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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

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Abstract Seasonal dynamics were studied by monthly monitoring of biological and environmental variables in permanent quadrats in two contrasting intertidal seagrass beds 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), was assumed to be related to riverine influences of the nearby Tallo River. The variation in seagrass variables at this site could, however, 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 *E. 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 during 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 of the seagrass bed on reef sediment 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.

Key words: Seasonal dynamics · Tropical seagrass beds
Tidal exposure · Terrigenous influences
Canonical correlation analysis

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 behind considerably with that from the temperate region and the tropical Caribbean. Only recently, have various structural and functional aspects of Indo-Pacific seagrass beds been studied (Brouns and Heijs 1986; Lindeboom and Sandee 1989; Nienhuis et al. 1989; Erftemeijer 1994). However, the study of structural and functional components of the seagrass system alone does not provide information on dynamics, and most seagrass communities are liable to changes (den Hartog 1979). With regard to conservation in particular, 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).
3. To compare the seasonal variations in environmental variables and seagrass response between a coastal muddy environment under the direct influence of a river, and an offshore reef environment under oceanic conditions.

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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. 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 *E. 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 PQs 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 *E. acoroides*, at both sites was determined monthly by 50 counts within an iron frame (50 × 50 cm), thrown randomly in the seagrass bed. Three replicate samples consisting of 6–8 shoots of *E. 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 square metre, using the average shoot density counted for that particular month. Biomass samples (three per month) of *T. hemprichii*, from Barang Lompo were collected randomly in the PQ using an aluminium frame (25 × 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 fresh water 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. Macro-algal biomass was sampled during periods of blooming, and was treated in a similar manner to the seagrass samples.

The plant parts were dried at 60–80°C to constant dry weight (DW) and stored for the determination of primary elemental constituents (C, N and P) and ash contents. The Carbon and nitrogen content of powdered plant tissue was measured using a Carlo-Erba NA 1500 CN Analyser. Phosphorus content was measured using 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 h at 550°C.

Leaf production was studied in random plots within the PQs using the leaf marking method described by Kirkman and Reid (1979). This method was recommended as being the most suitable for large-scale monitoring studies of seagrass primary production in tropical environments (Erftemeijer et al. 1993). An average of 10 plants in 4 plots (*E. acoroides*) or 20 plants in 3 plots (*T. hemprichii*) were arbitrarily selected and marked each month. Leaf growth was assessed after 6 days and expressed as relative growth rate (g g^{-1} day^{-1}).

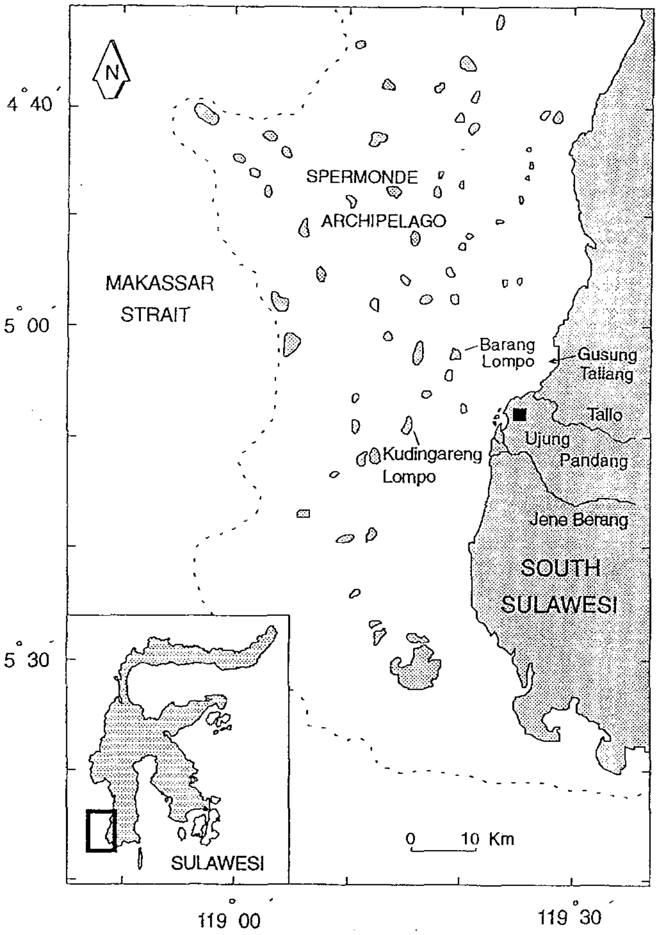


Fig. 1 Map of the study area, showing the locations mentioned in the text. *Dotted line* represents approximate edge of continental shelf

The exposure of the seagrass plants to water motion was studied by means of the clod card technique described by 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 of water. The blocks were glued to numbered plastic cards. Each month nine blocks (mounted on bricks) were placed at ca. 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 in 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 (*vol* = 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 using a refractometer, with an average of five replicate samples collected on different visits to each site. The 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 immediately analysed spectrophotometrically, using a Nanocolor 100D-MN filter photometer, for phosphate, ammonium and nitrate+nitrite as described by Strickland and Parsons (1972).

Sediment samples, of depth 10 cm, were taken randomly in the PQs once a month while snorkelling using small hand corers (diameter = 6 cm). Each core was separated into 2-cm sections in the field. The coinciding sections of every 12 successive cores were combined and treated as 1 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 and 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 1993).

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 multi-dimensional 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 *T. hemprichii* and *E. acoroides* 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 *T. hemprichii* and *E. acoroides*) were expressed as C:N ratio and C:P ratio. Relative growth rates (RGR) of *T. hemprichii* and *E. acoroides* 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 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. 2). During the months May–October, when south-easterly winds prevail, average monthly rainfall normally does not exceed 100 mm. From November to April northwesterly 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 Ni<1,57>o Southern Oscillation event (Kessler and McPhaden 1992; Murray et al. 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 Fig. 3. To deter-

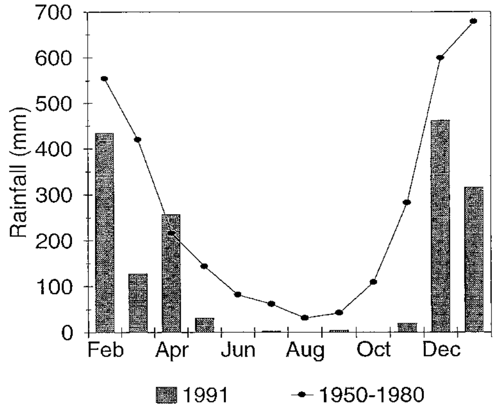


Fig. 2 Monthly rainfall (mm) in 1991 and average rainfall during 1950–1980, measured at Paotere harbour, Ujung Pandang, South Sulawesi. (source: Balai Metereologi dan Geofisika, Ujung Pandang)

mine 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) north-western 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 1800 hours and 0600 hours). From the second half of July until early February, however, the spring ebb tides occur during the daylight period (Fig. 4). This predicted 'seasonality' in the tidal regime was consistent in 5 successive years (1988–1992).

When a low-water of a spring tide occurs at midday, 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 months August–December over 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 (10–15 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. 5). 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.

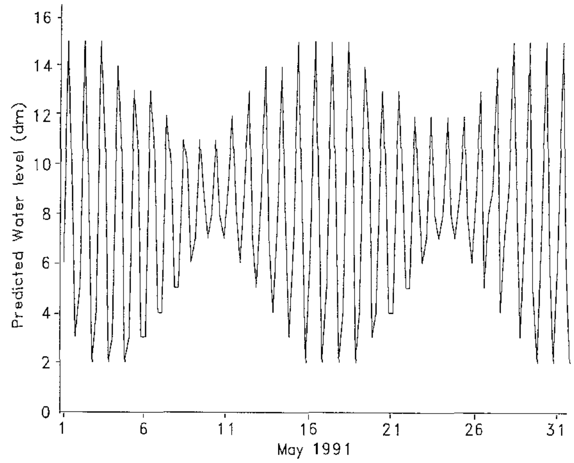


Fig. 3 Predicted tidal oscillation curve for Ujung Pandang harbour during May 1991 (source: Dinas Hidro-Oseanografi TNI-AL, Jakarta)

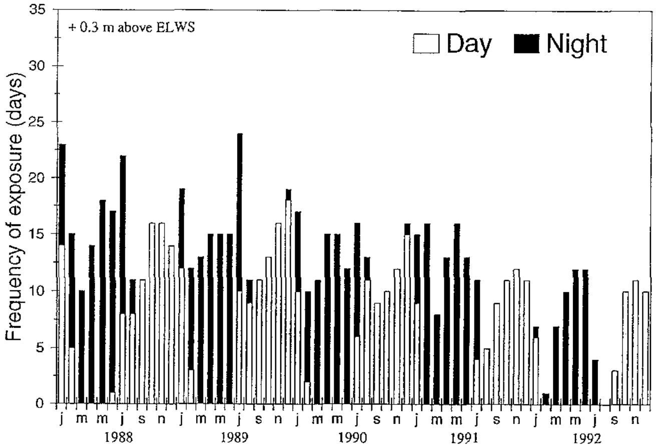


Fig. 4 Predicted frequency of spring low tide exposure (in days per month) during daylight (*white bars*) and at night (*black bars*) for stations situated +0.3 m above chart datum in the study area during 1988–1992 (source: predicted tide tables, Dinas Hidro-Oseanografi TNI-AL, Jakarta)

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). 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 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

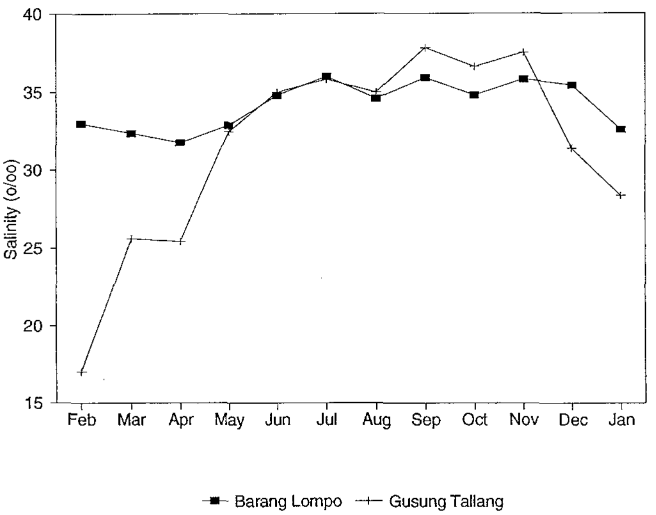


Fig. 5 Monthly variation in salinity of surface water (% S) above seagrass beds in the PQs at Barang Lompo and Gusung Tallang during 1991 and January 1992 (SD < 2%)

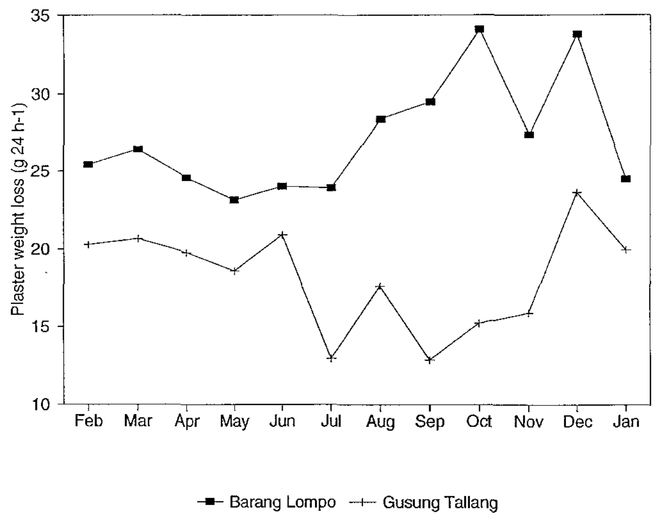


Fig. 6 Seasonal variation in clod card weight loss (in g 24 h^{-1}), as a measure of exposure to water movements in the PQs at Barang Lompo and Gusung Tallang during 1991 and January 1992 (SD < 1.9 g)

larger at Gusung Tallang than at Barang Lompo, and was most conspicuous for ammonium (Fig. 7). 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. 8). 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 depends 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 (*k*) of 0.34 ± 0.13 m^{-1}, with only minor variation during the year (Fig. 9). Turbidity levels at Gusung Tallang were much higher (mean $k = 1.59 \pm 0.75$ m^{-1}) and fluctuated

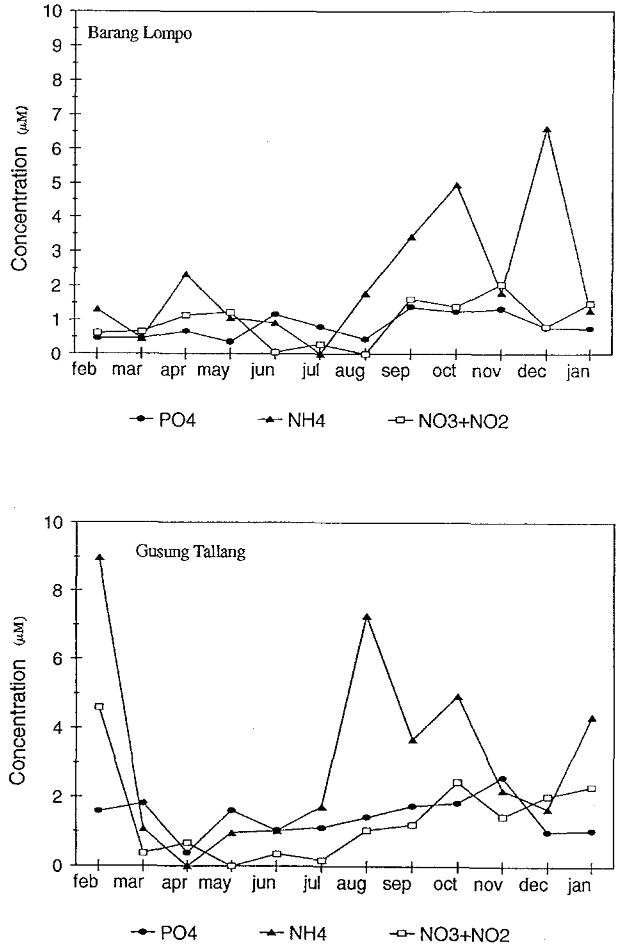


Fig. 7 Seasonal variation in the concentrations of phosphate, ammonium and nitrate+nitrite (monthly means) in the water column above the seagrass beds (PQs) at Barang Lompo and Gusung Tallang during 1991 and January 1992 [SD < 0.5 (PO_4 and NO_3+NO_2); SD < 2.0 (NH_4)]

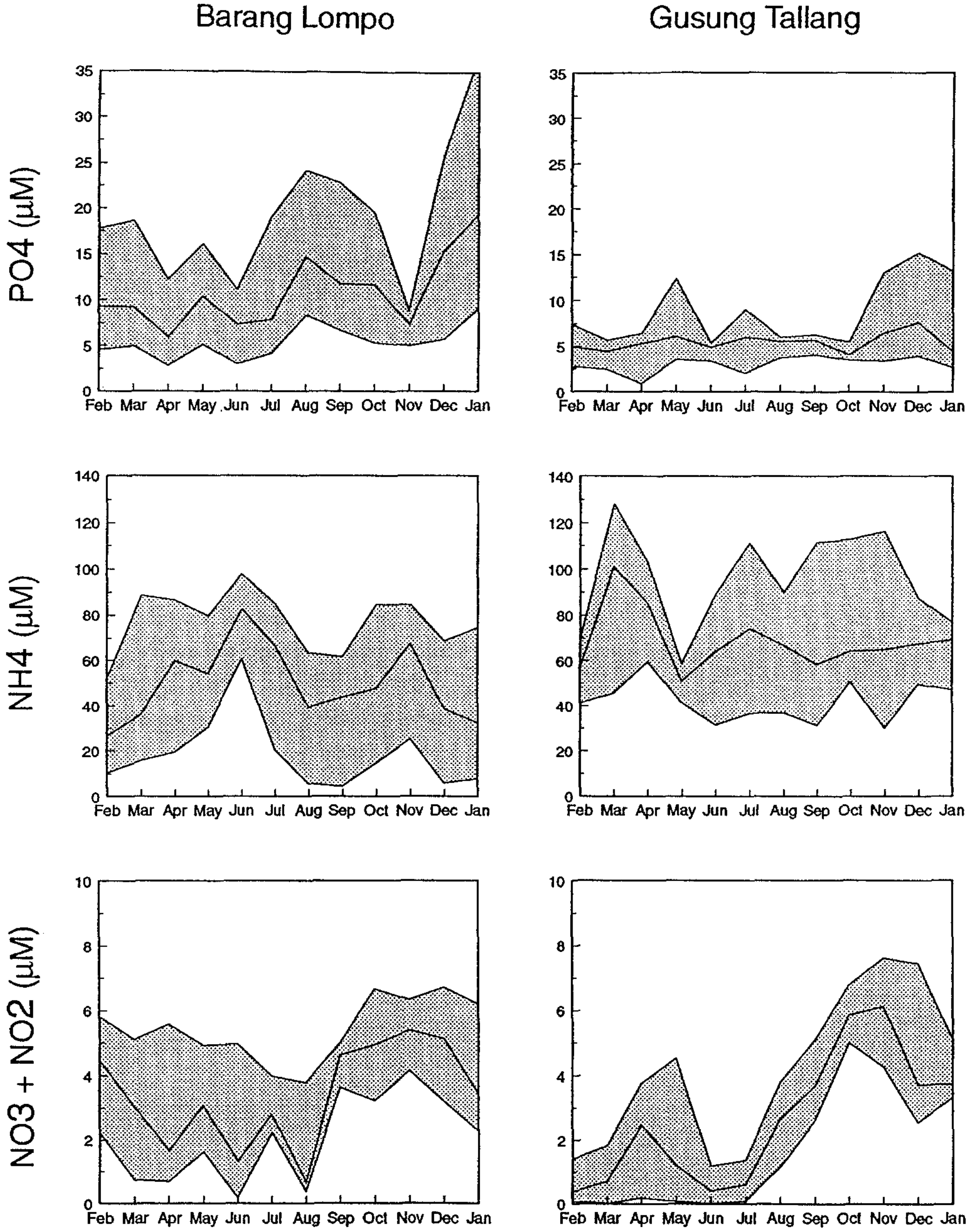


Fig. 8 Seasonal variation in the concentrations of sediment porewater nutrients (phosphate, ammonium and nitrate+nitrite) in the seagrass beds (PQs) at Barang Lompo and Gusung Tallang during 1991. Plots show median, minimum and maximum values for each month, recorded within the upper 10 cm of the sediment.

considerably, with maximum light attenuation measured in February, October and November (k > 2.5 m^{-1}).

Seagrass shoot density

Shoot density of *T. hemprichii* at Barang Lompo increased from 2064 ± 127 m^{-2} in February to 3733 ± 605 m^{-2} in July, but subsequently dropped to 1856 <6,1> 617 m^{-2} in August and remained low (around 2000 m^{-2}) during the rest of the year (Fig. 10). 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 *T. hemprichii* can gradually build up higher shoot densities. Shoot density of *E. acoroides* at Barang Lompo ranged from 18 to 28 m^{-2}, with only minor fluctuations which occurred in the period August-November (Fig. 10). 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. 10). Throughout the year, shoot density of *E. acoroides* was significantly lower at Barang Lompo than at Gusung Tallang. Annual mean shoot densities were 2380 ± 624 m^{-2} for *T. hemprichii* and 24 ± 3 m^{-2} for *E. acoroides* at Barang Lompo, and 39 ± 5 m^{-2} for *E. acoroides* at Gusung Tallang.

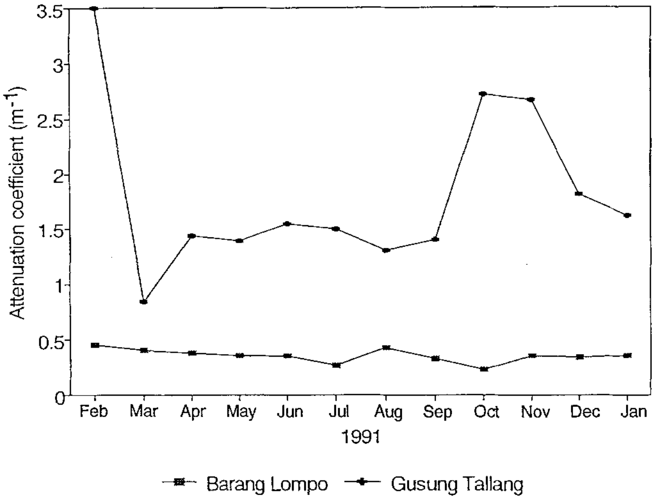


Fig. 9 Seasonal changes in turbidity (expressed as attenuation coefficient (*k*) in m^{-1}) of the water column (monthly averages) at Barang Lompo and Gusung Tallang during 1991 ($n = 3$–5; SD: Barang Lompo < 0.1; Gusung Tallang < 0.4)

Seagrass biomass

Total biomass of seagrasses at Barang Lompo showed a gradual increase to a maximum during June–July (*T. hemprichii* 1144–1401 g DW m^{-2}, *E. 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} (*T. hemprichii*) and 100 g DW m^{-2} (*E. acoroides*) until the end of the year (Fig. 11). The general picture for *E. acoroides* at Gusung Tallang is similar. Leaf blade biomass of *T. hemprichii* at Barang Lompo dropped considerably during August, September and October to levels below 30 g DW m^{-2} (Fig. 12). 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 10 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 *E. acoroides* at Barang Lompo followed a similar pattern as that of *T. hemprichii*, except that the steep drop in leaf biomass of *Enhalus* did not appear until September and that regeneration was slower (Fig. 12). Leaf biomass of *E. 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. 12).

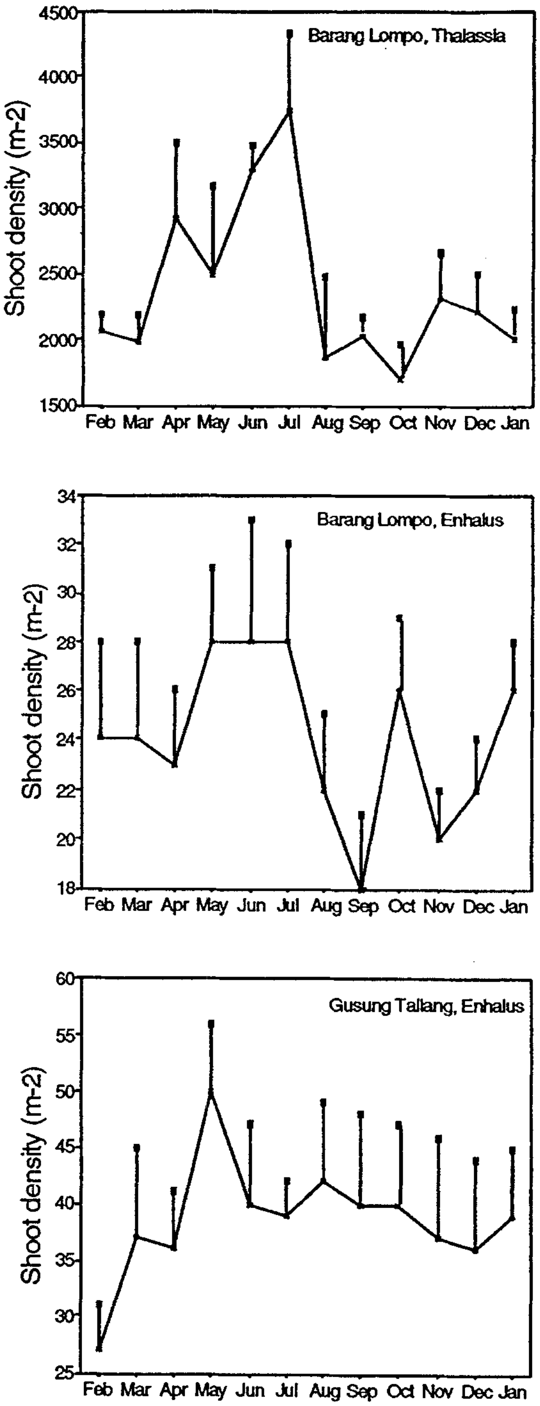


Fig. 10 Seasonal changes in shoot density of *Thalassia hemprichii* ($n = 3$) and *Enhalus acoroides* ($n = 50$) in the PQs at Barang Lompo and Gusung Tallang during 1991 (monthly means +SD)

Leaf production

Relative growth rates (RGR in g g^{-1} day^{-1}) ranged from 0.022 to 0.056 for *T. hemprichii* (Barang Lompo), and from 0.018 to 0.037 (Barang Lompo) and 0.012 to 0.024 (Gusung Tallang) for *E. acoroides*. Highest RGR were observed in July, August and September (Barang Lompo, both species) and July–August (Gusung Tallang) (Fig.

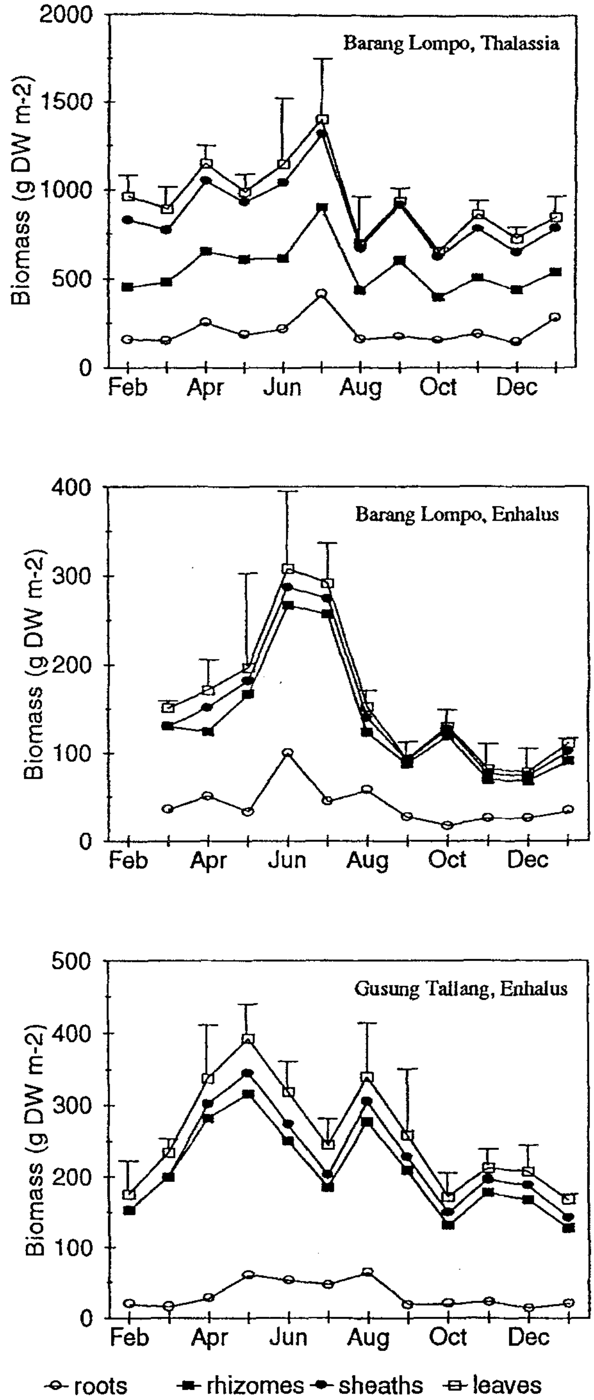


Fig. 11 Seasonal changes in seagrass biomass (in g dry wt m^{-2}) of *Thalassia hemprichii* and *Enhalus acoroides* (in PQs) at Barang Lompo and Gusung Tallang during 1991. Data are presented as cumulative weights of the monthly means of the biomass of different plant parts (roots, rhizomes, sheaths and leaves) SD values of total biomass are given on top of the cumulative graphs

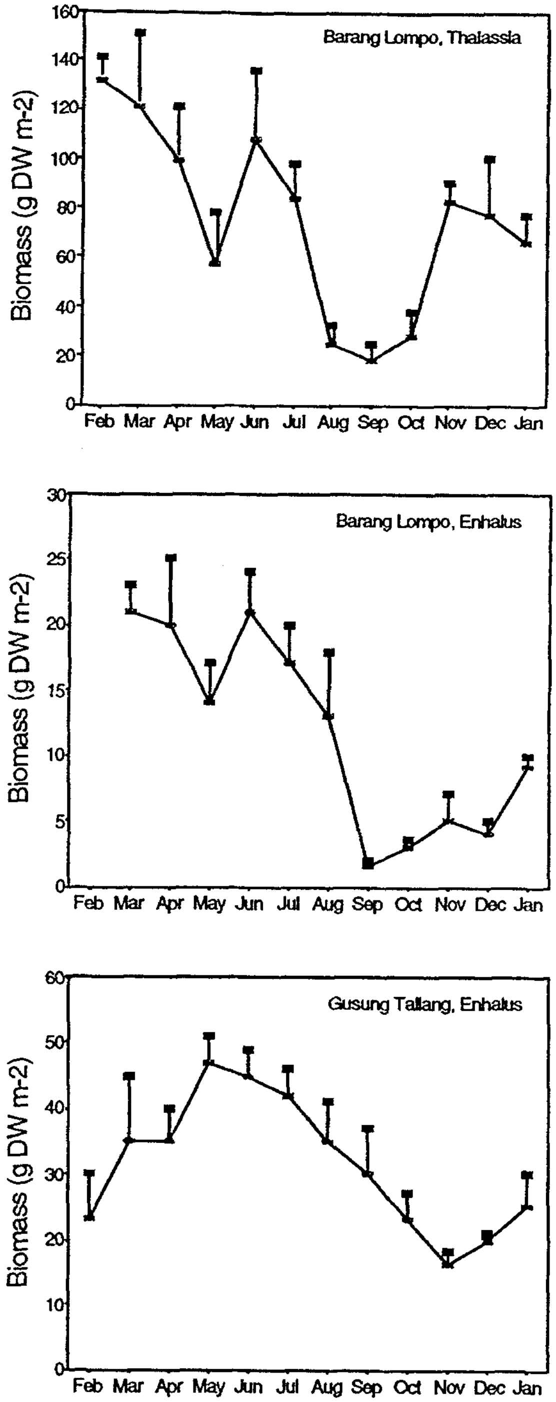


Fig. 12 Seasonal changes in leaf blade biomass (in g dry wt m^{-2}) of *Thalassia hemprichii* and *Enhalus acoroides* (in PQs) at Barang Lompo and Gusung Tallang during 1991 (monthly means + SD)

13). The annual average RGR for *E. acoroides* was significantly higher ($P < 0.05$) at Barang Lompo (0.028 ± 0.007 g g^{-1} day^{-1}) than at Gusung Tallang (0.019 ± 0.005 g g^{-1} day^{-1}). Leaf production per m^2 (calculated from RGR values and monthly standing crop data) ranged from 1.02 to 5.08 g DW m^{-2} day^{-1} (mean: 2.98 ± 1.29) for *T. hemprichii* (Barang Lompo), and from 0.09 to 0.57 g DW m^{-2} day^{-1} (mean: 0.33 ± 0.16) at Barang Lompo and 0.24–2.35 g DW m^{-2} day^{-1} (mean 0.63 ± 0.54) at Gusung Tallang for *E. acoroides*. Variation in leaf production per square metre for *T. hemprichii* was considerably larger than for *E. acoroides*, due to greater changes

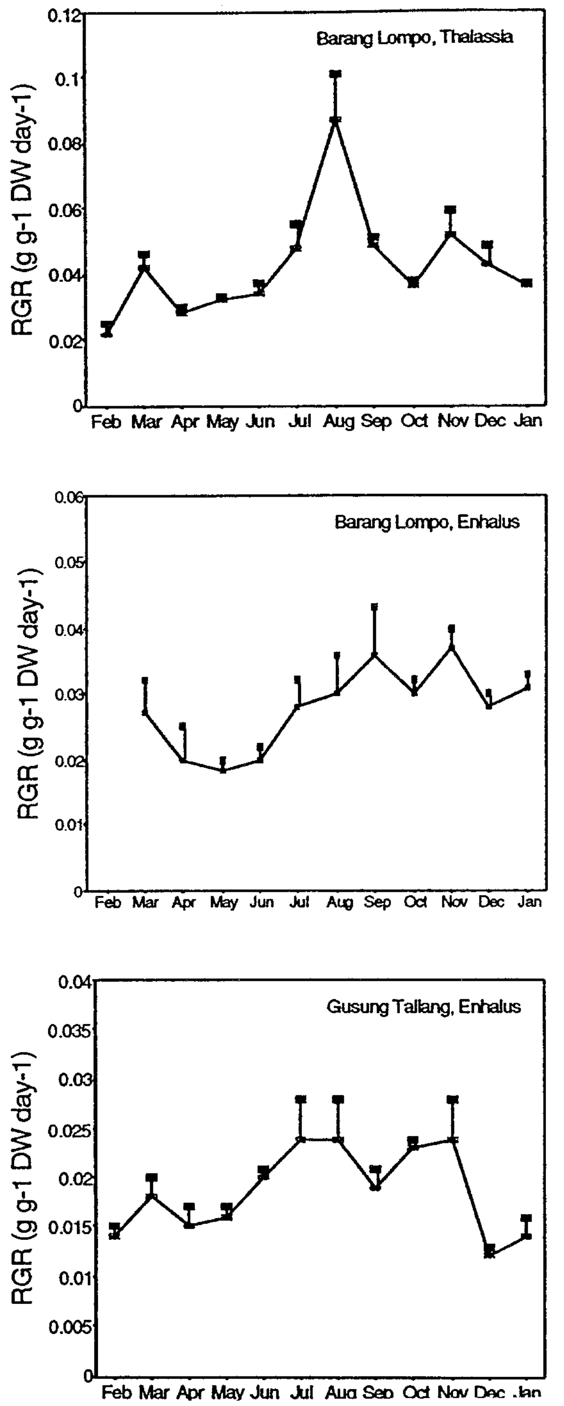


Fig. 13 Seasonal changes in relative growth rates (RGR, in g g^{-1} dry wt day^{-1}) of *Thalassia hemprichii* and *Enhalus acoroides* (in PQs) at Barang Lompo and Gusung Tallang during 1991 (monthly means + SD)

in standing crop. Total annual leaf production of *T. hemprichii* at Barang Lompo amounted to approximately 1 kg DW m^{-2} $year^{-1}$, which is equivalent to 390 g C m^{-2} $year^{-1}$. Total annual leaf production of *E. acoroides* ranged from c. 100 g DW m^{-2} $year^{-1}$ at Barang Lompo to ca. 200 g DW m^{-2} $year^{-1}$ at Gusung Tallang.

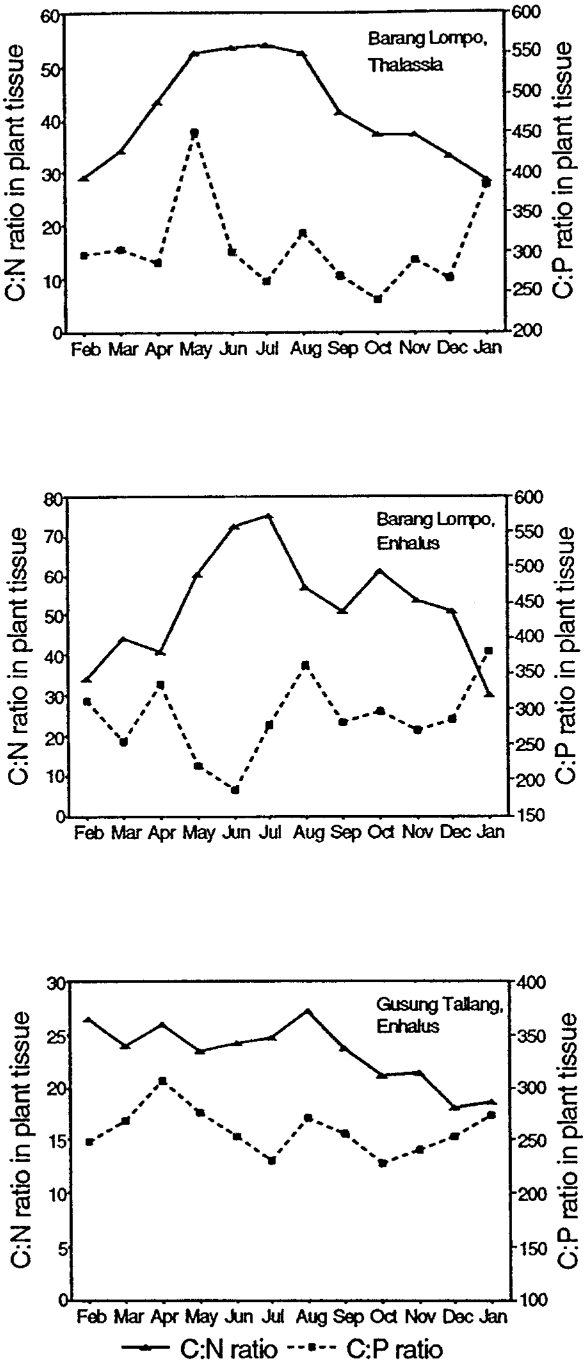


Fig. 14 Seasonal changes in C:N and C:P ratios in plant tissue of *Thalassia hemprichii* and *Enhalus acoroides* for the two sites. Ratios were calculated from total standing stocks of C, N and P in plant tissue (proportionally cumulated for the different plant parts); SD values ranged from 1 to 5 for C:N, and from 20 to 78 for C:P

Primary elemental constituents

Annual mean C, N, P and ash contents of leaf blades, leaf sheaths, rhizomes and roots of *T. hemprichii* and *E. acoroides* at the two stations are presented in Table 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 cor-

Table 1 Annual mean (± SD) tissue contents of primary elemental constituents (total C, N and P, in% dry weight) and ash (% dry weight) in the different parts of *Thalassia hemprichii* and *Enhalus acoroides* at the two study sites ($n = 36$)

		% C	% N	% P	% Ash
Barang Lompo					
T. 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
E. 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					
E. 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

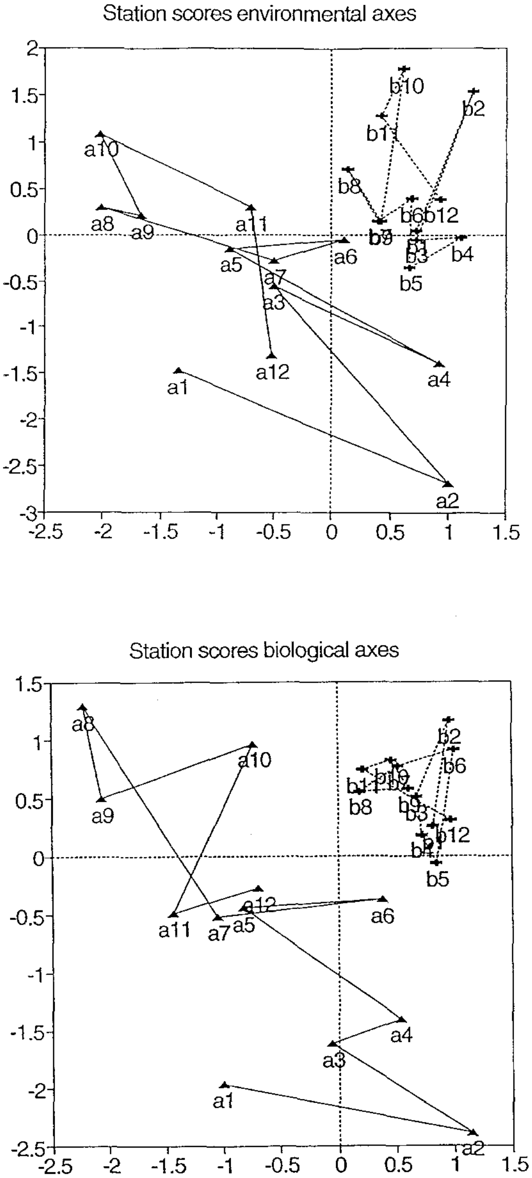
responded to fluctuations in nutrient availability in the ambient medium (water column and porewater). Monthly data on C, N and P contents in plant tissue (% of DW) were converted to standing stocks of C, N and P in the total biomass (cumulative of different plant parts) by multiplying these data with the corresponding biomass per square metre. Figure 14 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 *E. acoroides* at Gusung Tallang showed little seasonal variation.

Macroalgae

The biomass of macro-algae 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, macro-algae 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 3 times the mean above-ground seagrass biomass at this site), which lasted for approximately 3 weeks, and consisted of *Gracilaria salicornia*, *Gracilaria verrucosa*, *Gracilaria 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 *U. reticulata* gradually started to deteriorate and its biomass gradually decreased until hardly any *U. reticulata* was left at the end of January. While the *U. reticulata* mass was deteriorating, a new algal bloom appeared (end of December-January), which was dominated by *Gracilaria* spp. and *S. filamentosa*, with a biomass of 117–195 g DW m^{-2} (including deteriorating *U. reticulata*). The average ash content (in% DW) of macroalgae was 31.7 ± 7.6 with highest values obtained in December-January during the decay of the *U. reticulata* 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 (% DW) respectively (atomic ratio 448:34:1), without significant monthly changes. Multiple regression analysis of data from Gusung Tallang revealed no significant correlations between macro-algal 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 15). 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 in 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 pat-


Station scores environmental axes

Station scores biological axes

Fig. 15 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 (1–12) refer to months (1 = January etc.) For further explanation, see text

terns of biological and environmental variables, in which tidal exposure and water motion had the highest individual and overall contributions to the ordination (Table 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 reasonable to assume that seagrass dynamics at the coastal site (Gusung Tallang) are largely dependent on riverine influences from the nearby Tallo River, canonical correlation analysis of the data from this station (i.e. conducted 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 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). Biological variables are proportionally combined for *Enhalus acoroides* and *Thalassia hemprichii*; C:N and C:P ratios are of standing stocks in plant tissue; (*DIN* Dissolved inorganic nitrogen, RGR relative growth rates)

	Canonical coefficients	Canonical loadings
Environmental variables		
Tidal exposure	0.245	0.689
Water motion	0.903	0.886
Rainfall	-0.513	0.212
Turbidity (*k*)	0.478	-0.217
DIN-porewater	0.063	-0.218
PO_4-porewater	0.143	0.273
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 a unimodal seasonal pattern in which maximum shoot density (*T. hemprichii*: 3730 m^{-2}; *E. acoroides*: 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} and 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 *T. hemprichii* and up to 0.037 g DW g^{-1} day^{-1} for *E. acoroides*). 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 the daytime (August–December) caused a significant loss of aboveground 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[a]). 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 of 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 et al. 1979; Dawes and Lawrence 1980; 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 *T. hemprichii* and *E. acoroides* at Barang Lompo during the months of daytime exposure (Fig. 14) is indicative of such a mobilization of reserves.

In the seagrass bed at the coastal mudbank (Gusung Tallang), there was also a seasonal pattern in which maximum shoot density (*E. acoroides*: 50 m^{-2}), maximum biomass (*E. acoroides*: 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} and 0.43 g P m^{-2}) occurred in May. Macro-algae in this seagrass bed showed periods of blooming during April 1991 (*Gracilaria* spp.), August-November 1991 (*U. reticulata*), and December 1991-January 1992 (*Gracilaria* spp.). 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 macro-algae (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 macro-algal 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 being 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 most of the variability in seagrass biomass (>70%) 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 compared with those of temperate seagrasses in Australian waters.

The observed variability in shoot density and relative growth rate of *T. hemprichii* in the present study (at Barang Lompo) is within the range reported for *T. hemprichii* beds in Papua New Guinea (Brouns 1985). 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 (1985). As a consequence, estimates of leaf production per square metre 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. twofold) 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 RGR, which corresponds with the findings which show 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., in press[b]). It seems, therefore, more likely that the increase in porewater phosphate concentrations at Barang Lompo is related to 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 overall 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 (personal observation), and has also been observed in seagrass beds in Menado in North Sulawesi (personal observation), Ambon (H. de Iongh, personal communication), Papua New Guinea (Brouns and Heijs 1986), Kenya (E. Slim, personal communication), The Red Sea and the Gulf of Eilat (den Hartog, personal communication) and Mauritania (Van Lent et al. 1991; Hemminga, personal communication). 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 is a major difference between the situation in this region and that of 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 *Zostera noltii*, appear to be resistant to long periods of emersion, of 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 *Z. noltii* from Mauretania (Van Lent et al. 1991). Intertidal *Zostera* spp. 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, or 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 (*T. hemprichii* and *E. acoroides*, and locally some other species) can build up large and relatively stable biomasses, while macro-algae and phytoplankton components are relatively unimportant. At Gusung Tallang, however, where considerable fluctuations in environmental variables occur, large macro-algal biomasses and phytoplankton blooms appear rapidly at times of suitable conditions, but subsequently disappear when the environmental factors become unfavourable. Only the seagrass component is relatively stable in this vegetation, but suboptimal conditions (e.g. turbidity) allow development of only reduced biomasses of just one tall seagrass (*E. acoroides*). At other coastal sites in South Sulawesi, where environmental conditions are even less favourable, seagrasses are completely absent (personal observation).

The present study is among the few detailed studies monitoring seasonal changes in seagrass beds in the tropical Indo-Pacific region. Brouns (1985, 1987) 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 *A. antarctica* and *P. 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). In addition, it is unclear as to what extent the results have been affected by the prolongation of the dry season as a result of the 1991–1992 El Ni<1,57>o Southern Oscillation event. Several authors have stressed the importance of long-term measurements (two or more years) (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).

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 eight different species (e.g. Bira), and similar multispecies meadows occur in subtidal reaches on coastal terrigenous sands under limited riverine influences (e.g. Palanro) (Verheij and Erftemeijer 1993). Apparently, increased disturbance and stress in seagrass meadows, caused by large fluctuations in environmental conditions, leads to increased instability of the community, until no more seagrass growth is possible. A comparable relationship between disturbance and stability might be found in other (non-seagrass) ecosystems.

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