Diel growth in eelgrass *Zostera marina* *

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ABSTRACT: Growth of eelgrass *Zostera marina* leaves was determined by sequential measurements of leaf length at time intervals of 4 to 12 h. Leaf growth rates at night were consistently lower (30 to 40 %) compared to daytime rates, and night-time rates were highly correlated with growth during the previous day. Diel patterns of O_2 metabolism (measured at 2 to 4 h intervals) and leaf growth (at 4 h intervals) generally followed the daily irradiance cycle, with maximum growth and O_2 production rates both occurring near midday. Rapid (hours to days) responses to changes in environmental conditions such as light and sediment fertility were detected using this leaf growth method. Quantitative comparison of diel integrals of growth (increases in leaf, root, and rhizome biomass) and net O_2 production indicated that the 2 processes were in relative balance. Although eelgrass leaf growth was determined readily here on short time-scales, measurement of total plant growth required a longer study period approaching the plastochrone interval (leaf formation time). It was demonstrated, however, that separate calibration studies relating root-rhizome growth to leaf growth can be conducted (over 1 to 2 wk) to allow estimates of short-term (4 to 12 h) responses of total plant growth to changes in environmental conditions.

INTRODUCTION

The seagrass *Zostera marina* L. is a ubiquitous and abundant macrophyte species (den Hartog 1970), which contributes substantially to the organic budgets of many coastal marine systems (Petersen 1918, Zieman & Wetzel 1980). Leaf growth of this plant can be measured using a leaf-marking technique, first described over a decade ago (Sand-Jensen 1975) and based on earlier work with a tropical seagrass species (Zieman 1968). Since its introduction, this method has been widely used for *Z. marina* (eelgrass) and related species in Europe, North America and Asia (Jacobs 1979, Mukai et al. 1979, Nienhuis & De Bree 1980, Bulthuis & Woelkerling 1983, Robertson & Mann 1984, Wium-Andersen & Borum 1984). In general, leaf-marking represents a robust, highly interpretable method for estimating seagrass net production (Zieman & Wetzel 1980). However, the leaf marking method has been limited to studies involving relatively long intervals (1 wk to 2 mo) between sequential measurements of leaf length (e.g. Bittaker & Iverson 1976, Zieman & Wetzel 1980, Wium-Andersen & Borum 1984).

Rates of leaf elongation for *Zostera marina* in Danish coastal waters have been reported to range from 2 to 5 cm shoot^{-1}d^{-1} during summer, with most of this growth occurring on the 2 youngest leaves (Sand-Jensen 1975, Borum & Wium-Andersen 1980, Wium-Andersen & Borum 1984). Similar rates have been reported for plants from other geographic regions (e.g. Jacobs 1979). Thus, it appears that significant leaf growth would be measurable on much shorter time-scales, *viz.* 1 d or less. The capability of making such short-term growth measurements would allow investigators to address several important, but heretofore elusive, questions on physiology and ecology of this seagrass. The purposes of the present study were several-fold: (1) to demonstrate directly the ability to precisely determine *Z. marina* leaf growth rates on time-scales of ≤ 12 h; (2) to describe diel patterns of eelgrass growth in relation to photosynthesis and respiration; (3) to examine short-term (hours to days) temporal responses of eelgrass to changes in environmental conditions such as nutrient and light regimes.

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METHODS

Experiments were conducted during June and July 1985 at a small field station located adjacent to Vellerup Vig (55° 44.1' N, 11° 42.0' E), an arm of Isefjord, Denmark (Sand-Jensen 1975). Temperatures during this study were generally between 18 and 25 °C, with typical diel ranges being 4 to 6 C°. Salinity over the course of the experiment ranged from 16.5 to 18.0‰.

Zostera marina plants and associated sediment were collected by coring from a previously studied site in nearby Roskilde Fjord (55° 46.9' N, 12° 0.6' E), Denmark (Stn III in Borum 1985). For uniformity, 12 healthy vertical shoots with attached rhizome segment and roots were selected and transplanted into homogenized sediments in cylindrical pots (80 cm^2 area, 10 cm depth). Plants were generally free of visible epiphytic organisms; however, leaves were gently scraped with fingernails to remove all loosely attached material prior to planting. Four experimental units (plants and sediments in pot) were established and placed in clear acrylic cylindrical chambers holding 17 l water volume. Following pre-treatment sampling, one experimental unit was transferred from its chamber to the fjord for *in situ* incubation. A fifth experiment unit containing intact plants and sediments was collected from the same site (Roskilde Fjord) using a 25 cm diameter corer. An undisturbed experimental eelgrass-sediment unit (10 cm dia.), obtained by subcoring from the larger diamter plug, was then placed in a chamber. Each incubation chamber was filled with ambient fjord water, capped with an acrylic lid, and stirred continuously using submersible pumps (Eheim, flow rate 3 l min^{-1}). Chambers were placed in a clear glass tank (230 l) which served as a cooling bath with ambient fjord water drawn continuously at a rate of 15 l min^{-1}. Using this cooling system, temperatures were maintained within 2 C° of ambient conditions.

Chambers were covered with neutral density fiberglass screens which reduced irradiance by about 70 %, approximating light conditions at the field site. A 12 h photoperiod was created for experimental plants by covering the system with black polyethylene each day between 2000 and 0800 h. Daily irradiance was measured using a 2 π cosine-corrected quantum sensor (LICOR Model 1776) with integrator, and periodic instantaneous measurements were made in air and in chambers using another quantum sensor and meter (LICOR Model L1-185A).

Photosynthesis and respiration of experimental systems were estimated using sequential measurements of dissolved oxygen (O_2) in chambers. O_2 was measured at 2 to 4 h intervals during daylight and at beginning and end of the dark period using polargraphic Clark electrodes (YSI, Model 57) calibrated daily in air.

Whenever O_2 concentrations approached 120 % saturation (1 or 2 times per day), chamber water was bubbled with air back to 100 % saturation to minimize effects of O_2 diffusion losses, O_2 inhibition and CO_2 depletion. Walls of experimental chambers were cleaned of periphytic growth by scraping with a hard bristle brush, followed by a complete replacement of incubation water each day. O_2 metabolism of *Zostera marina* (and its few remaining epiphytes) was calculated from temporal changes in O_2 corrected for planktonic and benthic production and consumption rates. Plankton metabolism was estimated by O_2 changes in clear and opaque BOD bottles (300 ml) filled with experimental water and incubated for 3 to 6 h in the water bath. Benthic metabolism associated with plant sediments was measured as O_2 changes in small clear acrylic cylinders (2.5 cm diameter) inserted into unvegetated sediment cores throughout the study and into experimental sediments containing eelgrass during the last 2 d of the study. Benthic metabolism was measured during both daylight and dark periods. O_2 diffusion through the walls of acrylic incubation chambers was estimated by filling empty chambers with filtered (0.45 μm) ambient water, deoxygenating by bubbling with N_2 gas, and monitoring O_2 change over 8 h. Oxygen diffusion across chamber walls never accounted for more than 1.0% of the total rate. There was little visible epiphytic growth on experimental eelgrass leaves, and epiphyte O_2 metabolism, *per se*, was not considered here.

Elongation of eelgrass leaves was measured using the method of Sand-Jensen (1975), where a mark was placed on the sheath of the oldest leaf in each shoot, and length of each leaf was measured from this stationary mark using a clear acrylic ruler. Each shoot was marked also with a identification number (1 to 12) to allow sequential observations, and the relative age of leaves on each shoot was readily determined by its position in the leaf bundle (Wium-Andersen & Borum 1984). The appearance of new leaves was noted, with their growth beyond the reference mark also being measured. Distance from the basal meristem to the reference mark on the sheath was measured so that total growth of new leaves (initially hidden within the sheath of older leaves) could also be included. Belowground production was estimated as the product of the rhizome formation rate and the mean weight of internodal segments (including root bundle). The time required for formation of a each rhizome segment was assumed equivalent to the plastochrone interval (PI), which is the time between emergence of successive leaves on a shoot (Patriquin 1973).

At the end of the experiment, all plant material from each experimental unit was collected, sorted, dried (100 °C for 24 h) and weighed; 5 to 10 rhizome seg-

ments (first fully formed segment on a plant) were also selected randomly from each unit, dried, and weighed. In addition, 20 to 25 representative leaves were selected randomly from each of 3 leaf-width groups (3.0 to 3.5 mm, 3.6 to 4.2 mm, 4.3 to 4.8 mm); each leaf was measured for length, dried and weighed. Increments in eelgrass leaf length (L, cm) were converted to changes in dry weight (W, g) by applying appropriate length-weight regressions for leaves from respective width-classes. For leaves of 3.0 to 3.5 mm width, $W = 1.24 L - 7.78$ ($r^2 = 0.93$); for leaves 3.6 to 4.2 mm wide, $W = 1.60 L - 12.10$ ($r^2 = 0.93$); and for leaves 4.3 to 4.8 mm wide, $W = 1.92 L - 17.76$ ($r^2 = 0.94$). The slope of these regressions is equivalent to specific leaf weight, while the negative intercepts indicate a non-linearity of these relations for short leaves.

Eelgrass response to fertilization was examined on 2 occasions by comparing growth in experimental units with and without addition of commercial granular fertilizer pellets (N:P:K, 10:10:10) to the sediments. Approximately 10 g of fertilizer was added to each experimental system, where pellets were gently pushed (ca 3 cm) into sediments by hand (Orth 1977). On both occasions, experimental units were incubated for 6 to 7 d in the 17 l chambers, and leaf length measurements were made at dawn and dusk (12 h intervals). These fertilizer pellets were characterized by relatively rapid dissolution: it was observed that approximately 70 % of the salts were dissolved in unstirred fjord water after 48 h.

In addition, preliminary assessment of 3 methodological questions was provided by comparing eelgrass leaf growth rates under different (non-replicated) experimental conditions. In one case, effects of handling frequency was investigated comparing leaf growth measured at 12 and 96 h intervals (Units B and C, respectively). Eelgrass leaf growth was also compared for plants incubated in chambers (Unit C) versus *in situ* conditions (Unit D) and for intact (Unit E) versus planted experimental units (C).

RESULTS AND DISCUSSION

Growth of individual leaves

Most of the above-ground growth of each *Zostera marina* shoot was concentrated in the youngest 1 or 2 leaves. When measurable at all, growth of a third leaf was < 10 % of that in the 2 younger leaves. This general growth pattern of individual leaves is illustrated in Fig. 1, where intact leaf lengths are plotted at 12 h intervals over 8 d for 4 representative shoots selected from an unfertilized experimental unit (B). Leaves are numbered from youngest (No. 1) to oldest, with No. 0
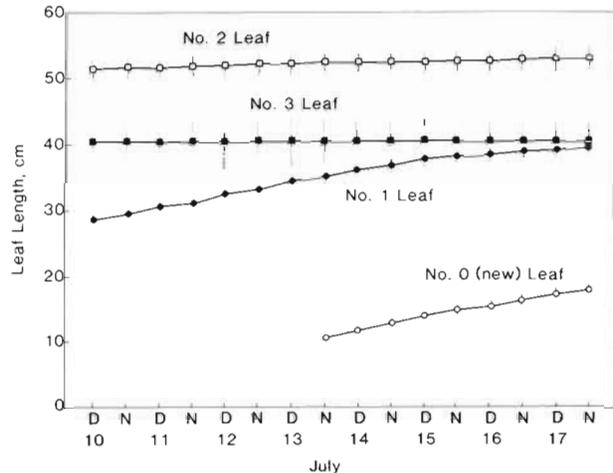

Fig. 1. *Zostera marina*. Temporal sequence of leaf lengths (± SE) in July measured at 12 h intervals (D = day, N = night) for 4 representative shoots selected from an experimental eelgrass unit (B)

indicating leaves which first emerged from the bundle sheath during the course of the experiment. During the initial 4 d of this incubation, growth was limited to the No. 1 (1.77 cm d^{-1}) and No. 2 (0.14 cm^{-1}) leaves. With the appearance of 2 new (No. 0) leaves after 3.5 and 5.5 d, the growth of No. 1 and No. 2 leaves slowed to 1.09 and 0.06 cm d^{-1}, respectively. The distribution of leaf growth for these shoots over the last 4 d was ca 2, 1 and 0.1 cm d^{-1} for Nos. 0, 1, and 2 leaves, respectively. This growth pattern is identical to those previously reported both for *Z. marina* populations off the French coast (Jacobs 1979) and for *Thalassia testudinum* near Barbados (Patriquin 1973), based on measurement intervals of 4 to 30 d.

Regressions of leaf length versus time were significant (t-test for non-zero slope, $p < 0.05$) for leaves No. 0, 1, and 2; however, no statistical time-trend was evident for leaves No. 3 and 4. Repetitive length measurements on leaves No. 3 and 4 therefore provided an estimate of the precision of this technique. For No. 3 leaves, the standard deviation was 0.4 mm, which is ca 0.1 % of the mean leaf length. Thus, for sequential observations, significant changes in leaf length of about 1 mm could be determined with confidence.

Length-frequency distributions for experimental *Zostera marina* shoots revealed greatest abundance of leaf Nos. 1, 2, 3, and 4 occurring in the length groups 21 to 30 cm, 51 to 55 cm, 46 to 50 cm, and 41 to 45 cm, respectively. Thus, the longest intact leaves were generally of intermediate age and growth rate. This is in contrast to reports of a direct, linear relation between leaf length and growth rate for *Thalassia testudinum* growing in tropical climates (Patriquin 1973, Zieman 1975). The non-linear relation between eelgrass leaf

length and growth observed here probably reflects a period of recently accelerated growth during the study, with older leaves (Nos. 3 to 5) being remnants of a previous period of slower elongation rates in late May and early June. Similar seasonal shifts in length-frequency distribution for different age leaves have been reported for other temperate seagrasses (Bulthuis & Woelkerling 1983).

Methods considerations

It appears that eelgrass growth was not affected by frequent handling of plants for length measurements at 12 h intervals (Unit B) compared to plants which were measured at a 4 d interval (Unit C). Daily growth for shoots in these 2 units were identical during the pretreatment period, and both decreased by about 30 % following initiation of treatment (Table 1). Diel leaf growth for plants incubated *in situ* (Unit D) also decreased (by 45 %) after the initial 4 d, but rates during the treatment period were similar to those for plants incubated in chambers (Unit C). Visually, plants grown *in situ* appeared to have more epiphytic fouling which may have offset any advantage of increased nutrition or water circulation that they might have experienced in nature (Borum 1985). Eelgrass shoots maintained with intact root-rhizome and sediment systems (Unit E) exhibited substantially higher (77 %) diel leaf growth rates than shoots removed from original substrate and replanted in homogenized sediments (Unit C). Evidently, during the process of mixing and rinsing, microzones of sediments were destroyed, resulting in a loss in fertility or in plant access to porewater nutrients (Kenworthy & Fonseca 1977).

Diel patterns of leaf growth

Overall, growth rates at night were consistently and significantly (t-test, $p < 0.05$) lower than rates during the day (by 30 to 40 %) for all experimental units (Table 1). Leaf growth at night was strongly correlated with growth during the previous daylight period (Fig. 2), indicating a close coupling. Presumably, a major portion of the energy captured during photosynthesis in a given day is used for growth in both that day and the following night. The small intercept in this relation (Fig. 2) is not significantly different from zero.

Growth of eelgrass leaves was also measured at time intervals of 4 h (Fig. 3). Daytime growth during each time interval exceeded 4 mm per shoot, a readily
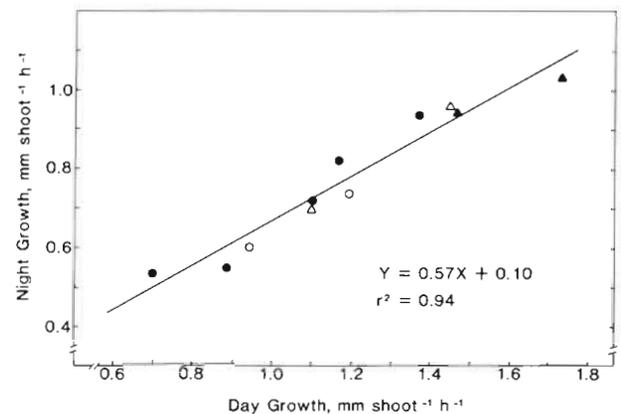
Fig. 2. *Zostera marina*. Correlation between leaf growth rates during night period and preceeding daytime period for experimental eelgrass units: (○) Unit A; (●) Unit B; (△) Unit C; (▲) Unit D. Growth data for fertilized plants (Unit A, 14 to 17 Jul) not included

Table 1. *Zostera marina*. Summary of leaf growth data for individual experiments units subjected to methodological tests. Pretreament period included 3 day and 3 night measurements (10 to 13 Jul); treatment period (14 to 17 Jul) included 4 day and 4 night measurements. Data given are mean values (± SE) for each time period (n = 3 or 4). Treatments include: handled every 12 h (H1) or every 96 h (H2); incubated in chamber (I1) or *in situ* (I2); planted shoots (S1) or intact shoots (S2)

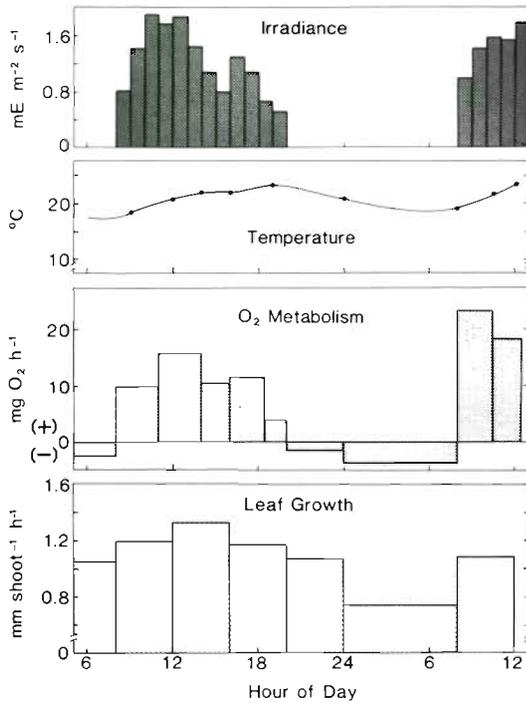| Eelgrass unit (Treatment) | Leaf growth rate (mm shoot^{-1} h^{-1}) | | | | |
| | Pre-treatment* | | Treatment* | | |
	Day	Night	Day	Night	Diel
B; handling (H1; I1; S1)	1.25 ±0.10	0.81 ±0.08	0.86 ±0.16	0.60 ±0.10	0.72 ±0.08
C; chamber (H2; I1; S1)	1.24 ±0.13	0.81 ±0.09	NA	NA	0.65 ±0.11
D; In situ (H2; I2; S1)	1.64 ±0.11	0.99 ±0.03	NA	NA	0.72 ±0.11
E; intact (H1; I1; S2)	NA	NA	1.25 ±0.00	1.04 ±0.07	1.15 ±0.06

NA: measurements not available

Fig. 3. *Zostera marina*. Diel pattern of net oxygen metabolism (production +, consumption −) and leaf growth for an intact eelgrass unit (E) in relation to daily cycles of irradiance (400 to 700 nm) and water temperature
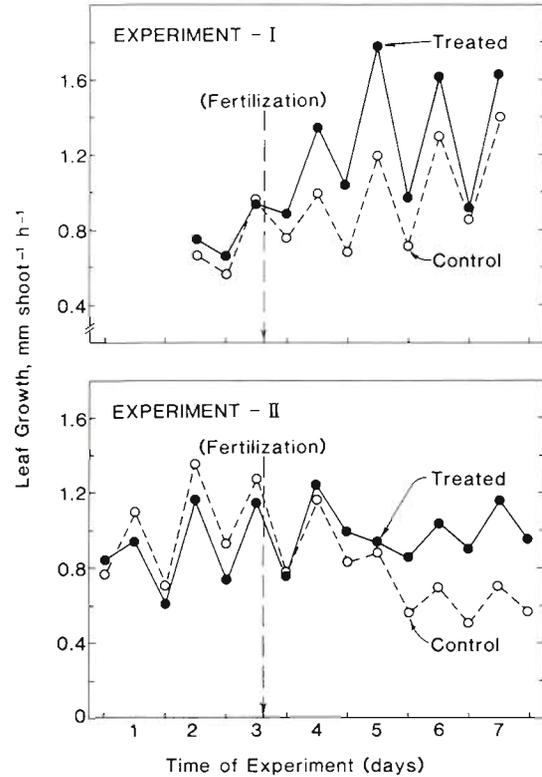

Fig. 4. *Zostera marina*. Temporal sequence of mean leaf growth rates measured at successive day and night intervals (12 h) for experimental eelgrass units with and without granular fertilizer added to sediments following daytime measurements on Day 3. Experiment I was conducted from 28 Jun to 4 Jul, with first measurement for daytime period; Experiment II was conducted from 10 to 17 Jul, with first measurement for night-time period

measurable change in length. Distinct patterns of O_2 metabolism and leaf growth were observed, with maximum and minimum rates occurring in early afternoon and early morning, respectively. Rates of night-time O_2 consumption constituted only 10 to 25 % of apparent (net) O_2 production during the day. There was an apparent lag of 1 to 3 h between the period of maximum irradiance and peak growth; however, this cannot be discerned clearly because sampling intervals were too long (Fig. 3). Oxygen production was depressed during a mid-afternoon period (3 h) of decreased irradiance (Fig. 3) associated with intermittent cloud-cover (cf. Kelly et al. 1983).

Response to environmental changes

Eelgrass growth response to sediment fertilization was evident within 24 to 60 h following treatment in both nutrient-addition experiments (Fig. 4). Leaf growth in the fertilized units averaged 25 and 33 % higher than in control units for the first and second experiments, respectively. Temporal patterns, however, were markedly different in the 2 experiments (Fig. 4). In the first study, growth rates continued to increase over the duration, and day–night differences in growth were pronounced. In contrast, leaf growth

increased only slightly with fertilization (compared to pre-treatment values) in the second experiment, while growth in the unfertilized unit declined from Day 2 to 7. Diel ranges in growth also declined with time in the second experiment.

Previous studies have reported increased growth over several weeks with *in situ* nutrient additions for *Zostera marina* and related species (Orth 1977, Bulthuis & Woelkerling 1981, Harlin & Thorne-Miller 1981). However, no previous study has investigated this response on time-scales of hours to days. The statistical significance of these fertilization responses cannot be discerned adequately in this study because of limited replication. The important thing here is that the observed response was rapid (ca 1 to 3 d) and detectable under 2 very different growth conditions.

Integrated daily irradiance (400 to 700 nm) levels during this study were relatively high, with mean values ranging from ca 600 to 1400 μE m^{-2} s^{-1}. Neutral density screening was effective in reducing irradiance in the chambers at plant height to ca 175 to 425 μE m^{-2}

s^{-1}. Experimental light levels were in the range of I_k (irradiance level for incipient light-saturated photosynthesis) values for eelgrass leaves (Penhale 1977, Sand-Jensen 1977, Dennison & Alberte 1985). A significant correlation was observed between integrated daily values of leaf growth (G, cm shoot^{-1} d^{-1}) and irradiance (I, E m^{-2} d^{-1}) for the fertilized experimental unit (A): G = 2.9 I/(3.1 + I), r^2 = 0.91. This correlation suffers from limited degrees of freedom (n = 6), and the estimate of I_k is probably too low (< 100 µE m^{-2}s^{-1}). Nonetheless, the relation demonstrates an ability of diel measurements of leaf growth to detect eelgrass response to changing daily light regimes.

Biomass growth versus oxygen production

Quantitative comparisons of diel growth and O_2 metabolism for these experimental eelgrass units were developed applying appropriate adjustments to the 2 rate measurements. Net diel O_2 production (daytime production minus night consumption) attributable to eelgrass (plus epiphytes) was calculated by subtracting rates of planktonic and benthic metabolism, and O_2 diffusion across the chamber walls, from the overall rates of O_2 concentration change in incubation water. Planktonic metabolism ranged from about 0.02 to 0.05 mg O_2 l^{-1}h^{-1}, which represents 5 to 15 % of the combined rate of O_2 change; rates of daytime net production and night-time consumption were similar to one another. Net benthic metabolism was always heterotrophic (negative), with respiration rates varying from about 20 to 40 mg O_2 m^{-2} h^{-1}, which amounts to 5 to 10 % of diel net O_2 production.

Growth of roots and rhizomes was assumed to be constant over the entire study period. This assumption was necessary because the plastochrone interval (PI) cannot be determined on a daily basis. Brouns (1985) has suggested a minimum of 7 to 12 d is required for a statistically accurate measurement of PI for the tropical seagrass *Thalassia hemprichii*. For the eelgrass units in this experiment, PI ranged from 10 to 14 d (averaging 12 d). These values are similar to that reported by Sand-Jensen (1975) for a nearby eelgrass population in July.

By integrating biomass growth and O_2 metabolism over full diel measurement periods, correcting O_2 rates to include only eelgrass (plus epiphyte) production, and converting biomass from dry weight to carbon (C:d.w. = 0.38, Sand-Jensen 1975), the 2 daily rates were compared (Fig. 5). Ratios of O_2 production to carbon incorporation (O_2:C) generally fell between 0.75 and 1.50, with three-quarters of these data exceeding unity. Mean O_2:C ratios for individual experimental units ranged from 0.84 to 1.40, with the maximum and

minimum ratios being significantly different from each other. This suggests that the variance in O_2:C was related as much to differences among plants as to daily physiological variations or to methodological uncertainties. If balances between both carbon and oxygen metabolism and photosynthesis and growth were maintained over diel periods of measurement, then these O_2:C ratios would approximate photosynthetic quotients (PQ). The mean ratio O_2:C for data in Fig. 5 is
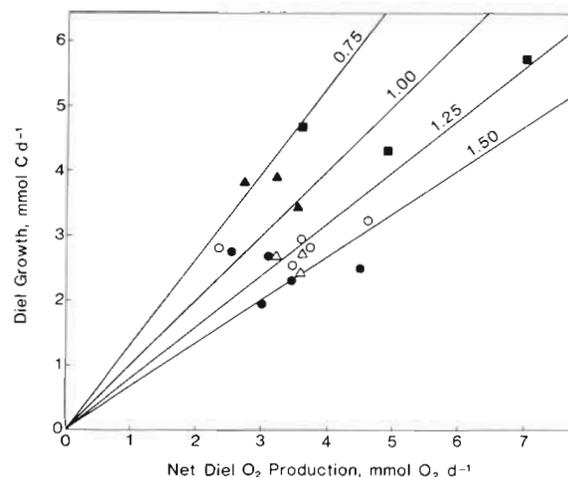

Fig. 5. *Zostera marina*. Comparison of diel rates of plant growth (total biomass increase converted to carbon units) and net oxygen production (daytime production minus night-time consumption) for experimental eelgrass units: (○) Unit A, fertilized; (●) Unit B, chamber incubated, handled every 12 h; (△) Unit C, chamber incubated, measured only after 96 h; (▲) Unit D, incubated *in situ*; (■) Unit E, intact core. Family of lines represents selected ratios of (O_2 metabolism):(carbon growth)

1.20 ± 0.07 (SE), which is similar to PQ values expected for aquatic macrophytes (e.g. Westlake 1965). A few other studies have demonstrated close correspondence between contemporaneous measurements of short-term (2 to 6 h) photosynthetic production and longer-term (7 to 10 d) biomass growth for macrophytes (e.g. Bittaker & Iverson 1976, Kemp et al. 1986). However, no previous investigation has reported comparisons of photosynthesis and growth based on incubations of the same (diel) time-scale.

Leaf growth versus total biomass production

The ability to determine eelgrass leaf growth successfully at 4 to 12 h measurement intervals has been demonstrated here (Fig. 1 to 4). Furthermore, by converting leaf-growth data to biomass units and accounting for root-rhizome production (assumed constant over PI), total biomass growth was shown to be comparable

with measurements of net diel O_2 production (Fig. 5). However, even though leaf growth rates can be determined with short-term incubations, translating such data to total plant growth requires measurement of PI over much longer incubations. The minimum study duration needed to estimate PI appears to be ca 70 to 120 % of the PI itself (Brouns 1985). In the present case, this would be 8 to 14 d. This limitation means that short-term leaf growth determinations cannot, *per se*, measure total plant production. However, under conditions of balanced growth where biomass accumulation of leaves is a consistent fraction of total production, leaf growth could be used as an index of that total and calibrated accordingly.

To investigate the possibility for developing such a calibration for 5 experimental eelgrass units, total biomass production was partitioned into growth of 3 component parts (Fig. 6): existing leaves; new leaves; roots
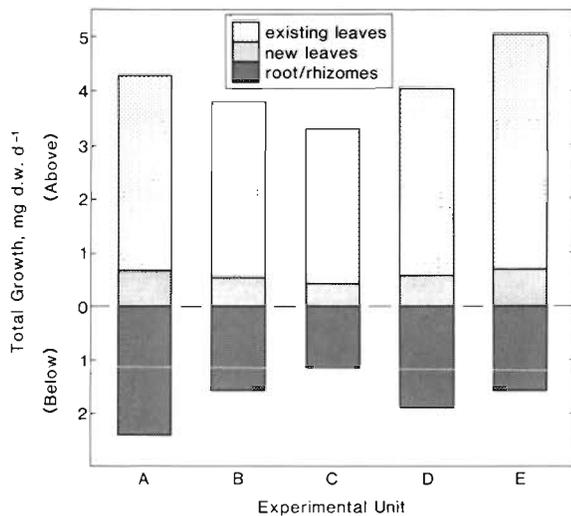

Fig. 6. *Zostera marina*. Biomass growth over study period (4 to 8 d) for 5 experimental eelgrass systems (Units A to E) partitioned into production of 3 plant components: leaves existing at beginning of incubation; leaves emerging during the incubation period; roots plus rhizomes. See Fig. 5 legend for description of treatments

and rhizomes. In combination the latter 2 components, which both require a minimum study duration approaching the PI, constituted 34 to 46 % of the total production. Growth of new leaves represented a constant proportion of existing leaf growth (13 to 15 %), while root-rhizome growth ranged from 24 to 36 % of leaf growth rates.

Final biomass of roots plus rhizomes correlated well with that of leaves, with the latter explaining 86 % of variations in the former (Fig. 7A). For the 4 replanted eelgrass units (A to D), a strong correlation between leaf and root-rhizome growth rates was likewise

obtained (Fig. 7B), with $r^2 = 0.97$ and a slope of about 1.0. This relation breaks down for the intact plant-sediment system (Unit E), where leaf production was more than 3 times that of roots plus rhizomes. This higher ratio of leaf to root-rhizome growth may have been associated with greater sediment fertility for the intact experimental Unit E which would be reflected by
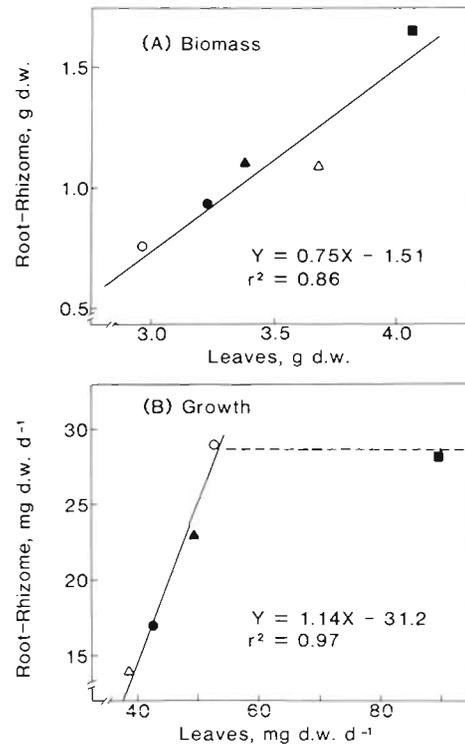

Fig. 7 *Zostera marina*. Comparison of eelgrass roots plus rhizomes versus leaves in terms of (A) biomass and (B) growth rate. Different symbols represent different experimental units: (o) Unit A; (●) Unit B; (△) Unit C; (▲) Unit D; (■) Unit E. See Fig. 5 legend for description of treatments

relatively lower investment in growth of roots for nutrient absorption (e.g. Denny 1972). Dry weight turnover times (biomass/production) were relatively consistent for leaves (10 to 20 d) and roots plus rhizomes (15 to 30 d). Total plant production, thus, can be readily calibrated to leaf growth for different plants incubated under similar conditions (e.g. Units A to D). Separate calibrations, however, are needed for plants growing under different environmental conditions.

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