean C-, N-, P- and ash-contents of leaf blades, leaf sheaths, rhizomes

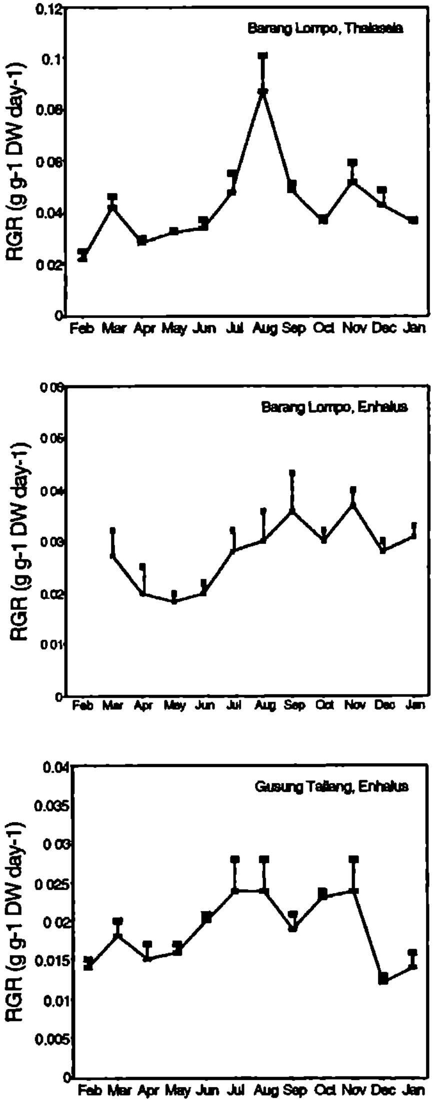


Fig. 6.12 Seasonal changes in relative growth rates (RGR, in g g^{-1} DW day^{-1}) of Thalassia hemprichii and Enhalus acoroides (in PQ's) at Barang Lompo and Gusung Tallang during 1991 (monthly means + SD).

and roots of Thalassia hemprichii and Enhalus acoroides at the two stations are presented in Table 6.1. Monthly variations in the concentrations of C, N and P were inconsistent among different plant parts and among plant species, without following obvious trends that corresponded to fluctuations in nutrient availability in the ambient medium (water column and porewater). Monthly data on C, N and P contents in plant tissue (% of dry wt) were converted to standing stocks of C, N and P in the total biomass (cumulative of different plant parts) by multiplying these data with the corresponding biomass per m^2. Figure 6.13 shows the seasonal changes in the C:N ratios and C:P ratios of the standing stocks of C, N and P in plant tissue of the two seagrass species at the two sites. The C:N ratio in plant material of both species at Barang Lompo showed a gradual increase from February to July (indicating a build-up of C-rich energy reserves) followed by a marked decrease in the period from August to January, coinciding with daytime tidal exposure (which might indicate a mobilization of energy reserves necessary for regeneration after exposure). C:N and C:P ratios in plant material of Enhalus acoroides at Gusung Tallang showed little seasonal variation.

Table 6.1

Annual mean (± SD) tissue contents of primary elemental constituents (total C, N and P, in % dry wt) and ash (% dry wt) in the different parts of Thalassia hemprichii and Enhalus acoroides at the two study sites (n = 36).

		% C	% N	% P	% Ash
Barang Lompo					
Thalassia hemprichii	leaf blades	32.02 ± 5.46	2.07 ± 0.55	0.15 ± 0.01	14.19 ± 5.20
	sheaths	29.73 ± 3.01	0.71 ± 0.26	0.13 ± 0.03	20.96 ± 4.26
	rhizomes	29.48 ± 3.81	0.48 ± 0.20	0.07 ± 0.01	15.93 ± 2.74
	roots	28.17 ± 2.97	0.82 ± 0.25	0.08 ± 0.04	29.17 ± 7.94
Enhalus acoroides	leaf blades	31.53 ± 5.44	1.99 ± 0.52	0.16 ± 0.01	10.54 ± 5.18
	sheaths	27.43 ± 4.34	1.13 ± 0.36	0.22 ± 0.11	23.39 ± 4.04
	rhizomes	29.49 ± 4.23	0.37 ± 0.07	0.13 ± 0.04	10.30 ± 3.72
	roots	29.85 ± 3.68	0.45 ± 0.23	0.04 ± 0.01	22.50 ± 3.55
Gusung Tallang					
Enhalus acoroides	leaf blades	30.96 ± 5.43	2.28 ± 0.60	0.22 ± 0.01	14.55 ± 5.30
	sheaths	25.59 ± 2.76	1.86 ± 0.45	0.20 ± 0.02	26.14 ± 6.28
	rhizomes	29.87 ± 3.83	1.06 ± 0.27	0.11 ± 0.03	9.23 ± 2.03
	roots	26.57 ± 3.65	1.20 ± 0.65	0.11 ± 0.03	26.37 ± 5.06

Macroalgae

The biomass of macroalgae in the seagrass beds at Barang Lompo was low throughout the year (average 5.1 g DW m^{-2}) and contributed less than 5 % to the total above-ground biomass. At Gusung Tallang, however, macroalgae showed periods of blooming. A first short period of blooming was observed in April 1991, with a mean biomass of 207 ± 39 g DW m^{-2} (more than three times the mean above-ground seagrass biomass at this site), which lasted for approximately three

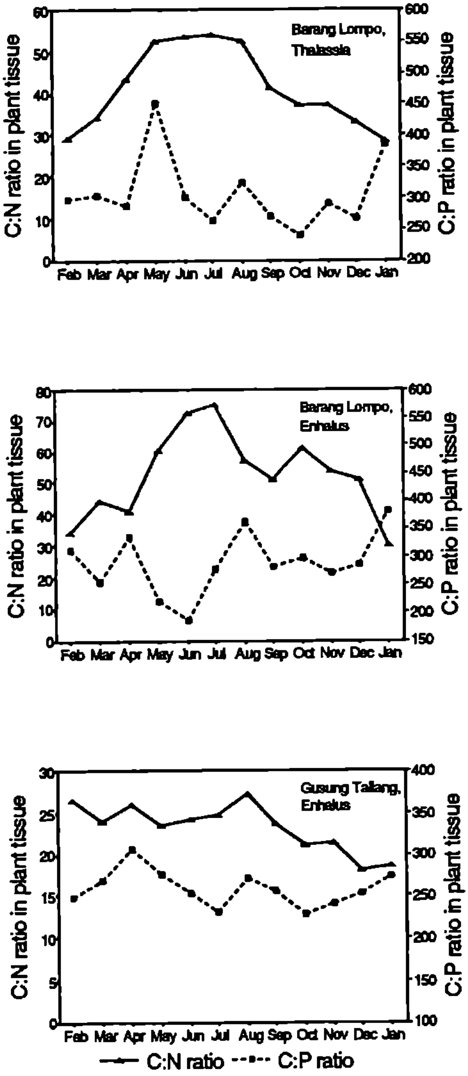


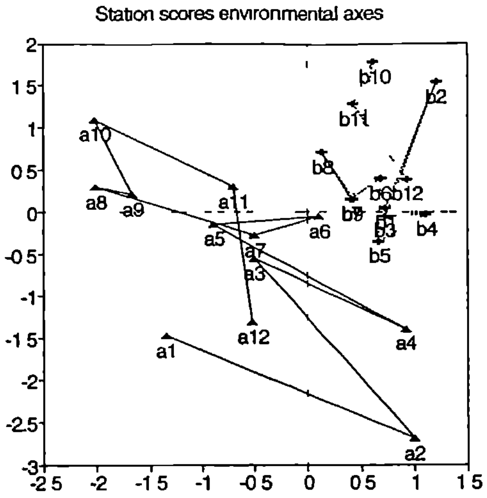
Fig. 6.13 Seasonal changes in C:N and C:P ratios in plant tissue of Thalassia hemprichii and Enhalus acoroides for the two sites. Ratios were calculated from total standing stocks of C, N and P in plant tissue (proportionally cumulated for the different plant parts); SD values ranged from 1 to 5 for C:N and from 20 to 78 for C:P.

weeks, and consisted of Gracilaria salicornia, G. verrucosa, G. blodgettii and Spyridia filamentosa. A second period of blooming started at the end of July 1991 and lasted until the end of November 1991, with a peak biomass of 257 ± 44 g DW m^{-2} observed in September. This bloom consisted of Ulva reticulata and had an average biomass of 206 ± 46 g DW m^{-2}. Towards the end of November the thick layer of Ulva gradually started to deteriorate and its biomass gradually decreased until hardly any Ulva was left at the end of January. While the Ulva mass was deteriorating, a new algal bloom appeared (end of December-January), which was dominated by Gracilaria spp. and Spyridia filamentosa, with a biomass of 117 to 195 g DW m^{-2} (including deteriorating Ulva). The average ash content (in % dry wt) of macroalgae was 31.7 ± 7.6 with highest values obtained in December-January during the decay of the Ulva mass (up to 45 %). Average (± SD) concentrations of carbon, nitrogen and phosphorus in the algal tissue were 24.29 ± 1.82, 2.14 ± 0.50 and 0.14 ± 0.02 (% dry wt) respectively (atomic ratio 448:34:1), without significant monthly changes. Multiple regression analysis of data from Gusung Tallang revealed no significant correlations between macroalgal biomass and measured environmental parameters, except with the predicted pattern of spring low tide exposure ($p < 0.05$).

Canonical correlation analysis

The canonical correlation analysis of data from both locations revealed significant correlations between variations in environmental and biological variables. Correlations were statistically significant along the first two ordination axes (canonical correlations: 0.917 and 0.844 respectively). This overall analysis provided data, which mainly indicated that the two stations differ considerably in the values and relative importance of the different environmental variables in explaining the observed dynamics (Fig 6.14). The analysis also revealed correlations (mainly along the second ordination axis) that seem to represent a seasonal trend (notably at Barang Lompo), roughly separating the scores of Barang Lompo for both biological and environmental variables of the months August-November from those of January-April (with the remaining months representing the transition). However, the interference effect of locality on the results was large. Therefore, we carried out additional canonical correlation analyses for each of the two localities separately. The analysis of data from Barang Lompo revealed a highly significant correlation between the seasonal patterns of biological and environmental variables, in which tidal exposure and water motion had the highest individual and overall contributions to the ordination (Table 6.2). In this analysis only the ordination over the first axis was significant (canonical correlation: 0.997) indicating that the observed dynamics could be largely explained by correlations over the first ordination axis.

Although it may seem likely to assume that seagrass dynamics at the coastal site (Gusung Tallang) are largely dependent on riverine influences from the nearby



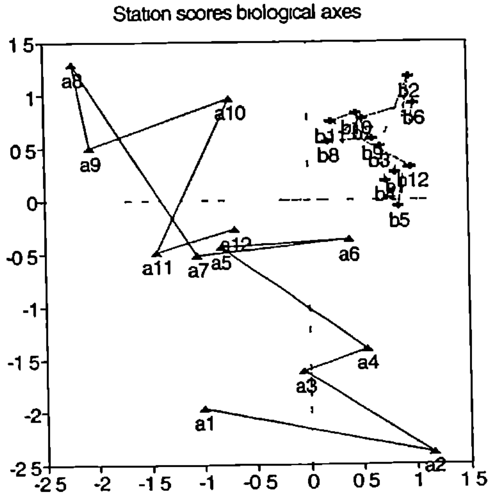


Fig. 6.14 Station scores of biological and environmental variables over the first two ordination axes derived from canonical correlation analysis. Stations: a = Barang Lompo; b = Gusung Tallang. Numbers (1 to 12) refer to months (1 = January, etc.). Explanation: see text.

Tallo River, canonical correlation analysis of the data from this station (separately from the data of Barang Lompo) revealed no significant correlation between the seasonal variation in measured environmental variables and the observed dynamics in seagrass variables.

Table 6.2

Canonical coefficients and canonical loadings for the first ordination axis derived from a canonical correlation analysis of monthly means of biological and environmental variables measured at Barang Lompo (see text for explanation). (DIN = Dissolved Inorganic Nitrogen); Biological variables are proportionally combined for Enhalus acorides and Thalassia hemprichii; C:N and C:P ratios are of standing stocks in plant tissue)

	Canonical Coefficients	Canonical Loadings
Environmental variables		
Tidal exposure	0.245	0.689
Water motion	0.903	0.866
Rainfall	-0.513	0.212
Turbidity (k)	0.478	-0.217
DIN-p	0.069	-0.218
PO_4-p	0.149	0.279
Biological Variables		
RGR	-0.185	-0.632
Total biomass	0.946	0.765
Leaf biomass	0.071	0.672
C:N ratio	-0.404	0.110
C:P ratio	0.405	0.384

DISCUSSION

This study has demonstrated that in some tropical marine habitats (i.e. coastal and intertidal areas), within-year variation in seagrass biomass, production and nutrient contents is considerable. In the seagrass bed at the offshore reef site (Barang Lompo) there was an unimodal seasonal pattern in which maximum shoot density (Thalassia: 3730 m^{-2}, Enhalus: 28 m^{-2}), maximum biomass (Thalassia: 1400 g DW m^{-2}, Enhalus: 300 g DW m^{-2}) and maximum standing stocks of nutrients in plant tissue (494 g C m^{-2}, 8.6 g N m^{-2}, 1.86 g P m^{-2}) occurred in July. Leaf production followed a less clear and different pattern, with maximum relative growth rates observed between August and November (up to 0.056 g DW g^{-1} d^{-1} for Thalassia and up to 0.037 g DW g^{-1} d^{-1} for Enhalus). Tidal exposure and water motion were identified in a canonical correlation analysis as the environmental variables contributing most significantly to the observed (seasonal) variation in seagrass variables at this site (Barang Lompo). Low waters at spring tide that occurred during day-time (August-December) caused a significant loss of above-ground material due to the deleterious effect of intense midday insolation, high temperatures, and, when the seagrass plants became fully emerged, of severe desiccation and 'burning'. Subsequent tidal currents (generally strongest at spring tide) may cause a considerable export of dead leaf material. High mortality as a result of exposure to air has also been reported among reef-edge corals from South Sulawesi (Whitten et al., 1987: p.107) and among macrobenthic invertebrates inhabiting the seagrass beds (Erftemeijer et al., in press). The die-off of above-ground seagrass material over vast areas of the reef flat of Barang Lompo during such spring low waters was generally followed by a rapid regeneration (periods of maximum RGR), usually within approximately 10 days after exposure.

Substantial evidence exists, that the rhizomes of seagrasses function as major storage organs from which the energy required for regeneration is mobilized (Dawes and Lawrence, 1979; Dawes and Lawrence, 1980; Dawes et al., 1979; Dawes et al., 1985; Libes and Boudouresque, 1987). Soluble carbohydrate was found to be the primary reserve mobilized in the rhizome after defoliation in Thalassia testudinum (Dawes and Lawrence, 1979) Halodule wrightii and Syringodium filiforme (Dawes and Lawrence, 1980) in Florida. In the present study, the considerable drop in C:N ratio of seagrass tissue of Thalassia hemprichii and Enhalus acoroides at Barang Lompo during months of daytime exposure (Fig. 6.13) is indicative of such mobilization of reserves.

In the seagrass bed at the coastal mudbank (Gusung Tallang), there was also a seasonal pattern in which maximum shoot density (Enhalus: 50 m^{-2}), maximum biomass (Enhalus: 392 g DW m^{-2}) and maximum standing stocks of nutrients in seagrass tissue (109 g C m^{-2}, 4.7 g N m^{-2}, 0.43 g P m^{-2}) occurred in May. Macroalgae in this seagrass bed showed periods of blooming during April 1991 (Gracilaria), August-November 1991 (Ulva), and December 1991-January 1992 (Gracilaria). Transect studies indicated considerable river inputs of dissolved and particulate constituents to the inshore waters by the Jene Berang and Tallo rivers, notably in the rainy season (Erftemeijer, unpublished data). Although seasonal dynamics in this coastal seagrass bed were expected to be largely determined by riverine influences of the Tallo River, canonical correlation analysis revealed no significant correlations between measured seasonal fluctuations in rainfall, salinity, nutrients, turbidity, tidal exposure and water motion and the observed dynamics in seagrass variables at this site. The applied methodologies and accuracy of sampling and analyses may have contributed to some irregularity in the datasets, but it is more likely to suggest that other factors are responsible for (at least part of) the observed dynamics at this site than those taken into consideration during the present study. It may be speculated that the occurrence and biomass of colonizing macroalgae (and probably also that of epiphytes and phytoplankton) at Gusung Tallang are more likely to follow the seasonal fluctuations in environmental variables rather than the seagrasses themselves, which appear to be a more stable and relatively more constant factor in the system, with limited response to large environmental fluctuations. The data on macroalgal biomass, however, revealed no significant correlation with measured environmental variables in a multiple regression analysis.

The absence of low-tide exposure to air of extensive parts of the seagrass meadow at Gusung Tallang (despite of its situation at approximately 30 cm above ELWS) is attributed to wind-stress and lens retention. A similar case of lens retention was reported by Holmquist et al. (1989) for seagrass-covered mudbanks in Florida.

The seasonal changes in total biomass and production observed in the seagrass beds in the present study area are relatively large for a tropical region. The relatively uniform temperature in tropical regions sustain a persistent biomass with substantial growth throughout the year, but tidal exposure (reef site) and river input-related influences (coastal site) may cause considerable variation in biological variables. Duarte (1989) found that the most (>70%) of the variability in seagrass biomass reflects seasonal responses, and concluded that the extent of variability is constrained by the latitudinal position of the plant stands, with biomass seasonality usually being small in tropical regions. Hillman et al. (1989) also reported smaller seasonal changes in the biomass of tropical seagrasses than those of temperate seagrasses in Australian waters.

The observed variability in shoot density and relative growth rate of Thalassia hemprichii in the present study (at Barang Lompo) is within the range reported for Thalassia hemprichii beds in Papua New Guinea (Brouns, 1985b). Leaf biomass variability, however, was much larger in the present study area (18-132 g DW m^{-2}) than reported for Papua New Guinea (100-160 g DW m^{-2}) by Brouns (1985b). As a consequence, estimates of leaf production per m^2 also differed considerably among the two studies (Sulawesi: 0.9-5.1 g DW m^{-2} d^{-1}; Papua New Guinea: 3.3-6.5 g DW m^{-2} d^{-1}). The seasonal variation in standing stock of nutrients (N and P) (maximum range c. two-fold) in seagrass plant tissue observed in the present study is comparable to that reported by Walker and McComb (1988) for Amphibolis antarctica and Posidonia australis in Shark Bay, Western Australia.

With the exception of porewater phosphate (Barang Lompo), which scored relatively high in the canonical correlation analysis, the availability of dissolved nutrients showed no significant correlation with the observed seasonal dynamics in the seagrass variables at both sites. Relatively higher porewater phosphate concentrations at Barang Lompo in months of daytime tidal exposure corresponded with increased relative growth rates, which corresponds with the findings of strong indications for P-limitation of seagrass growth on carbonate sediments in the Caribbean (Short et al., 1985; 1990). Recent evidence from fertilization experiments in seagrass beds in South Sulawesi, however, indicates that seagrass growth on carbonate sediments in this area is not significantly limited by the availability of nutrients and that nutrient supply meets the demands of the seagrasses (Erftemeijer et al., submitted). It seems therefore more likely, that the increase in porewater phosphate concentrations at Barang Lompo is related with the significant drop in seagrass biomass, suggesting that a major part of the dead seagrass material was retained and decomposed in situ within the meadow.

The overal significance of tidal exposure as a phenomenon that may induce considerable seasonal variability in biomass, production and nutrient contents in shallow-water seagrass beds in tropical regions is probably large. The phenomenon is certainly not restricted to the island of Barang Lompo, but is common throughout the study area in South Sulawesi (pers. obs.), and has also been observed in seagrass beds in Menado in North Sulawesi (pers. obs., June 1991), Ambon (H. de Iongh, pers. comm. 1992), Papua New Guinea (Brouns and Heijs, 1986), Kenya (E. Slim, pers. comm. 1993), Red Sea and Gulf of Eilat (den Hartog, pers. comm., 1993) and Mauritania (Van Lent et al., 1991; Hemminga, pers. comm., 1993). Bulthuis and Woelkerling (1983) similarly attributed a bimodal seasonal pattern with a midsummer minimum standing crop and density of the temperate seagrass Heterozostera tasmanica in Victoria (Australia) to exposure and desiccation stress at spring low tides during summer months.

The importance of daytime tidal exposure in determining within-year dynamics in shallow-water seagrass beds in the Indo-Pacific region may be considered as a major difference with the situation in the Caribbean, where the tidal amplitude is small, and where the only changes of considerable magnitude appear to be caused by hurricanes or cyclones (Zieman, 1987).

Some populations of temperate seagrass species, such as Zostera marina and Z. noltii, appear to be resistant to long periods of emersion, up to 6 h twice daily (Leuschner and Rees, 1993). In tropical regions, however, high intertidal populations of seagrasses may suffer negative effects from high insolation and dehydration, as reported for Zostera noltii from Mauretania (Van Lent et al., 1991). Intertidal Zostera populations in temperate waters have been shown to be able to maintain high rates of net photosynthesis under exposure to air (Leuschner and Rees, 1993). It is not known whether intensive photosynthetic activity during periods of emersion also occurs in the intertidal seagrass beds in the tropical Indo-Pacific region and how significant this process is for the carbon balance of these plants.

On the reef flat at Barang Lompo, where most environmental variables show only minor seasonal fluctuations (with the exception of tidal exposure and water motion), seagrasses (Thalassia hemprichii and Enhalus acoroides and locally some other species) can build up large and relatively stable biomasses, while macroalgae and phtyplankton components are relatively unimportant. At Gusung Tallang, however, where considerable fluctuations in environmental variables occur, large macroalgal biomasses and phytoplankton blooms appear rapidly at times of suitable conditions, but subsequently dissappear when the environmental factors turn unfavourable. Only the seagrass component is relatively stable in this vegetation, but suboptimal conditions (e.g. turbidity) allow development of only reduced biomasses of only one tall seagrass (Enhalus acoroides). At other coastal sites in South Sulawesi, where environmental conditions are even less favourable, seagrasses are completely absent (Verheij and Erftemeijer, in press).

So, increased disturbance and stress from large fluctuations in environmental conditions leads to an increased instability of the community, until no more seagrass growth is possible. Some subtidal carbonate sedimentary environments in the study area, which do not experience stress from low tide exposure, harbour mixed species vegetations with up to 8 different species (e.g. Bira), and similar multi-species meadows occur in subtidal reaches on coastal terrigenous sands under limited riverine influences (e.g. Palanro) (Verheij and Erftemeijer, in press).

The present study is among the few detailed studies monitoring seasonal changes in seagrass beds in the tropical Indo-Pacific region. Brouns (1985b, 1987b) studied seasonal dynamics of biomass and production of several seagrass species in Papua New Guinea and found relatively small variations. Similarly, Walker and McComb (1988), who reported on seasonal dynamics of the temperate seagrasses Amphibolis antarctica and Posidonia australis in tropical Australian waters, found relatively small variations in biomass and production. Whereas most studies in tropical waters revealed little seasonal variation in biomass and production of seagrasses, the present study has shown that in some habitats seasonal changes in seagrass variables can be considerable, although less pronounced than those of temperate seagrasses.

The results of the present study are from only one annual cycle; no data on year to year variation are available. It is significant that the magnitude of the measured parameters did not always return to their initial values, suggesting that there may be year to year variations in environmental conditions (see Walker and McComb, 1988). Besides, it is not clear to which extent the results have been affected by the prolongation of the dry season as a result of the 1991-1992 El Niño-Southern Oscillation event. Several authors have stressed the importance of long-term (two or more years) measurements (e.g. den Hartog, 1987), as recent research has shown that climatic differences can cause considerable variation between successive years in both the seasonal pattern and maximum standing crop reached at any one site (Hillman et al., 1989).

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CHAPTER SEVEN

GENERAL DISCUSSION

Seagrass beds are recognized for their importance as nursery grounds for many fish and crustacean species. Here, a woman collects fry of milkfish (*Chanos chanos*) at a seagrass-dominated coast at Selayar (January 1992).

Productivity and nutrient demand

Gross primary production in seagrass beds in South Sulawesi (0.9-4.4 g C m^{-2} day^{-1}, Chapter 3) was within the range of values reported for other tropical and subtropical seagrass beds (Zieman and Wetzel, 1980) and approaches the 5 to 7 g C m^{-2} day^{-1} primary production rates of reef flats reported from the Great Barrier Reef region (Furnas et al., 1990). Calculated annual gross production in these seagrass communities amounted up to c. 1600 g C m^{-2} $year^{-1}$, which supports the view that seagrass beds rank among the most productive of submerged aquatic ecosystems (Zieman and Wetzel, 1980, Hillman et al., 1989) along with coral reefs, mangrove forests and salt marshes (Table 7.1).

Table 7.1. Annual primary productivity of some submerged aquatic ecosystems of the world (in g C m^{-2} $year^{-1}$).

	Gross P	Net P	Source
Coral reefs	4500	650	Lewis, 1977; Mann, 1982
Mangrove forests	2700	1095	Lugo & Snedaker, 1974
Salt marshes	1750	470	Long & Mason, 1983
Seagrass beds	1600	180	This study

Relatively high rates of community respiration in these seagrass beds (1.4 to 5.1 g C m^{-2} day^{-1}) resulted in low net production rates (by the entire community) of less than 0.5 g C m^{-2} day^{-1}. This confirms similar findings by Lindeboom and Sandee (1989) in seagrass beds in the Flores Sea (Indonesia) and supports the hypothesis that the major part of the high primary production in tropical seagrass beds is used within the ecosystem for several consumption processes (Nienhuis et al., 1989). The fact that net community productivity was slightly negative on seven out of twelve occasions indicates that these systems may depend on some input of nutrients or organic material and that total net export of nutrients to adjacent ecosystems is probably insignificant or episodic.

The high productivity of the seagrass beds implies a high demand for phosphorus and nitrogen, two of the main elements which are essential to plant growth. There is little literature on the nutrient demand of tropical seagrasses, but available information suggests the annual requirement of seagrasses for nitrogen to range from 6.6 to 50 g N m^{-2} $year^{-1}$ (Hemminga et al., 1991). Assuming an average N:P ratio of 20 in seagrass tissue, this would indicate that the annual requirement for phosphorus would range from 0.3 to 2.5 g P m^{-2} $year^{-1}$. Net annual leaf production of Thalassia hemprichii at Barang Lompo reached 1000 g DW m^{-2} $year^{-1}$ (Chapter 6). Annual mean nutrient contents in leaf material of this species at Barang Lompo were 2.07 %N and 0.15 %P. This implies that the annual nutrient requirement of Thalassia hemprichii at this site is 20.7 g N m^{-2} $year^{-1}$ for nitrogen, and 1.5 g P m^{-2} $year^{-1}$ for phosphorus, which is within the range reported by Hemminga et al. (1991). Annual requirements of Enhalus acoroides were 2.0 g N m^{-2} $year^{-1}$ and 0.2 g P m^{-2} $year^{-1}$ at Barang Lompo, and 4.6 g N m^{-2} $year^{-1}$ and 0.4 g P m^{-2} $year^{-1}$ at Gusung Tallang respectively (similar calculations).

Nutrient availability

A quantitative study of nutrient concentrations and resources in shallow-water seagrass beds at six selected field sites in South Sulawesi (Chapter 2) revealed significant differences between seagrass communities on carbonate sediments (on the reef flats of the various coral islands) and seagrass communities on terrigenous sediments (along the west coast). Increased loads of phytoplankton and suspended particulate organic matter originating from terrigenous river discharges, high epiphyte cover, occasional macroalgal blooming, lower shoot densities and lower biomass (m^{-2}), increased leaf lengths and increased N and P contents of seagrass plant material at coastal terrigenous sites suggested an increased nutrient availability in comparison with the carbonate reef sites, which had clear oligotrophic waters, low epiphyte cover and much higher seagrass biomasses.

The concentration of dissolved inorganic forms of nitrogen and phosphorus in the ambient medium (water column, porewater) is largely determined by the rate of decomposition of organic material, molecular diffusive fluxes across the sediment-water interface, water-flow rates and adsorption-desorption characteristics of the sediment (Chapter 4). Simple measurements of nutrient concentrations, however, are not sufficient to draw conclusions on the availability of nutrients to plant growth. The complexity of the processes responsible for the balance between regeneration and removal cannot easily be entangled in the field. The ratio of C, N and P in plant tissue, however, is regarded to reflect the availability of N and P in the environment where the plant tissue was collected (Duarte, 1990). Mean C:N:P atomic ratios of above-ground seagrass tissue (leaf blades + sheaths) collected at six localities in the study area (Sulawesi) in 1990 ranged from 340:19:1 in terrigenous coastal areas to 565:18:1 in carbonate reef environments. Overall annual mean C:N:P ratios in seagrass tissue (above+below ground material) collected monthly during 1991 was 639:19:1 at the reef site Barang Lompo and 456:22:1 at the coastal site Gusung Tallang. The mean ratio in leaf blade material during 1991 was 530:29:1 at Barang Lompo and 363:23:1 at Gusung Tallang. These data indicate a richer supply of both N and P in the terrigenous environment than in the carbonate environment.

Nutrient concentrations in the water column were very low (often below detectable limits) at all localities investigated (annual means: phosphate 0.8-1.4 µM, ammonium 2.2-3.2 µM, nitrate+nitrite 0.9-1.4 µM). Even at coastal sites under significant influence of river inputs, the extremely favourable tropical conditions of maximum insolation and a constant water temperature of approximately 30 °C allow an immediate and rapid incorporation of dissolved nutrients in suspended particulate components (phytoplankton and microorganisms). Turn-over times of tropical phytoplankton populations in reef environments can be less than half a day, and uptake rates of dissolved nutrients by the phytoplankton are rapid and efficient (Furnas et al., 1990).

Porewater nutrient concentrations generally are much higher and vary with sediment depth. Annual mean porewater concentrations of phosphate, ammonium and nitrate+nitrite in the upper 10 cm of the sediment reached 11, 50 and 3 µM in carbonate sand and 5, 69 and 3 µM in terrigenous mud, respectively. Porewater nutrient concentration gradients with sediment depth and ratios between ammonium and phosphate porewater concentrations in terrigenous sediment could well be explained by stoichiometric modelling based on decomposition of organic material, and molecular diffusion. Vertical gradients of porewater nutrient concentrations in carbonate sediments seem to be determined by a more complex interaction of decomposition, molecular diffusion, bioturbation, accumulation depth of detritus, structure of the root zone, oxic-anoxic transitions, nitrification-denitrification, sorption of phosphate and other geochemical processes (Chapter 4).
The coarse carbonate sediments in the study area maintained relatively high phosphate concentrations (ranging from 5 µM in deeper layers up to c. 20 µM in the upper two cm of the sediment) in comparison with the extremely low phosphate concentrations (< 2 µM) reported from fine-grained carbonate sediments in the tropical Caribbean and Florida (Patriquin, 1972; Short et al., 1990; Fourqurean et al., 1992). It has been demonstrated in this study (Chapter 4) that the capacity of calcium carbonate sediments to adsorb phosphate is strongly dependent on the particle-size composition of the sediment, with fine-grained sediments having the highest adsorption capacity.

Implications for decomposition and flushing rates

Whereas water column nutrient concentrations mainly depend on inputs (e.g. from land-runoff or upwelling) and diffusion across the sediment-water interface, dissolved nutrients in the sediment porewater are largely replenished through decomposition of organic material (although adsorption-desorption processes may also be important: Chapter 4). The high leaf productivity and relatively stable standing crop of the seagrasses suggest a high turn-over of leaf material (e.g. Thalassia hemprichii at Barang Lompo: annual net leaf production = 1000 g DW m^{-2} $year^{-1}$; mean standing crop = 100 g DW m^{-2}; thus turn-over = 10 times per year; similarly I calculated a turn-over of approximately 7 times per year for the leaf biomass of Enhalus acoroides at both sites). Since no large amounts of seagrass litter were regularly observed accumulating on beaches or along the coast (as reported for example by Hemminga and Nieuwenhuize (1990) from an area in Mauritania), and organic matter contents of the sediments in the study area were low (organic C: 0.3 % in carbonate sediment, 0.6-1.9 % in terrigenous sediments), these data imply a rapid decomposition of organic material in situ, or a considerable export from the system.

Recent studies indicate that decomposition rates of seagrass material in carbonate sediments in the study area in Sulawesi are very fast: over 50% of the initial dry weight of seagrass material in litter bags had decomposed within two weeks of burial (Bogert, 1993; Stapel, in prep. and pers. comm., 1993). Export of considerable amounts of leaf litter from seagrass beds seems to occur at some of the islands located along the edge of the Spermonde continental shelf, which are subjected to stronger currents and water motions, but export is less important at most other localities (Stapel, in prep. and pers. comm. 1993). Only in periods when low waters of spring tides occur at day-time, intertidal seagrass beds may loose significant amounts of above-ground plant material by exposure and desiccation stress.

The locally considerable export of seagrass litter and the periodically significant loss of above-ground material from intertidal beds support the view that the seagrass meadow must be considered as an open system (Hemminga et al., 1991). The openness of the seagrass system is also related to the residence time of the water in the water column over the vegetation. Residence times of lagoonal water are related to the tidal amplitude, tidal currents around the reef and the strength of wind-driven currents overtopping the reef or flowing through the lagoon (Pickard, 1986). Residence times of water over reef flats in the central Great Barrier Reef were on the order of several days during calm periods, but were less than a day during a period of high winds (Furnas et al., 1990).

Nutrient limitation

Various authors have addressed the issue of nutrient limitation in seagrass growth in different parts of the world and have come to a wide range of often contradictionary results (Chapter 5). Short (1987) reviewed available information on nutrient limitation in seagrass beds and suggested that seagrasses growing in northern temperate climates (and) in habitats with terrigenous sediments typically experience nitrogen-limitation, whereas seagrasses occurring in tropical environments (and) on carbonate sediments appear to experience phosphorus limitation due to sorption of phosphate to the sediments.

It has been shown by experimental evidence, presented in Chapter 5 of this thesis, that nutrient limitation of seagrass growth in the study area does not occur. Nutrient supply apparently meets the demand of the seagrasses in environments characterized by terrigenous sediments as well as those characterized by carbonate reef sediments. Phosphorus limitation, which is generally regarded as typical for seagrass beds on carbonate sediments in tropical reef environments, could not be demonstrated. The adsorption of phosphate by the carbonate sediment, which has been generally acknowledged to be the responsible process for the observed P-limitation in these seagrass meadows, was found to be dependent on the particle-size composition of the sediment. The coarse sandy composition of the carbonate sediments in the study area (>80% larger than 63 µm of which > 40% larger than 312 µm) was responsible for a limited adsorption capacity of phosphate onto the carbonate mineral surfaces, thus maintaining relatively high porewater phosphate concentrations (Chapter 4). As a result of the limited effect of adsorption by the sediment on the availability of phosphate, P-limitation of seagrass growth did not occur. The importance of grain-size in processes affecting nutrient availability adds a new perspective to the general discussion on nutrient limitation of seagrass growth. Apparently, the generally accepted opinion that the growth of tropical seagrasses on reef sediments is limited by the availability of phosphorus needs to be revised, given its dependence on grain-size characteristics of the sediment.

Dynamics

Tidal exposure was found to be responsible for a seasonal pattern of considerable changes in biomass and production in intertidal seagrass beds on reef flats (Chapter 6). Exposure of the seagrass vegetation at these sites to air on hours of low water during spring tides occurs during the daylight period from the end of July until the beginning of January, with an average of 20 hours (daylight) exposure per month in this period. Exposure posed a serious stress of desiccation to the plants and resulted in a considerable loss of above-ground material during these months. Regeneration of the standing crop was fast and apparently occurred through mobilization of reserves stored in the rhizomes.

Seasonal dynamics in coastal seagrass beds were considerable, but statistical analyses did not reveal significant correlations between the large fluctuations in environmental variables and those in the seagrass variables. Nevertheless, the observed changes seemed to be largely determined by fluctuations in riverine influences related to the seasonal pattern in rainfall. The coastal meadows were characterized by occasional periods of blooming of phytoplankton and macroalgae.

The meadows depicted for the study of seasonal dynamics consisted of a vegetation of two (Barang Lompo) or one seagrass species. Apparently, the considerable stress from periodic tidal exposure (reef habitat) and salinity and turbidity fluctuations (coastal habitat) permits the establishment of Thalassia hemprichii and Enhalus acoroides in relatively dense meadows, but does not allow the development of full-grown multi-species vegetations of up to 7 or 8 species, as found at some other localities in the study area and also reported by Brouns and Heijs (1986).

The considerable seasonal dynamics in seagrass biomass observed in the study area is in contrast with reports compiled by Duarte (1989), who concluded that, in general, seasonal biomass changes are relatively small in tropical regions. It seems to appear, however, that much of the data on tropical seagrass communities are derived from the Caribbean region, where the effect of tidal exposure on seagrass biomass is insignificant due to the small tidal amplitude in those areas.

Nutrient acquirement

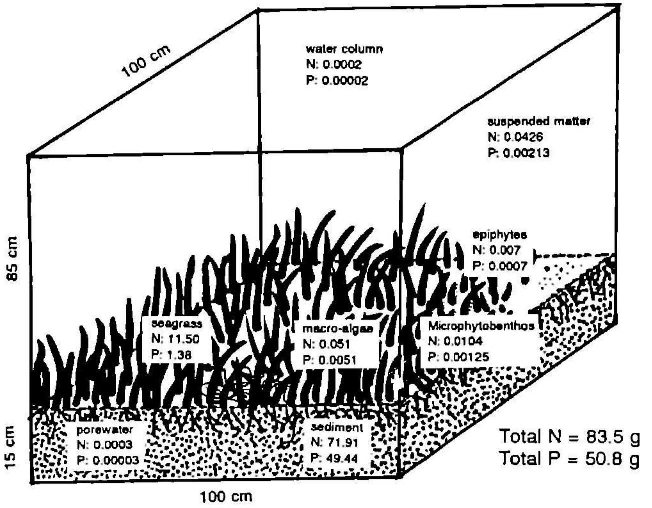
The site of nutrient uptake by seagrasses (roots or leaves) remains an ongoing dispute. Evidence from partitioned chamber experiments (Thursby and Harlin, 1982; Short and McRoy, 1984) and studies using labelled isotopes of phosphorus and nitrogen (McRoy and Barsdate, 1970; Iizumi and Hattori, 1982; Borum et al., 1989) have demonstrated that seagrasses are capable of nutrient uptake with leaves and roots, as has also been demonstrated for other submerged rooted aquatic macrophytes (Rattray et al., 1991). Yet, it remains unclear how the majority of nutrients required for plant growth are acquired in the field situation. McRoy and McMillan (1977) suggested that the sediments are the principle site of nutrient adsorption for most seagrasses and that leaf uptake was relatively unimportant. Although this theory was merely a speculation based on little evidence, it has been widely adopted in further studies. Results obtained in partitioned chambers by Penhale and Thayer (1980) suggested root-uptake in Zostera marina to be dominant over leaf uptake.

One might speculate that both the leaves and roots are simultaneously used in the uptake process, and that their relative contribution to the total uptake of nutrients by the plant depends on the availability of nutrients in the corresponding medium (water column versus porewater, see also Borum et al., 1989) and the ratio between leaf surface area and active sorptive root surface (Smith et al., 1979). It seems logical to assume that the majority of nutrient uptake will take place by the roots, since the sediment and interstitial water contain considerable reserves of nitrogen and phosphorus. At times of increased nutrient concentrations in the water column (which is more likely to be of episodic nature in tropical oceanic waters) leaf uptake might be the dominant process (temporarily). This might perhaps be regarded as a meachanism by which the seagrass plants are able to capture excess pulses of nutrients in the water column which are stored in rhizomes for later use.

Nutrient uptake from the water column, however, seems to be more favourable than from sediment porewaters, since the roots need to actively pump oxygen into the sediment. Oxygen transported into the root zone is involved in several biogeochemical processes, including oxidation of toxic reduced compounds such as ferrous iron and sulphide (Reddy et al., 1989). Another aspect that pleads for leaf uptake as the main process of nutrient acquisition is the effect of water velocity. Current flow may enhance nutrient uptake at the leaf surface of seagrasses. Uptake rates of compounds by aquatic organisms (e.g. nutrients by seagrass leaves) have been shown to be dependent on mass transfer of water along the diffusive boundary. The effect of water velocity on nutrient uptake in coral reef-flat communities has been recently elaborated for phosphorus by Atkinson and Bilger (1992). Rates of phosphate uptake increased as water velocity increased. It should be born in mind that coral reef ecosystems, which rely entirely on nutrient resources in the water column, usually reach very high primary productivities that exceed seagrass productivities (Table 7.1). The open character of the water column and the continuous flow of the water along the seagrass leaves greatly enhances the uptake of nutrients by the leaves. As such, leaf uptake of nutrients from the nutrient-poor water column might exceed root-uptake from porewaters, which, although they hold much higher concentrations, are much less mobile and replenishment of nutrients that are removed by uptake processes largely depends on (relatively slow) diffusion processes and regeneration. Solute transport of porewaters through shallow marine sediments may occur as a result of wave-induced pressure gradients, current-obstruction interactions and convection due to salinity changes (estuarine sediments), and bioturbation may significantly increase porewater exchange (Webster, draft paper). These porewater movements are, however, considered negligible in comparison to those taken place in the water column.

It seems reasonable to assume that the capacity of seagrasses to utilize sediment nutrients with their well-developed root systems plays an important role in their dominance over algae in soft sedimentary environments. Algae (which clearly dominate over seagrasses on hard substrates) are considered to solely depend on nutrient resources in the water column, although a few rhizophytic species have been shown to acquire nutrients directly from sediment sources via rhizoid holdfasts (Williams, 1984; McGlathery et al., 1992). Increased nutrient availability in the water column usually leads to a decline in seagrass biomass and a gradual take-over by algae (Jensen and Gibson, 1986; Burkholder et al., 1992) with macroalgae dominating over seagrasses under conditions of marked eutrophication (Walker and McComb, 1992). Human-induced eutrophication has been marked as the major cause of world-wide seagrass decline (Walker and McComb, 1992).

BARANG LOMPO



GUSUNG TALLANG

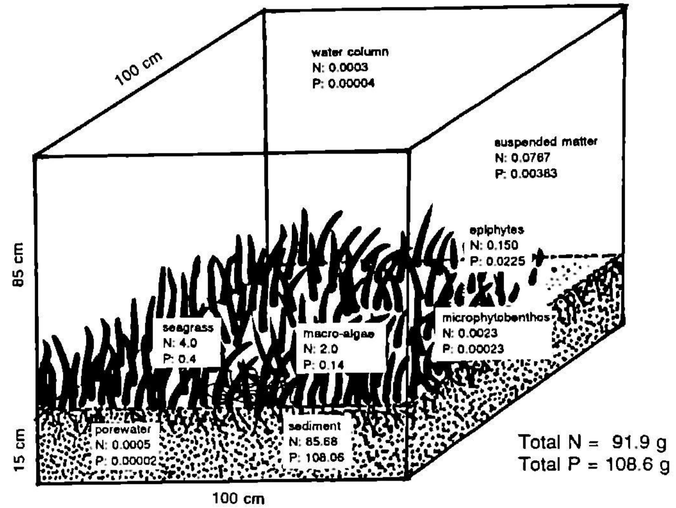


Fig. 7.1 Absolute quantities (in g) of nitrogen (N) and phosphorus (P) in the various components in a cubic metre of seagrass ecosystem containing 850 l of seawater (water column) and 150 l of sediment. Data presented for Barang Lompo (reef site) and Gusung Tallang (coastal site).

A substantial proportion of the total nutrient requirement of seagrasses may be met by internal recycling (Borum et al., 1989; Hemminga et al., 1991). As with many plants, nutrients are withdrawn from ageing leaves, remobilized during senescence and translocated to sites of growth and storage. This process of internal recycling has been estimated to provide about 25 % of the annual requirement of seagrasses for nitrogen (Hemminga et al., 1991). For phosphorus no such data are available, but there is no reason to assume that this process would differ considerably from that observed for nitrogen.

Nutrient pools and fluxes

The absolute quantities of nitrogen and phosphorus present in the various components in a cubic metre of seagrass ecosystem containing 850 l of seawater (water column) and 150 l of sediment (including 75 to 100 l of porewater, depending on the porosity) were calculated for a typical carbonate site and a typical terrigenous site, from the data presented in the various chapters of this thesis (Figure 7.1). These data were then expressed as relative proportions to the total pool of N and P (Figure 7.2). In both sedimentary environments, the majority of the entire pool of nutrients (> 85%) is present in the sediment, largely unavailable to the plants [note: This remained virtually unchanged when the relative proportions of water:sediment in the box of the model was changed from 850:150 to a 950:50 or a 500:500 basis]. Only a tiny fraction (< 0.001%) of the total pool of nutrients is present in the water column and porewater in dissolved forms directly available for uptake by the plants (both environments). Approximately 13.8 % of the nitrogen and 2.7 % of the phosphorus is contained in the seagrass biomass in meadows at reef sites. The amount of N and P contained in other biota (epiphytes, macroalgae, phytoplankton, microphytobenthos) is negligible (< 0.1 %) at these sites. In seagrass beds on coastal terrigenous sediments, only 4.3 % of the total pool of N and 0.4 % of the total pool of P is captured in the plant biomass. In this environment, an additional 2 to 3 % of the total pool of N and 0.1 to 0.2 % of the total pool of P may be contained in macroalgae.

Data on nutrient incorporation rates by the seagrass vegetation (see above; notice that for Barang Lompo both species are taken together) and diffusion fluxes of nutrients from sediment to water column (see Chapter 4) are summarized in Table 7.2. These data allow mass-balance calculations of fluxes necessary to maintain the observed productivities. I performed such calculations according to three different approaches:

1). Assumption: Seagrasses take up all nutrients with their leaves from the water column, and nothing with their roots. The appropriate mass-balance then reads: incorporation = diffusive flux + input of new nutrients. If this is correct, the data from Table 7.2 suggest an input of 22.05 g N m^{-2} $year^{-1}$ and 1.25 g P m^{-2} $year^{-1}$ at

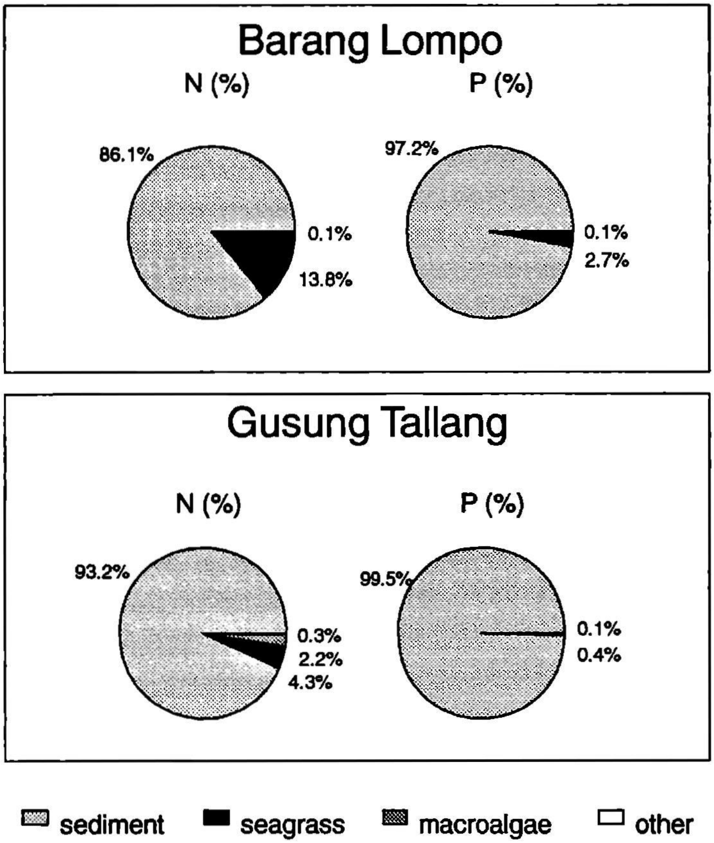


Fig. 7.2 Relative proportions of N and P (in %) in the various components of the seagrass ecosystem to the total pool of N and P, for Barang Lompo and Gusung Tallang.

Barang Lompo and an input of 3 g N m^{-2} $year^{-1}$ and 0.3 g P m^{-2} $year^{-1}$ at Gusung Tallang. This implies that [assuming a 100% uptake efficiency of the leaves resulting in complete stripping of the water] the amount of dissolved nutrients available in the water column needs to be replaced between 57000 (P) and 120000 (N) times at Barang Lompo and between 7800 (N) and 11000 (P) times at Gusung Tallang.

Table 7.2
Summary of data on annual incorporation of N and P in the seagrass biomass and on diffusive fluxes of N and P from the sediment porewater into the overlying water column for seagrass beds at Barang Lompo and Gusung Tallang.

	Barang Lompo	Gusung Tallang
Rate of incorporation:		
g N m^{-2} $year^{-1}$	22.55	4.56
g P m^{-2} $year^{-1}$	1.65	0.44
Diffusive porewater flux:		
g N m^{-2} $year^{-1}$	0.53	1.56
g P m^{-2} $year^{-1}$	0.42	0.14

This suggests that the observed productivity requires a turn-over of the water column of at least 240 times per day at Barang Lompo and at least 25 times per day at Gusung Tallang. Given the estimated residence time of water on reef flats (minimum: 0.5 days), this approach does not seem to lead to satisfactory results.

2). Assumption: Seagrasses take up all nutrients with their roots from the sediment porewater, and nothing with their leaves. The appropriate mass-balance then reads: incorporation = regenerated nutrients - diffusive flux. If this is correct, the data from Table 7.2 indicate that regeneration should account for 23.05 g N m^{-2} $year^{-1}$ and 2.05 g P m^{-2} $year^{-1}$ at Barang Lompo, and for 6.12 g N m^{-2} $year^{-1}$ and 0.58 g P m^{-2} $year^{-1}$ at Gusung Tallang. Given the average N and P contents of plant material at these sites (Chapter 6), this would imply decomposition of 1124-1367 g DW m^{-2} $year^{-1}$ at Barang Lompo and 264-268 g DW m^{-2} $year^{-1}$ at Gusung Tallang. This is slightly more than the total net seagrass leaf production at both sites, and implies that all organic matter produced by the seagrasses is decomposed within the system. To account for the loss of nutrients by diffusion from the sediment to the water column, the system depends on some import of organic material, and total net production of the entire ecosystem is slightly negative. [Note: This is supported by the data on primary productivity presented in Chapter 3]. Nitrogen fixation may contribute substantially to the available pool of N in the sediment (1 to 6 g N m^{-2} $year^{-1}$ (Hemminga et al., 1991)). However, no such additional sources of nutrient input exist for phosphorus, which implies that the calculated decomposition rates are necessary at least to account for the phosphorus demand of the plants.

3). Assumption: Seagrasses take up nutrients with both their roots and leaves from porewater and water column. Model:

I : N-incorporation = N-regeneration + N-conc.(water) * flushing.
II: P-incorporation = P/N ratio * N-regeneration + P-conc.(water) * flushing.

These two mass-balances could be solved (two equations with two unknown values) to determine flushing rates and N-regeneration rates. The data suggest flushing rates of 37450 times per year at Barang Lompo and 8416 times per year at Gusung Tallang (i.e. 103 and 23 times per day respectively). The higher flushing rates at Barang Lompo compared to Gusung Tallang are consistent with the results of plaster block experiments presented in Chapter 6. N-regeneration rates in this situation should be in the order of 15.7 g N m^{-2} $year^{-1}$ at Barang Lompo and 2.2 g N m^{-2} $year^{-1}$ at Gusung Tallang. These data imply that decomposition of at least 766 g DW m^{-2} $year^{-1}$ at Barang Lompo and 97 g DW m^{-2} $year^{-1}$ at Gusung Tallang is necessary to support the observed productivities (i.e. nearly 70% (at BL) and 48% (at GT) of total organic production). [Note: this model assumes a 100% efficiency of uptake of water column and porewater nutrients].

From these calculations it can be concluded, that the majority uptake of nutrients by seagrasses is done by the rhizome-root system from the sediment sources, while leaf uptake from the water column can only supply a maximum of 2% (Barang Lompo) to 10% (Gusung Tallang) of the nutrient demand (assuming an actual flushing rate of the water column of twice a day). The data also imply that the majority of the produced organic matter has to be rapidly decomposed inside the seagrass meadow to support observed productivities, and that internal recycling through remobilization of nutrients from old plant parts during senescence is very likely to supply an important part of the required nutrients. The limited amount of data available suggest that internal recycling may account for approximately 25% of the annual requirement for nutrients of seagrasses (Hemminga et al., 1991). In some terrestrial plants even higher rates have been reported (Clark, 1977; Pugnaire and Chapin, 1993). It seems to occur that terrestrial plants in low-nutrient environments generally have a higher nutrient resorption efficiency than those growing on more fertile soils (Pugnaire and Chapin, 1993). Nothing on this is known with respect to seagrasses, and it is clear that the process of internal nutrient resorption deserves special attention in future seagrass research.

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SUMMARY

Seagrasses are flowering marine plants with well-developed root systems. They form extensive meadows in shallow coastal waters throughout the world. In tropical regions they have reached optimal development, with a high species diversity and mixed-species vegetations being characteristic of the Indo-Pacific region. Here, the seagrass beds have important ecological functions, including the stabilisation of the substratum (thus reducing coastal erosion and preventing sedimentation of coral reefs) and functioning as nursery ground for various fishes and crustaceans (including several species of economic importance). The key to a better understanding of the functioning of the seagrass ecosystem lies in the factors regulating growth, production, decomposition and regeneration processes. Whereas light is considered to be one of the most important limiting factors to seagrass growth in the often turbid coastal waters of the temperate region, this is not likely to be the case in most tropical seas, which are usually characterized by low turbidity. In these waters, seagrass growth is more likely to be limited by the availability of nutrients. This Ph.D thesis describes the results of a four-year research into the role of the nutrients most likely to be limiting to seagrass growth (phosphorus and nitrogen) in seagrass beds in the Spermonde Archipelago and adjacent coastal waters in South Sulawesi, Indonesia.

A detailed quantitative study of nutrient concentrations and resources in seagrass beds at six different localities in the study area (Chapter 2) indicated significant structural and functional differences between seagrass beds growing on terrigenous sediments along the coast (sand and mud deposited by rivers) and seagrass beds growing on carbonate sediments on the shallow reef flats of the various coral reef islands in the study area. Increased loads of phytoplankton and suspended particulate organic material in the water column, high epiphyte cover, occasional macroalgal blooming, lower seagrass shoot densities and biomass, increased leaf lengths of seagrass plants, and C-, N- and P-contents of seagrass plant tissue in seagrass beds at coastal sites (on terrigenous sediments) were all indicative of an increased nutrient availability in comparison to the seagrass beds on offshore reef platforms, which had cristal-clear waters, low epiphyte cover of seagrass leaves and much higher seagrass densities and biomass.

Measurements of primary production in the seagrass beds using different techniques (leaf- and rhizome marking methods, plastochron interval technique, and oxygen evolution studies with electrodes in bell jars) revealed similar results (Chapter 3). The seagrass communities in the study area are characterized by a high gross primary production (0.9 to 4.4 g C m^{-2} per day), which is within the range of values reported from seagrass beds in other tropical areas and supports the view that seagrass beds rank among the most productive of submerged aquatic ecosystems, along with coral reefs, mangrove forests and salt marshes. The oxygen evolution measurements indicated high rates of community respiration in these

seagrass beds, resulting in very low net production rates by the entire community (in some cases even negative rates were found). This indicates that a major part of the high primary production is used within the ecosystem for several consumption processes. Pioneering seagrass species, such as Halodule uninervis and Cymodocea rotundata, showed considerably higher growth rates than constant (climax) species, such as Thalassia hemprichii and Enhalus acoroides. The leaf growth of Enhalus acoroides was significantly higher in coastal areas than at offshore reef sites, but areal production (per m^2) was lower in coastal areas due to much lower shoot densities.

Chapter 4 describes the major geochemical interactions between nutrients and sediments in seagrass beds. Depth profiles of measured porewater nutrient concentrations in coastal terrigenous sediments could well be explained by modelling based on stoichiometric decomposition of organic material and molecular diffusion. Measured porewater phosphate concentrations in carbonate reef sediments, however, were significantly higher in the upper few cm of the sediment than would be expected based on stoichiometry. This apparent phosphate enrichment is attributed to rapid regeneration of both N and P in the rhizosphere and subsequent rapid removal of ammonium by nitrification. The capacity of carbonate sediments to adsorb phosphate was directly related to their grain-size composition. The coarse-grained carbonate sediments in the study area maintained relatively high porewater phosphate concentrations as a result of their limited adsorption capacity, in contrast with extremely low porewater phosphate concentrations reported from fine-grained carbonate sediments in the Caribbean, where strong evidence for P-limitation of seagrass growth has been found.

Experimental in situ fertilization of three seagrass beds (two on carbonate sediment, one on terrigenous sediment) with N and P by various additions of slow-release fertilizers (4-5 months) to the sediment had no significant effects on the biomass, shoot density and leaf production of the seagrasses (Chapter 5). The C-, N- and P-contents of seagrass tissues changed significantly in response to N addition and P addition (but not N+P additon), and indicated an increase in N (and to a lesser extent P) incorporation (luxury uptake). The coarse grain-size composition of the carbonate sediments in the study area and their consequently high porewater phosphate concentrations are considered to explain the absence of P-limitation of seagrass growth, which is generally considered to be characteristic of tropical carbonate-rich environments.

Chapter 6 describes the seasonal dynamics in a seagrass bed on a reef flat (carbonate sediment) and a seagrass bed on muddy substrate along the coast (terrigenous sediment). Both seagrass beds showed distinct seasonal dynamics, with relatively large variations in seagrass biomass, shoot densities, production and nutrient contents during the year. A canonical correlation analysis indicated a significant correlation between the observed dynamics in biological (seagrass) variables at the reef flat environment and the measured set of environmental variables. Periodic exposure of the (intertidal) seagrass bed on hours of low water during spring tides at daylight (during the months July-January) and seasonal changes in the exposure to water motion (measured with the clod card technique) were found to be the most important environmental variables explaning the seasonal changes in seagrass variables. Daylight tidal exposure resulted in a significant loss of above-ground plant biomass due to desiccation and burning of the leaves, but regeneration is rapid through immobilization of reserves from the rhizomes. This phenomenon is not restricted to South Sulawesi, but is common throughout the Indo-Pacific region as well as in parts of Africa and is in sharp contrast with the Caribbean, where the tidal amplitude is small. The observed seasonal changes in biological variables in the coastal seagrass bed on terrigenous mud showed no significant correlation with measured variations in environmental variables, despite of the expectation that these were largely caused by the riverine influences of the nearby Tallo River. The occurrence and biomass of colonizing macro-algae at this site was not significantly correlated either with the seasonal changes in environmental variables.

In Chapter 7, the results of the previous chapters are evaluated and combined. Data on concentrations and resources of phosphorus and nitrogen from these chapters are processed in a box-model of one cubic metre of a seagrass ecosystem, in which the individual contribution of the various components of the ecosystem to the total pool of N and P in the system is calculated. The majority (86 to 99%) of the total pool of N and P is contained in the sediment. These data, together with data on productivity, are evaluated in mass balance calculations, in which the implications for the site of nutrient uptake (leaves or roots), decomposition and flushing rate of the water column are discussed. Based on these calculations it is concluded that the seagrasses in the study area collect the majority (90% or more) of the nutrients required for their growth from the porewater with use of their root system. Leaf uptake (maximum 10%) seems to be less important, which is in contrast with findings of some nutrient-uptake experiments with seagrasses in the laboratory. These data also suggest that internal recycling of nutrients by remobilisation from older plant parts during senescence is likely to be an important process that might substantially contribute to the nutrient demand of the actively growing parts of the seagrass plants. This process deserves special attention in future research.

SAMENVATTING

Zeegrassen zijn bloeiende mariene planten met goed ontwikkelde wortelstelsels, die uitgestrekte velden vormen in de ondiepe kustwateren in grote delen van de wereld. In tropische gebieden zijn ze tot maximale ontwikkeling gekomen, zoals in het Indo-Pacifische gebied, waar ze in grote soortsverscheidenheid en als gemengde vegetaties voorkomen. Zeegrasvelden vervullen hier belangrijke oecologische functies, waarvan substraatstabilisatie (waardoor kusterosie en sedimentatie van koraalriffen wordt voorkomen) en het functioneren als kinderkamer voor allerlei soorten vissen en schaaldieren (waaronder soorten van economisch belang) de voornaamste zijn. De sleutel tot het beter begrijpen van het functioneren van het zeegras-oecosysteem ligt in de factoren die de groei en productieprocessen alsmede de afbraak- en regeneratieprocessen reguleren. Over het algemeen beschouwt men de beschikbaarheid van licht in de vaak troebele kustwateren in de gamatigde streken als een van de belangrijkste factoren die beperkend zijn voor de groei van het zeegras. Maar in de doorgaans zeer heldere oligotrofe wateren van tropische gebieden speelt deze factor een ondergeschikte rol. Daar is het waarschijnlijk de beschikbaarheid van voedingsstoffen die beperkend is voor de groei van het zeegras. Dit proefschrift beschrijft de resultaten van vier jaar onderzoek naar de rol van de meest waarschijnlijke groei-limiterende voedingsstoffen (stikstof en fosfor) in zeegrasvelden in de Spermonde Archipel en aangrenzende kustwateren in Zuid Sulawesi (Indonesië).

Een gedetailleerde kwantificering van nutrienten-concentraties en -gehalten in zes verschillende zeegrasvegetaties in dit gebied (Hoofdstuk 2) toonde aan dat er grote verschillen bestaan tussen zeegrasvelden op terrigene sedimenten langs de kust (modder en zand dat door rivieren is afgezet) en zeegrasvelden op carbonaatsedimenten op de ondiepe rifplatforms van de diverse koraaleilanden in het onderzoeksgebied. Hogere gehalten van fytoplankton en gesuspendeerd organisch materiaal in het water, een sterk ontwikkelde epifytenbegroeiing op de zeegrasbladeren, het incidenteel optreden van macroalgenbloei, de beduidend lagere scheutdichtheden en biomassa's van het zeegras, de opvallend grotere bladlengte en de gehalten aan C, N en P in het plantenmateriaal bij de zeegrasvelden langs de kust (op terrigene sedimenten) duidden allen op een hogere beschikbaarheid van nutrienten in vergelijking met de zeegrasvelden op de rifplatforms, die gekarakteriseerd werden door zeer helder water met zeer lage gehalten van gesuspendeerd materiaal, veel lagere epifytenbedekking van zeegrasbladeren en veel hogere zeegrasbiomassa's en -dichtheden.

Productiemetingen in de zeegrasvelden met verschillende meetmethoden (blad- en rhizoommarkering, plastochrone interval en zuurstofevolutie met electroden in transparante meetklokken) leverden vergelijkbare resultaten op (Hoofdstuk 3). De zeegrasgemeenschappen in het onderzoeksgebied worden gekarakteriseerd door een hoge bruto primaire productie (0.9 tot 4.4 g C m^{-2} per dag), overeenkomstig met de gegevens in de literatuur over andere tropische gebieden en in orde van grootte vergelijkbaar met andere hoogproductieve mariene oecosystemen, zoals mangrovebossen, koraalriffen en schorren. De zuurstof-metingen toonden verder aan dat de zuurstofconsumptie in de zeegrasvelden zeer hoog is, wat resulteert in een uiterst lage netto productie van het gehele systeem (in sommige gevallen zelfs negatief). Dit wijst erop dat een zeer groot deel van het geproduceerde organische materiaal in het zeegrassysteem zelf wordt afgebroken. Pioniersoorten, zoals Halodule uninervis en Cymodocea rotundata, toonden veel hogere groeisnelheden dan konstante soorten, zoals Thalassia hemprichii en Enhalus acoroides. De groeisnelheid van bladeren van Enhalus acoroides in kustgebieden was signifikant hoger dan in rifgebieden, maar door lagere scheutdichtheden in kustgebieden was de bladproductie per m^2 hier toch beduidend lager.

Hoofdstuk 4 beschrijft de voornaamste geochemische interacties tussen nutrienten en sedimenten in de zeegrasvelden. Diepteprofielen van gemeten poriënwater-nutriëntenconcentraties in kustsedimenten konden goed worden verklaard op grond van modellering van stoichiometrische afbraak van organisch materiaal en molekulaire diffusie. De gemeten poriënwater fosfaatconcentraties in rifsedimenten waren echter veel hoger in de bovenste paar centimeter van het sediment dan zou worden verwacht op basis van stoichiometrie. Deze schijnbare fosfaatverrijking wordt toegeschreven aan een snelle regeneratie van zowel N en P in de rhizosfeer, gevolgd door een snelle verwijdering van ammonium door nitrificatie. De capaciteit van carbonaatsedimenten om fosfaat door middel van adsorptie te onttrekken aan het poriënwater blijkt direkt gerelateerd te zijn aan de korrelgrootte van het sediment. De relatief grove sedimentsamenstelling van de carbonaatsedimenten in het onderzoeksgebied resulteerde daarom in relatief hoge fosfaatgehalten in het poriënwater, hetgeen in kontrast staat tot de zeer lage fosfaatgehalten in poriënwaters van fijnkorrelige carbonaatsedimenten in het Caraibische gebied, waar sterke aanwijzingen zijn gevonden voor fosfaatlimitatie van zeegrasgroei.

Kunstmatige bemesting van drie zeegrasvelden (twee op carbonaatsediment, een op terrigeen sediment) met N en P door middel van het toevoegen van "slow-release" kunstmestkorrels in het sediment had (na 4-5 maanden) geen signifikante effecten op de biomassa, scheutendichtheid en bladproductie van het zeegras (Hoofdstuk 5). N additie en P additie afzonderlijk (maar niet N+P additie) leidden tot wel tot een signifikante verandering in de C-, N- en P-gehalten in het plantenmateriaal, hetgeen wijst op een verhoogde mate van N- (en in mindere mate ook P-) incorporatie ("luxury-uptake"). De grove korrelsamenstelling van de carbonaatsedimenten in het onderzoeksgebied en de daarmee samenhangende hoge fosfaatconcentraties in het poriënwater worden beschouwd als de belangrijkste verklaring voor het verschijnsel, dat de fosfaatlimitatie, die doorgaans als karakteristiek wordt beschouwd voor zeegrasvelden op tropische koraalsedimenten, hier niet optreedt.

Hoofdstuk 6 beschrijft de seizoensdynamiek in twee kontrasterende zeegrasvelden. Een zeegrasveld op een rifplatform (carbonaat) en een zeegrasveld op een modderbank langs de kust (terrigeen) vertoonden beide een duidelijke seizoensdynamiek, met relatief vrij grote veranderingen in zeegrasbiomassa, scheutendichtheden, productie en nutrientengehalten gedurende het jaar. Een canonische correlatieanalyse toonde aan, dat de gevonden dynamiek in biologische (zeegras) variabelen op het rifplatform een signifikante correlatie vertoonde met de gemeten set aan omgevingsvariabelen. Het periodiek overdag droogvallen van grote delen van dit zeegrasveld bij laag water tijdens spring-tij (gedurende de maanden juli-januari) en seizoensveranderingen in de blootstelling aan de waterbewegingen (gemeten met de 'clod card' techniek) werden aangemerkt als de belangrijkste omgevingsvariabelen die de veranderingen in zeegrasvariabelen veroorzaken. Het overdag droogvallen bij spring-tij veroorzaakt het afsterven van het merendeel van de bovengrondse biomassa van het zeegras, dat zich evenwel daarna snel weet te regenereren door het mobiliseren van reserves uit de rhizomen. Dit verschijnsel is niet beperkt tot Zuid-Sulawesi, maar komt getuige literatuur en mondelinge mededelingen voor in het gehele Indo-Pacifische gebied en zelfs in Afrika, en vormt zo een scherp kontrast met het Caraibische gebied, waar de getijdebeweging minimaal is. De gevonden seizoensveranderingen in biologische variabelen in het zeegrasveld op de modderbank aan de kust vertoonden geen signifikante correlatie met de gemeten veranderingen in milieufactoren, ondanks de verwachting dat deze vooral door de rivierinvloed van de Tallo Rivier zouden zijn veroorzaakt. Ook de periodiek optredende macro-algenbloei die hier werd waargenomen kon niet signifikant worden gecorreleerd aan de seizoensvariatie in milieuvariabelen.

In Hoofdstuk 7 worden de gevonden resultaten van de voorafgaande hoofdstukken tenslotte nog eens geëvalueerd en met elkaar in verband gebracht. Data van stikstof en fosfor uit deze hoofdstukken worden uiteindelijk verwerkt in een boxmodel van een kubieke meter zeegras-oecosysteem, waarin de bijdrage van iedere komponent aan het totale N en P budget in het systeem wordt berekend. Het meerendeel (86 tot 99%) van de totale hoeveelheid N en P zit in het sediment. Deze gegevens worden uiteindelijk tezamen met de productiegegevens verwerkt in een massa-balans berekening, waarbij de implicaties voor de vermoedelijke plaats van nutrienten-opname (bladeren of wortels), decompositie en retentietijd van de waterkolom worden besproken. Uit deze gegevens volgt, dat de zeegrassen ruim 90% van de voedingsstoffen die zij voor de groei nodig hebben, uit het poriënwater halen door middel van hun wortelstelsel. Bladopname (maximaal 10%) lijkt dus minder belangrijk, in tegenstelling tot wat soms wordt verondersteld. Bovendien lijkt interne recycling van nutrienten, door remobilisering uit oude plantendelen gedurende het afsterven daarvan, een belangrijk proces dat in substantiële mate bijdraagt aan de nutrientenbehoefte van de planten. Dit proces verdient in toekomstig onderzoek speciale aandacht.

RINGKASAN

Lamun (seagrass) adalah tumbuhan berbunga dengan sistem akar yang lengkap. Di seluruh dunia dapat ditemukan padang rumput Lamun yang terbenam di perairan laut yang dangkal. Di daerah tropis Lamun itu paling tinggi perkembangannya di mana dijumpai padang Lamun yang keanekaragam jenis tinggi yang begitu khas untuk kawasan Indo-Pasifik. Di sini padang rumput Lamun ini merupakan ekosistem yang penting fungsi ekologisnya, termasuk (1) stabilisasi dari substratum (yaitu melindungi pantai dari erosi dan melindungi terumbu karang dari sedimentasi), dan (2) sebagai tempat pembibitan dari berbagai jenis ikan, udang dan crustaceae lain (termasuk beberapa jenis yang bernilai ekonomis). Kunci utama untuk lebih memahami mengenai fungsi dari ekosistem rumput Lamun terdapat di faktor-faktor yang mengatur pertumbuhannya, produktivitas, dekomposisiserta proses regenerasi. Cahaya matahari dianggap sebagai salahsatu faktor pembatas (limiting factor) terpenting pada pertumbuhan Lamun di perairan (yang seringkali keruh) di daerah yang beriklim sedang. Walaupun demikian, mungkin lain halnya di kebanyakan perairan tropis, yang biasanya sangat jernih. Di perairan ini kemungkinan besar pertumbuhan Lamun dibatasi oleh persediaan nutrien. Tesis Ph.D ini adalah uraian tentang hasil penelitian yang diadakan selama empat tahun mengenai fungsi ekologisnya dari beberapa nutrien, yaitu amonium dan nitrat di dalam endapan yang berasal dari daratan, dan fosfat di dalam sedimen karbonat, yang keduanya kemungkinan besar merupakan faktor pembatas terhadap pertumbuhan Lamun. Riset ini diadakan di padang rumput Lamun di Kepulauan Spermonde dan daerah pesisir di sekitarnya di Sulawesi Selatan.

Analisa terpenci yang kuantitatif mengenai konsentrasi nutrient dan sumber daya padang rumput Lamun di enam lokasi berlainan di daerah penelitian ini (Bab 2) menunjukkan adanya perbedaan nyata dalam struktur dan fungsi di antara padang Lamun yang terdapat sepanjang pesisir pada sedimen terrigenous (yaitu pasir atau lumpur yang berasal dari daratan dibawa sungai), dibanding padang Lamun yang terdapat di sekitar pulau-pulau terumbu karang pada sedimen carbonate (yaitu pasir yang berasal dari erosi terumbu karang). Pada sedimen terrigenous di padang Lamun, (1) konsentrasi tinggi dari fytoplankton dan partikel organik dalam suspensi kolom air, (2) daun Lamun yang ditumbuhi epifit yang rapat, (3) terjadinya kadang-kadang pertumbuhan massal dari makroalga, (4) kerapatan batang serta biomassa Lamun yang lebih rendah, (5) daun Lamun yang lebih panjang, dan (6) kadar C, N dan P dalam jaringan Lamun menunjukkan persediaan nutrien yang tinggi dibanding padang Lamun di lingkungan gosong terumbu karang di pulau-pulau, yang sedimennya carbonate. Di sini airnya yang jernih menyebabkan penutupan epifit yang jarang serta kerapatan dan biomassa Lamun yang jauh lebih tinggi.

Pengukuran produktifitas di padang Lamun dengan memakai beberapa tehnik

(metoda menandai daun dan akar; interval plastochron; studi evolusi oksigen dengan elektrode di kubah transparan) menunjukkan hasil yang sama (Bab 3). Produksi primer yang tinggi (0.9 sampai 4.4 g C m^{-2} per hari), adalah khas untuk komunitas Lamun di daerah riset dan masih di dalam kisaran yang dilaporkan untuk daerah tropis yang lain.Ini juga mendukung pendapat bahwa padang Lamun termasuk ekosistem perairan terendam yang paling produktif di samping ekosistem hutan bakau, terumbu karang dan rawa payau. Pengukuran oksigen menunjukkan konsumpsi zat asam oleh komunitas ini yang tinggi, sehingga produktifitas bersih dari komunitas pada keseluruhannya sangat rendah (bahkan dengan nilai di bawah nol). Ini menunjukkan bahwa sebagian besar dari produksi primer yang tinggi dipergunakan untuk berbagai proses konsumptif di dalam ekosistemnya. Daya tumbuh dari jenis Lamun pionir, misalnya Halodule uninervis dan Cymodocea rotundata, jauh lebih tinggi daripada jenis mantap (klimaks), misalnya Thalassia hemprichii dan Enhalus acoroides. Pertumbuhan daun pada Enhalus acoroides lebih tinggi di lokasi pinggir pantai daripada di lokasi pulau terumbu karang, akan tetapi produksi per meter persegi lebih rendah di pinggir pantai karena kerapatan batang yang lebih rendah.

Interaksi-interaksi geokimia yang utama di antara nutrien dan sedimen di ekosistem padang Lamun diuraikan di Bab 4. Profil kedalaman konsentrasi nutrien yang larut pada air interstisial (air yang terdapat di antara butir-butir pasir) di sedimen terrigenous di perairan pantai, dengan mudah dapat diuraikan oleh model dekomposisi stoikhiometris dari bahan organik serta proses difusi molekular. Akan tetapi di beberapa cm paling atas di sedimen carbonate di lokasi terumbu karang, konsentrasi fosfat larutan di air interstisial jauh lebih tinggih daripada yang dapat diharapkan berdasarkan stoikhiometrinya. Diperkirakan, bahwa kelebihan akan fosfat ini disebabkan oleh regenerasi N dan P di rhizosfer, dan kemudian penghilangan amonia yang cepat melalui nitrifikasi. Kapasitas sedimen carbonate untuk menyerap fosfat berkaitan langsung dengan ukuran butirnya. Sedimen carbonate yang berbutir kasar di daerah studi menahan konsentrasi cukup tinggi dari fosfat larutan di air interstisial dikarenakan daya serap yang terbatas. Ini berbeda dengan konsentrasi fosfat di air interstisial yang sangat rendah seperti dilaporkan untuk sedimen carbonate di daerah Carribean di mana dibuktikan adanya P sebagai faktor pembatas untuk pertumbuhan Lamun.

Pemupukan in situ dengan memakai butir N dan P (yang slow release, artinya dengan pelan melepaskan unsur hara: 4-5 bulan) pada tiga lokasi padang Lamun (dua di sedimen carbonate, satu di sedimen terrigenous) tidak mempengaruhi biomassa, kerapatan batang dan produktifitas Lamun (Bab 5). Pemupukan N dan pemupukan P (bukan N+P) mempengaruhi kadar C, N dan P dalam jaringan Lamun, yang menunjukkan adanya kenaikan inkorporasi N (dan P, tapi agak kurang) oleh Lamun (luxury uptake). Diperkirakan bahwa tidak-adanya dampak pemupukan ini disebabkan oleh komposisi butir sedimen carbonate yang kasar dan konsentrasi tinggi akan fosfat interstisial yang berkaitan dengan ukuran butir itu. Jadi, walaupun P sebagai faktor pembatas dianggap sebagai cirikhas di lingkungan tropis yang kaya akan carbonate, ini tidak demikian di daerah penelitian ini.

Dinamika musiman di dua padang Lamun intertidal yang berbeda diuraikan di Bab 6. Kedua padang Lamun di sekitar pulau terumbu karang (carbonate) dan di daerah berlumpur di perairan pesisir (terrigenous) menunjukkan dinamika musiman yang jelas, dengan perubahan-tajam dalam biomassa, kerapatan batang, produktifitas, dan kadar nutrien sepanjang tahun. Analisa statistik (canonical correlation analysis) menunjukkan korrelasi nyata di antara dinamika yang diamati pada variabel biologi dari Lamun di lingkungan gosong terumbu karang dan kumpulan variabel lingkungan yang diukur. Sebagai variabel lingkungan utama yang menyebabkan perubahan musiman pada variabel Lamun itu ditemukan (1) keterbukaan pada siang hari secara periodik selama surut purnama (Juli-Januari) dan (2) perubahan musiman pada kekuatan arus laut (diukur dengan tehnik clod card). Keterbukaan pada siang hari selama surut itu menyebabkan kehilangan biomassa dari bagian tumbuhan yang di atas tanah karena Lamun berada dalam kisaran suhu besar dan mengalami kekeringan dan kematian daunnya. Akan tetapi, regenerasi Lamun cukup cepat melalui mobilisasi simpanan dari rhizom. Fenomena ini tidak hanya ditemukan di Sulawesi Selatan, tapi agak umum di perairan intertidal di seluruh daerah Indo-Pasifik dan sebagian dari Afrika. Ini sangat berbeda dengan situasinya di Carribean yang mengalami fluktuasi pasang-surut yang kecil. Perubahan musiman dari variabel-variabel biologis yang ditemukan di padang Lamun berlumpur di sepanjang pesisir tidak ada korelasi dengan variabel lingkungan yang diukur, walaupun itu dapat diharapkan karena dampaknya sungai Tallo yang muarahnya tidak jauh dari padang Lamun ini. Juga tidak ada korelasi antara perubahan musiman dari variabel lingkungan dan kelimpahan dan biomassa makro-alga yang diamati beberapa kali selama penelitian ini.

Sebagai penutupan, hasil dari bab-bab sebelumnya dibahas dan digabungkan di Bab 7. Data mengenai nitrogen dan fosfor diproses dalam model kotak meliputi satu meter kubik dari ekosistem Lamun, di mana diperhitungkan seluruh masukan dari masing-masing komponen di ekosistem ke anggarannya N dan P. Sebagian besar (86-99%) dari anggaran ini termuat di dalam sedimen. Data ini, dan data mengenai produktifitas, dievaluasi dalam perhitungan keseimbangan massa, di mana dibahas akibat-akibat untuk tempat penyerapan nutrien (daun atau akar), dekomposisi dan daya gelontor dari kolom air. Berdasarkan perhitungan ini, ditarik kesimpulan, bahwa rumput Lamun di daerah studi ini mengumpulkan sebagian besar (90% ke atas) dari nutrien yang diperlukan untuk tumbuh diserap dari air interstisial melalui sistem akar. Penyerapan melalui daun kelihatan kurang penting (10% maksimal), yang bertentangan dengan beberapa eksperimen dengan Lamun yang dilakukan di laboratorium mengenai penyerapan nutrien. Data ini juga memberi gambaran mengenai proses daurulang dari nutrien melalui remobilisasinya dari bagian tumbuhan lama yang menua. Ini merupakan proses yang penting karena masukannya yang besar kepada permintaan nutrien pada bagian rumput Lamun yang sedang tumbuh. Proses ini patut mendapat perhatian khusus di penelitian lanjutan.

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CURRICULUM VITAE

Paul Erftemeijer was born on 11 April 1963 in 's-Gravenhage, the Netherlands. Between 1975 and 1981 he attended secondary school at the Sint Janscollege in 's-Gravenhage. In 1981 he started his biology study at the Catholic University of Nijmegen, where he graduated in 1988, with aquatic ecology, nature conservation and animal ecology as his main specializations. As part of his masters degree, he carried out two studies in Indonesia. In 1986 he studied mixed-species flocks of insectivorous forest birds in mountain and lowland forests in West Java under supervision of the department of nature conservation of the Agricultural University of Wageningen. In 1988 he carried out surveys of coastal wetlands and waterbirds in the Brantas and Solo deltas, Segara Anakan and Pulau Rambut on Java in cooperation with the Asian Wetland Bureau in Bogor. From January to August 1989 he was employed as project officer at the Asian Wetland Bureau in Indonesia to make an inventory of natural resources in Bintuni Bay (Irian Jaya) and to provide recommendations for its conservation and sustainable management. From August 1989 to August 1993 he was employed by the Netherlands Organization for Scientific Research (NWO) to carry out the study presented in this thesis. The major part of the preparations and writing was performed at the Netherlands Institute of Ecology, Centre for Estuarine and Coastal Ecology (formerly Delta Institute of Hydrobiological Research) in Yerseke, The Netherlands.