

Meadow maintenance, growth and productivity of a mixed Philippine seagrass bed

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ABSTRACT: Leaf production, shoot demography and rhizome growth and branching were quantified for the common seagrass species in a mixed seagrass bed on the Bolinao reef flat (Luzon, The Philippines) to assess the contribution of these species to canopy maintenance, meadow biomass and productivity. We tested the hypothesis that seagrass growth rates correlated negatively with shoot size and age when compared across species, and found that shoot recruitment, leaf turnover and horizontal rhizome elongation and branching rates were lower for species with older and larger shoots. Median shoot ages for the short-lived species were generally less than a year; those for the longer-lived *Enhalus acoroides* (L. f.) Royle and *Thalassia hemprichii* (Ehrenb.) Aschers. were slightly more than 1.5 yr. The oldest *E. acoroides* had almost reached 10 yr. Generally, shoot mortality and recruitment balanced each other fairly well. The rhizomes of longer-lived *E. acoroides* and *T. hemprichii* elongated at rates of 5 and 21 cm yr⁻¹, respectively, and those of the short-lived *Syringodium isoetifolium* (Aschers.) Dandy and *Halophila ovalis* (R. Br.) Hook f. at rates of 135 and 141 cm yr⁻¹. Vertical shoot elongation ranged from 2 to 13 cm shoot⁻¹ yr⁻¹ and was not correlated with size or age. The meadow had a total biomass of 624 g dry wt (DW) m⁻² (roots excluded), to which the larger and longer-lived species *T. hemprichii* and *E. acoroides* contributed substantially (52 and 37%, respectively). Leaf production dominated total annual productivity, constituting 91% of 2143 g DW m⁻² yr⁻¹ (roots excluded); this productivity was mainly due to *T. hemprichii* (74%), and not to the oldest and slowest-growing *E. acoroides* (10%).

KEY WORDS: Tropical seagrasses · Shoot life spans · Recruitment and mortality · Pioneer vs climax species · Allometry

INTRODUCTION

With at least a dozen species, of which 7 are common, the Philippine seagrass flora is among the richest in the world (Den Hartog 1970, Fortes 1988, 1989, Phillips & Meñez 1988). As in most of the Indo-Pacific region (Brouns 1987a, b, Nienhuis et al. 1989, Brouns & Heijs 1991), Philippine seagrass beds are generally mixed (Meñez et al. 1983, Tomasko et al. 1993, M.D.F. pers. obs.). Whereas the dynamics of monospecific seagrass meadows are well studied (e.g. review in Duarte

1991a), little is known about those of mixed beds, or how the different species contribute to canopy maintenance and productivity (Brouns 1987b, Williams 1990).

A comparative analysis of the growth dynamics of different seagrass species forming monospecific meadows has shown that differences in shoot growth and population dynamics were associated with differences in seagrass size (Duarte 1991a): larger species were found to be longer-lived and slow-growing, whilst smaller species were shorter-lived and grew faster. Duarte (1991a) formulated this association as allometric relationships between rhizome diameter or shoot size and module (sensu Harper 1976, Duarte et al.

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1994; i.e. shoots, leaves, rhizome internodes, or roots) life span and production rates.

This finding suggests that the large differences in size of the seagrass species present in Philippine mixed beds (cf. Meñez et al. 1983, Duarte 1991a) may help explain differences in their contribution to canopy maintenance and meadow productivity. We expect the larger, more longevous species to behave as 'climax' species, whereas the smaller, short-lived and fast-growing species may act as 'pioneer' species (cf. e.g. Birch & Birch 1984, Brouns 1987a, b). The allometric relations given in Duarte (1991a), however, were derived for monospecific beds, and may for example be confounded by differences in growth conditions along the distributional range of the many species studied or by interspecific interference in the mixed bed; hence their relevance in mixed meadows remains to be tested.

In this paper we quantify life-span, mortality and recruitment patterns of shoots, as well as rhizome branching patterns and vertical and horizontal rhizome growth, of 7 seagrass species from mixed meadows on the Bolinao reef flat (NW Luzon, The Philippines). Our aims were: (1) to test the hypothesis that an allometric relation also exists between module size or age and growth of co-occurring seagrass species in a mixed bed; and (2) to assess the contribution of these species to canopy maintenance, meadow biomass and productivity. We rely on the age reconstruction technique of Duarte et al. (1994) and an assessment of the size of the different seagrass modules.

MATERIALS AND METHODS

The data were collected in April 1992 in the Cape Bolinao area, which has approximately 37 km² of mixed seagrass beds (Fortes 1988, 1989, Klumpp et al. 1992; Fig. 1) and experiences a maximum semi-diurnal tidal range of 1 m. The species present in these mixed beds are *Cymodocea rotundata* Ehrenb. & Hempr. ex Aschers., *Cymodocea serrulata* (R. Br.) Aschers. & Magnus, *Enhalus acoroides* (L. f.) Royle, *Halodule uninervis* (Forssk.) Aschers., *Halophila ovalis* (R. Br.) Hook f., *Syringodium isoetifolium* (Aschers.) Dandy and *Thalassia hemprichii* (Ehrenb.) Aschers. All species except *Enhalus acoroides* and *Halophila ovalis* have differentiated vertical or 'short' shoots that are placed at different intervals along the horizontally creeping rhizome [the basic architecture of seagrasses is illustrated e.g. in Den Hartog (1970), Tomlinson (1974), Phillips & Meñez (1988) and Duarte et al. (1994)]. Sampling was carried out at 3 stations (Fig. 1): a subtidal station (3 m mean depth; *C. rotundata*, *C. serrulata*, *E. acoroides*, *H. ovalis*, *H. uninervis*, *S.*

isoetifolium, *T. hemprichii*), an intertidal station (0.5 m; *C. rotundata*) off Silaqui island on coral rubble, and a shallow subtidal station on shallow silty sand overlying hard coral rock at Pislatan (1 m; *C. serrulata*, *E. acoroides*, *H. uninervis*). Most of the data presented here have been pooled across stations, since between-station differences were generally insignificant.

Seagrass samples were collected with a stainless steel cylindrical corer (20 cm diameter) pushed about 30 cm into the sediment. In a total of 30 cores we collected 342 shoots of *Cymodocea rotundata*, 156 of *Cymodocea serrulata*, 55 of *Halodule uninervis*, 61 of *Syringodium isoetifolium* and 533 shoots of *Thalassia hemprichii*. The cores were gently washed out on-site, carefully maintaining the connections between rhizomes and shoots. The large shoots of *Enhalus acoroides* had a patchy distribution and were, therefore, collected by hand to obtain a sample size of 20 shoot clusters. A shoot cluster is a group of shoots (or ramets; Harper 1977) attached as branches to a common rhizome axis.

The samples were washed once more upon return to the laboratory, and the plants were carefully sorted to the species level. The rhizome axes sampled were then examined to estimate the number of rhizome apices, shoot size (length and number of vertical internodes, as well as leaf number, length and width) and age (as the sum of the number of leaf scars and standing leaves, i.e. in plastochron intervals; cf. Duarte et al.

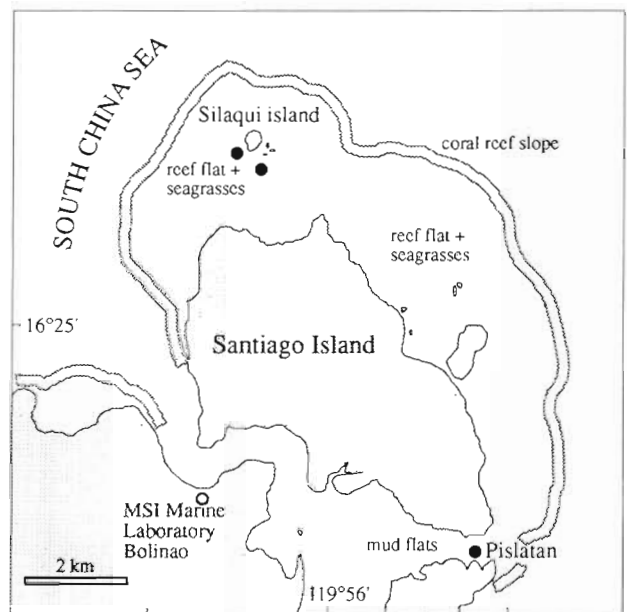


Fig. 1 Location of the study sites in the mixed seagrass beds of the Bolinao reef lagoon. The Philippines: a subtidal and an intertidal station off Silaqui (the latter is closer to the island), and a shallow subtidal station at Pislatan

1994), the number of rhizome internodes between shoots, rhizome internode length and diameter, and the occurrence and angle of rhizome branches. Vertical shoot length (mm) was measured from the insertion of the vertical stem on the horizontal rhizome to the apical leaf-producing meristem. The length of the petioles of *Halophila ovalis*, which lacks vertical shoots, was also measured. Shoot leaf area (single-sided) was calculated as leaf width times the sum of leaf lengths, except for the subulate leaves of *Syringodium isoetifolium* for which leaf area was calculated assuming a conical shape: $\text{Area} = \pi \times \text{Leaf radius} \times \text{Leaf length}$. The age of *Enhalus acoroides* shoots could only be determined precisely for lateral shoots, whereas for apical shoots only a minimum estimate was possible: either up to the first branch, or to the decaying distal end of the rhizome. The latter measurement is also a minimum age estimate for the whole shoot cluster.

Subsamples of leaves, complete shoots, and vertical and horizontal rhizomes of each species were dried (105°C) to constant weight to estimate specific module weights (i.e. mg DW cm⁻² leaf, mg DW shoot⁻¹, mg DW internode⁻¹; DW = dry weight). Shoot abundance was represented as mean annual density, estimated from 10 replicate 0.25 m² quadrats sampled monthly between July 1992 and October 1993 at the subtidal Silaqui station (Vermaat et al. 1994). These mean annual density estimates were used to calculate the single-sided leaf area index (LAI, m² m⁻²) and shoot biomass (g DW m⁻²) for the separate species and the meadow.

Shoot age and estimates of time in plastochron intervals (PI) were converted to days using the annual mean PI equivalence in days as measured at the study sites (cf. Duarte et al. 1994) for *Cymodocea rotundata* (11.4 ± 0.3 d), *C. serrulata* (12.7 ± 1.2 d), *Enhalus acoroides* (35.6 ± 1.8 d) and *Thalassia hemprichii* (10.9 ± 0.3 d). The PI for *Syringodium isoetifolium* was taken from the literature (33.2 d; Duarte 1991a) and for *Halophila ovalis* and *Halodule uninervis* from short-term marking measurements at the subtidal Silaqui station. For *H. uninervis* the leaves of 36 shoots were marked by punching them with a hypodermic needle at the level of the ligula of the oldest leaf (Zieman 1974). *H. ovalis* rhizomes (n = 20) were tagged with a ribbon around the last fully developed internode. The marked plants were harvested after 4 d, and the appearance of new, unmarked *H. uninervis* leaves, and new *H. ovalis* internodes with their corresponding leaf pair, were used to calculate the PI in days of these species (Duarte et al. 1994).

Vertical elongation rates were estimated from the slope of a linear regression of vertical shoot length to shoot age (in PI; Duarte et al. 1994). Similarly, horizontal rhizome growth was estimated from the slope of the

distance between shoots connected along a section of rhizome against the difference in age between these shoots (Duarte et al. 1994).

Annual shoot recruitment rates (R , ln units yr⁻¹) were calculated from the total number of live shoots (N_{total}) and the number of shoots older than 1 yr ($N_{\text{age}>1\text{yr}}$), both present in the sampled shoot population, using the equation (Duarte et al. 1994):

$$R = \ln(N_{\text{total}}) - \ln(N_{\text{age}>1\text{yr}}) \quad (1)$$

N_{total} and $N_{\text{age}>1\text{yr}}$ were derived from frequency distributions of age (in PI). Shoot life expectancy was estimated as the median age at death of dead shoots (i.e. those without leaves but ending in a round tip; cf. Duarte et al. 1994) present in the samples. Exponential shoot mortality rates (M , ln units yr⁻¹) were estimated as the slope of a linear regression fitted to the natural log-transformed age distribution tails of living shoots using the equation (Duarte et al. 1994):

$$N_t = N_0 e^{-Mt} \quad (2)$$

where N_0 and N_t are the numbers of shoots present at times 0 and t . The use of living shoots to estimate M assumes interannual homogeneity in recruitment and mortality rates (Harper 1977, Duarte et al. 1994). Statistical analyses were done with SPSS/PC⁺ (Norusis 1986). Multiple comparisons among species were made with least significant difference (LSD) tests at a reduced comparisonwise error rate to maintain an overall error rate of 0.05, and after log-transformation to homogenize variances whenever needed (Steel & Torrie 1980).

RESULTS

The seagrasses that form this mixed bed encompass a considerable size range, from the smallest (*Halophila ovalis*) to the largest (*Enhalus acoroides*). Most module dimensions differed significantly between species (Table 1). The different species had a comparable number of leaves, but leaf dimensions differed widely, so that shoot leaf area and weight differed by 2 orders of magnitude. Rhizome diameter and (vertical and horizontal) internode lengths differed 10-fold.

As demonstrated before (Duarte et al. 1994), the length of the vertical internodes of *Cymodocea rotundata*, *C. serrulata*, *Thalassia hemprichii* and *Enhalus acoroides* showed distinct annual cycles, indicating seasonal changes in vertical growth. Moreover, especially *C. rotundata* (Fig. 2) but also *T. hemprichii* showed 2 minima in a year: an absolute minimum in early January, the time of the shortest daylength, and a secondary minimum in August/September, i.e. when the rainy SW monsoon results in low salinity and temperature of the reef lagoon water (Vermaat et al. 1994). These 2 minima were

Table 1 Weight and size of the modules of seagrasses present in the mixed meadows at Bolinao (Luzon, The Philippines). Mean module biomass in dry weight was derived from large pooled samples ($n > 30$ modules); means are given ± 1 standard error; sample size is in parentheses; na: not applicable. Where multiple comparisons (modified LSD) revealed significant differences between species, these are indicated with different letters in superscript

	<i>Cymodocea rotundata</i>	<i>Cymodocea serrulata</i>	<i>Enhalus acoroides</i>	<i>Halophila ovalis</i>	<i>Halodule uninervis</i>	<i>Syringodium isoetifolium</i>	<i>Thalassia hemprichii</i>
Vertical internode weight (mg)	0.4	5.6	na	na	3.0	3.0	3.2
Horizontal internode weight (mg)	12.6	15.9	312.6	2.9	11.4	11.3	7.0
Leaf weight (mg)	35.8	44.2	568.4	3.5	18.3	44.9	79.3
Leaves per shoot	$3.41^b \pm 0.10$ (70)	$3.37^b \pm 0.07$ (107)	$4.38^c \pm 0.70$ (40)	2 ^a	$2.73^{ab} \pm 0.11$ (51)	$2.07^{ab} \pm 0.08$ (61)	$3.29^b \pm 0.05$ (309)
Shoot leaf area (mm ² , single-sided)	$3703^d \pm 0.47$ (51)	$3322^a \pm 6.88$ (9)	$35870^b \pm 24.4$ (37)	$416^a \pm 0.70$ (10)	414 ^a	799 ^a	$2656^d \pm 2.32$ (50)
Leaf length (mm)	$222.6^c \pm 0.26$	$92.2^b \pm 1.36$	$500.8^d \pm 1.82$	$15.4^a \pm 0.09$	48.9 ^{ab}	$136.6^b \pm 0.68$	$86.8^b \pm 0.53$
Leaf width (mm)	$5.5^b \pm 0.04$	$8.7^c \pm 0.08$	$15.7^d \pm 0.04$	$8.5^c \pm 0.08$	$3.1^{ab} \pm 0.03$	$1.8^a \pm 0.08$	$8.0^c \pm 0.04$
Vertical shoot length (mm)	$13.3^a \pm 0.02$ (69)	$79.8^c \pm 0.51$ (90)	$103.9^c \pm 1.45$ (27)	$14.9^a \pm 0.17$ (10)	$53.5^b \pm 0.64$ (39)	$47.6^b \pm 0.41$ (56)	$62.4^b \pm 0.45$ (114)
Vertical internode length (mm)	0.47 ± 0.04	4.49 ± 0.46	na	na	1.07 ± 0.56	7.77 ± 0.60	0.87 ± 0.06
Rhizome diameter (mm)	$2.87^a \pm 0.76$ (5)	$2.88^a \pm 0.25$ (2)	$13.25^b \pm 1.25$ (2)	$1.09^a \pm 0.07$ (8)	1.25 ^a	$2.18^a \pm 0.86$ (5)	$3.43^a \pm 0.00$ (2)
Horizontal internode length (mm)	$13.5^{bc} \pm 0.01$ (98)	$39.3^a \pm 0.19$ (66)	$4.7^a \pm 0.00$ (28)	$17.0^c \pm 0.13$ (45)	$8.6^{ab} \pm 0.14$ (24)	$25.3^d \pm 0.11$ (40)	$3.7^a \pm 0.01$ (30)

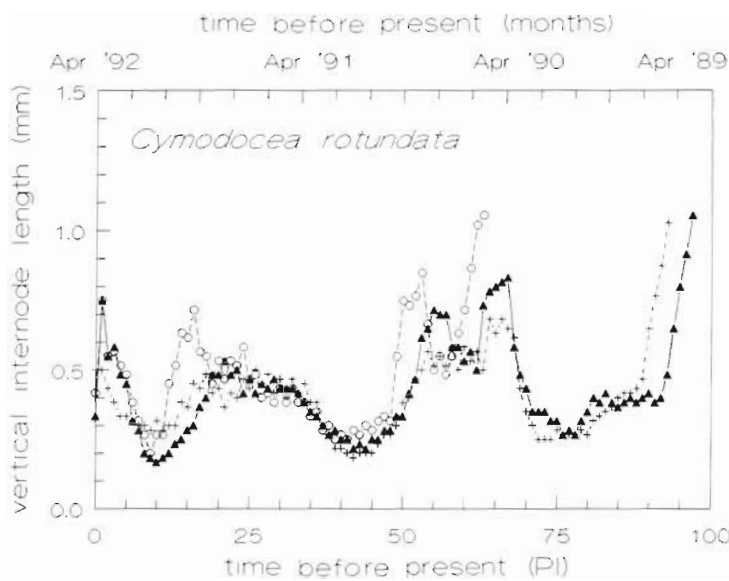


Fig. 2. *Cymodocea rotundata*. Seasonal variation in vertical internode length of 3 shoots from samples taken at the subtidal Silaqui station. Different symbols identify the different shoots. Time in months along the upper horizontal axis is computed using the mean annual plastochron interval (PI) duration in days for this species

also observed in seasonal leaf marking studies (Vermaat et al. 1994).

The PI estimates for *Enhalus acoroides* and *Syringodium isoetifolium* were relatively high (about a month) compared to the 9 to 12 d for the remaining species; for *Halophila ovalis* we found an even shorter PI of 2 d (Table 2). Comparison of the number of leaves produced in a year (Table 2) with the average number of leaves on a shoot (Table 1) suggests rapid leaf turnover (about 10 leaves shoot⁻¹ yr⁻¹ or more) for most species except *S. isoetifolium* (5 leaves shoot⁻¹ yr⁻¹) and *E. acoroides* (2.5 leaves shoot⁻¹ yr⁻¹).

For all species with differentiated vertical stems, vertical growth was significantly correlated with shoot age ($p < 0.001$; Fig. 3), which allowed the calculation of vertical elongation rates (Table 2). The shoots showed substantial vertical growth, ranging from 1.5 to 13.1 cm shoot⁻¹ yr⁻¹. Differences between stations were not significant, except for *Halodule uninervis* (Fig. 3), which had a significantly higher vertical growth rate at Pislatan than at the subtidal Silaqui station (F -test comparing regressions: $p < 0.001$).

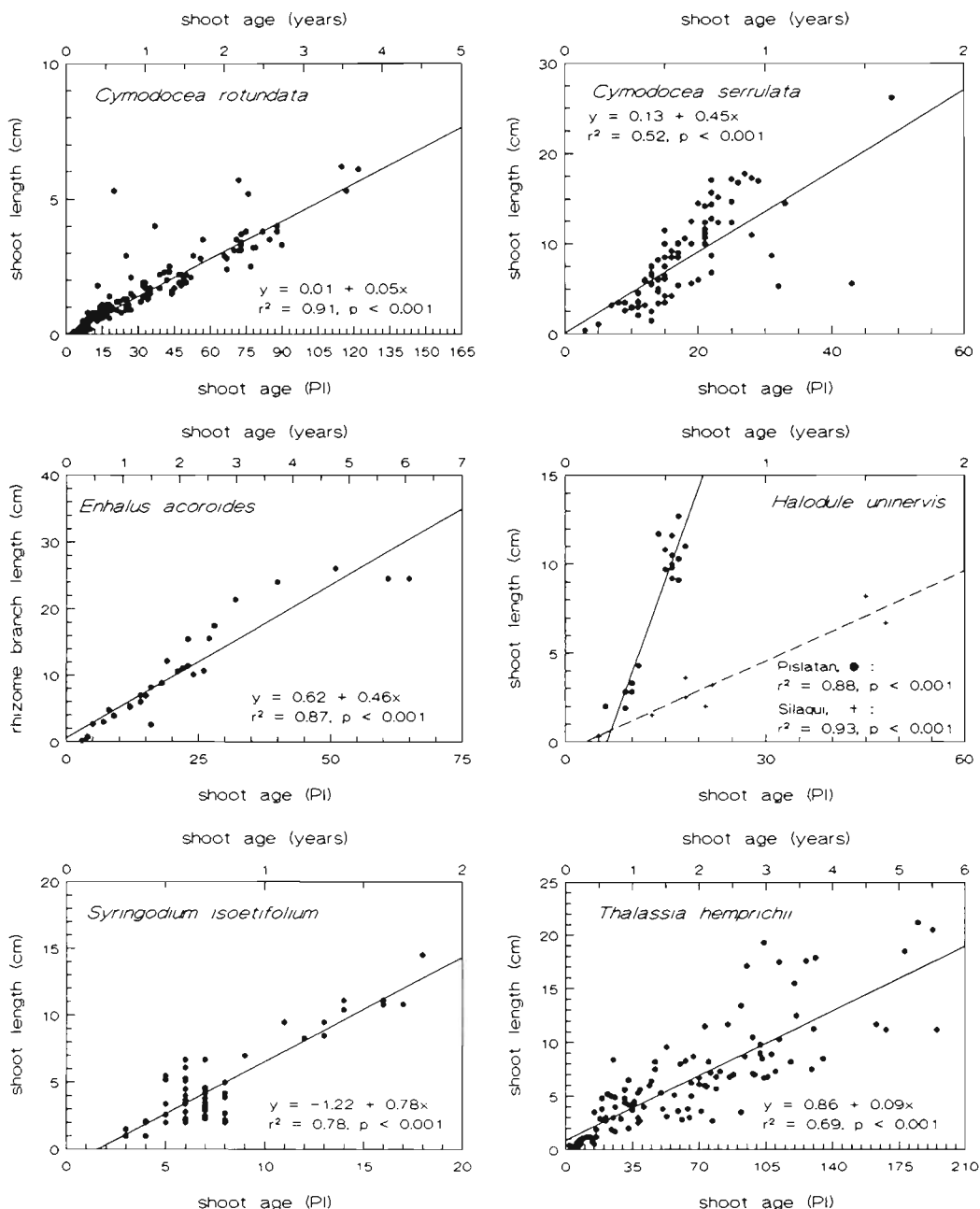


Fig. 3. Vertical shoot length versus shoot age of the seagrasses at Bolinao. Rhizome apex length of *Enhalus acoroides* is included, although strictly speaking it has no differentiated vertical shoots. Shoot age is expressed in terms of leaf plastochron intervals (PI) and years (based on the mean annual PI duration in days for each species)

Horizontal rhizome growth rates were lowest for *Enhalus acoroides* (5 cm yr^{-1} ; Table 2) and highest for *Halophila ovalis* (141 cm yr^{-1}). Rhizomes branched at angles of about 60° (Table 2: 40° for *Cymodocea serrulata* to 72° for *H. ovalis*), but no branches were observed in the large sample of horizontal rhizomes of *Thalassia hemprichii* examined (Table 2). Branch production per year tended to correlate positively with

horizontal rhizome growth (excluding *T. hemprichii*, $r^2 = 0.70$, $p < 0.10$).

Enhalus acoroides and *Thalassia hemprichii* had fairly long-lived shoots, with median ages of about 1.5 yr and maximal observed longevities of 9.8 and 6.1 yr, respectively (Table 3). The remaining species had mean shoot ages rarely exceeding 1 yr, although the oldest *Cymodocea rotundata* shoot sampled had an

Table 2. Number of leaves produced per shoot per year, and the corresponding plastochron intervals (PI), rhizome elongation and branching rates, and shoot spacing on the rhizomes, of the seagrasses present in the mixed meadows at Bolinao (Luzon, The Philippines). Means are given ± 1 standard error; sample size is in parentheses, na: not applicable; -: data were not collected. Leaf PI in *Halophila ovalis* was calculated as half the measured rhizome PI of 4.4 d, because a pair of leaves is produced for each rhizome internode. Vertical elongation rate for *Halodule uninervis* was averaged over the Silaqui and Pislatan stations

	<i>Cymodocea rotundata</i>	<i>Cymodocea serrulata</i>	<i>Enhalus acoroides</i>	<i>Halophila ovalis</i>	<i>Halodule uninervis</i>	<i>Syringodium isoetifolium</i>	<i>Thalassia hemprichii</i>
PI (d)	11.4 \pm 0.3 (29)	12.7 \pm 1.2 (3)	35.6 \pm 1.8 (46)	2.2 (12)	9.6 (36)	33.2	10.9 \pm 0.31 (59)
Leaves shoot ⁻¹ yr ⁻¹	32.5 \pm 0.8	29.3 \pm 3.0	11.5 \pm 0.6	165.9	38.0	11.0	34.8 \pm 0.9
Vertical elongation rate (cm shoot ⁻¹ yr ⁻¹)	1.5 \pm 0.1 (69)	13.1 \pm 1.8 (90)	na	na	4.1 \pm 2.1 (39)	8.6 \pm 0.7 (56)	3.0 \pm 0.2 (115)
Horizontal elongation rate (cm apex ⁻¹ yr ⁻¹)	33.9	78.3	5.3	141.0	28.4	134.7	20.6
Horizontal elongation rate (internodes apex ⁻¹ PI ⁻¹)	0.77 \pm 0.03 (98)	0.68 \pm 0.21 (15)	1	0.5	0.87 \pm 0.19 (46)	4.84 \pm 2.10 (14)	1.60 \pm 0.28 (17)
Rhizome branching angle (degrees)		39.5 \pm 4.9 (9)	56.6 \pm 4.1 (25)	72.0 \pm 4.2 (27)	55.5 \pm 6.8 (9)	58.0 \pm 9.0 (7)	na
Branching rate (branches apex ⁻¹ yr ⁻¹)		1.15	0.29	13.4	0.39	2.93	<0.01
Horizontal internodes between shoots	7.52 \pm 0.10 (98)	1.61 \pm 0.21 (66)	14.22 \pm 2.48 (9)	1	5.17 \pm 1.50 (24)	1.50 \pm 0.12 (40)	20.18 \pm 2.11 (28)
Shoot spacing along the rhizome (cm)	4.8	5.3	6.9	1.7	2.7	3.7	6.9
Distance between horizontal branches (cm)		68.1	19.2	10.5	62.8	45.9	>2846.0

Table 3. Age of live and dead shoots, as well as shoot mortality and recruitment (gross and net) rates, of seagrass species forming the mixed meadow at Bolinao (Luzon, The Philippines). Means are given ± 1 standard error; sample size is in parentheses; na: not applicable; -: data were not collected. In *Enhalus acoroides* and *Halophila ovalis*, shoot age was calculated for branches up to the connection with the main rhizome axis, and for apices up to the first rhizome branch

	<i>Cymodocea rotundata</i>	<i>Cymodocea serrulata</i>	<i>Enhalus acoroides</i>	<i>Halophila ovalis</i>	<i>Halodule uninervis</i>	<i>Syringodium isoetifolium</i>	<i>Thalassia hemprichii</i>
Age of living shoots (d)	343 \pm 20 (269)	202 \pm 9 (126)	787 \pm 125 ^a (34)	27 \pm 4.2 (25)	145 \pm 16 (55)	244 \pm 15 (61)	668 \pm 27 (346)
Median [maximum] age of living shoots (d)	286 [1510]	190 [622]	570 [3564]	22 [79]	134 [461]	232 [598]	584 [2215]
Life expectancy (median age of dead shoots \pm SE)	57 \pm 24 (73)	57 \pm 7 (30)	-	-	-	166 \pm 10 (9)	229 \pm 17 (187)
Recruitment rate, <i>R</i> (yr ⁻¹); [annual recruits m ⁻²]	1.08 [258]	3.10 [170]	0.26 [9]	-	2.06 [471]	2.05 [738]	0.77 [320]
Mortality rate, <i>M</i> (yr ⁻¹)	0.80 \pm 0.10 (26)	2.86 \pm 0.40 (9)	0.23 \pm 0.05 (18)	-	1.81 \pm 0.42 (12)	2.46 \pm 0.50 (4)	0.48 \pm 0.05 (39)
Net recruitment, <i>R</i> - <i>M</i> (yr ⁻¹)	0.28	0.24	0.03	-	0.25	-0.41	0.29

^aAlternatively, minimal age of the apical shoots of *E. acoroides* was calculated by summing all internodes of the main rhizome axis up to its distal end: 1673 \pm 229 (18), with median and maximum age being 1869 and 3564 d, respectively. This is also the minimal age of a shoot cluster

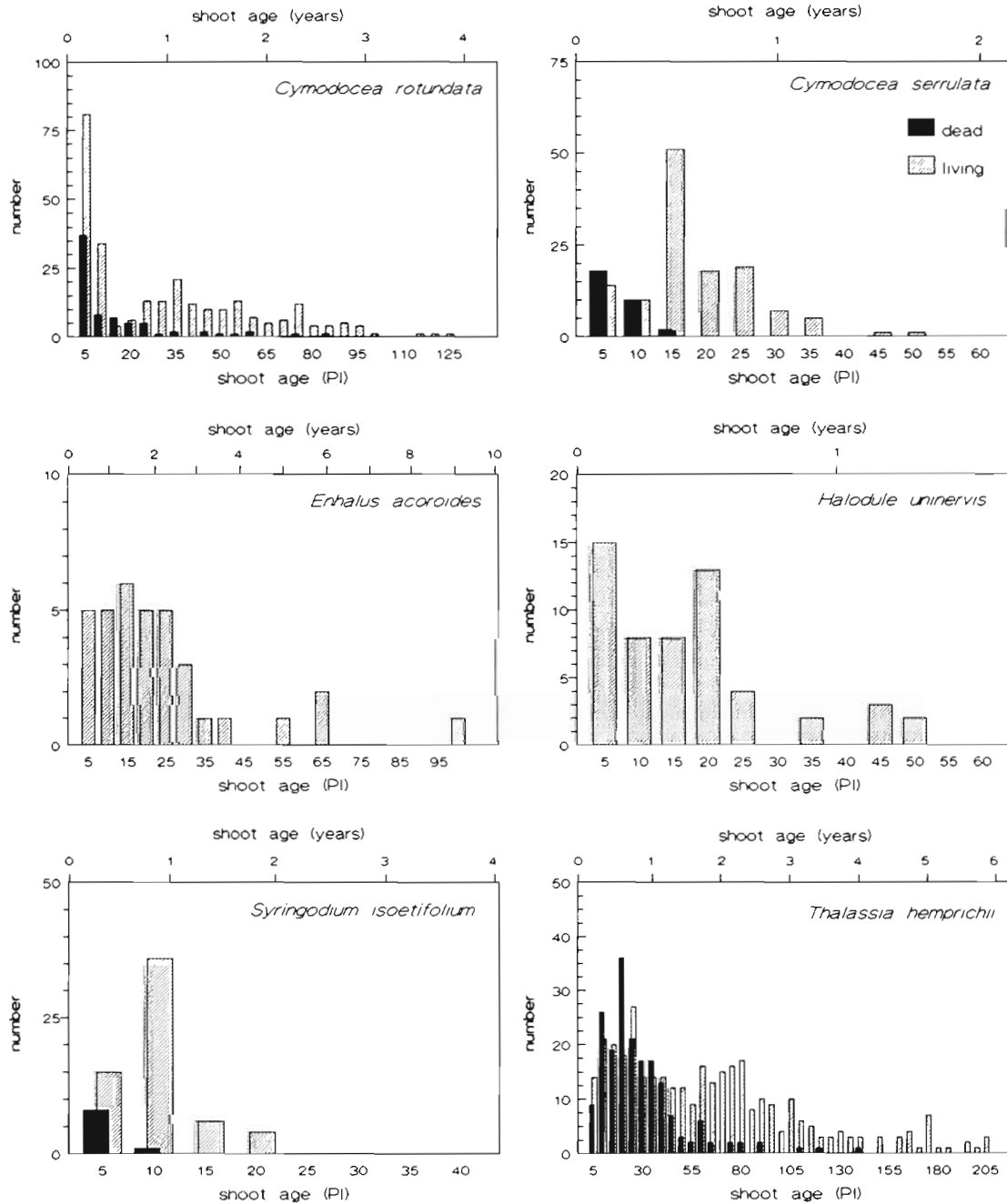


Fig. 4. Shoot age frequency distributions of the seagrass species at Bolinao. Filled bars indicate dead shoots, hatched bars are living shoots; no dead shoots were encountered for *Enhalus acoroides* and *Halodule uninervis*. Shoot age is expressed in leaf plastochron intervals (PI, lower horizontal axis) and in years (upper horizontal axis), computed from the mean annual plastochron interval (PI) duration of each species in days

age of 4.1 yr. Shoot age distributions were considerably skewed (Fig. 4), indicating substantial mortality (Table 3). Mortality rates ranged from 0.2 (*E. acoroides*) to 2.9 ln units yr⁻¹ (*C. serrulata*), and were also high for *Halodule uninervis* and *Syringodium isoetifolium*. Mortality rates were closely correlated with recruitment rates ($r^2 = 0.94$, $p < 0.001$, slope = 1.01 ± 0.13). *T.*

hemprichii and *C. rotundata* had positive net recruitment rates considerably larger than the standard errors estimated for the mortality rates (Table 3), suggesting that they were proliferating in the mixed meadow.

In support of our hypothesis, the allometric correlation between shoot weight and (median) age was significant (Fig. 5a), as was that between rhizome diame-

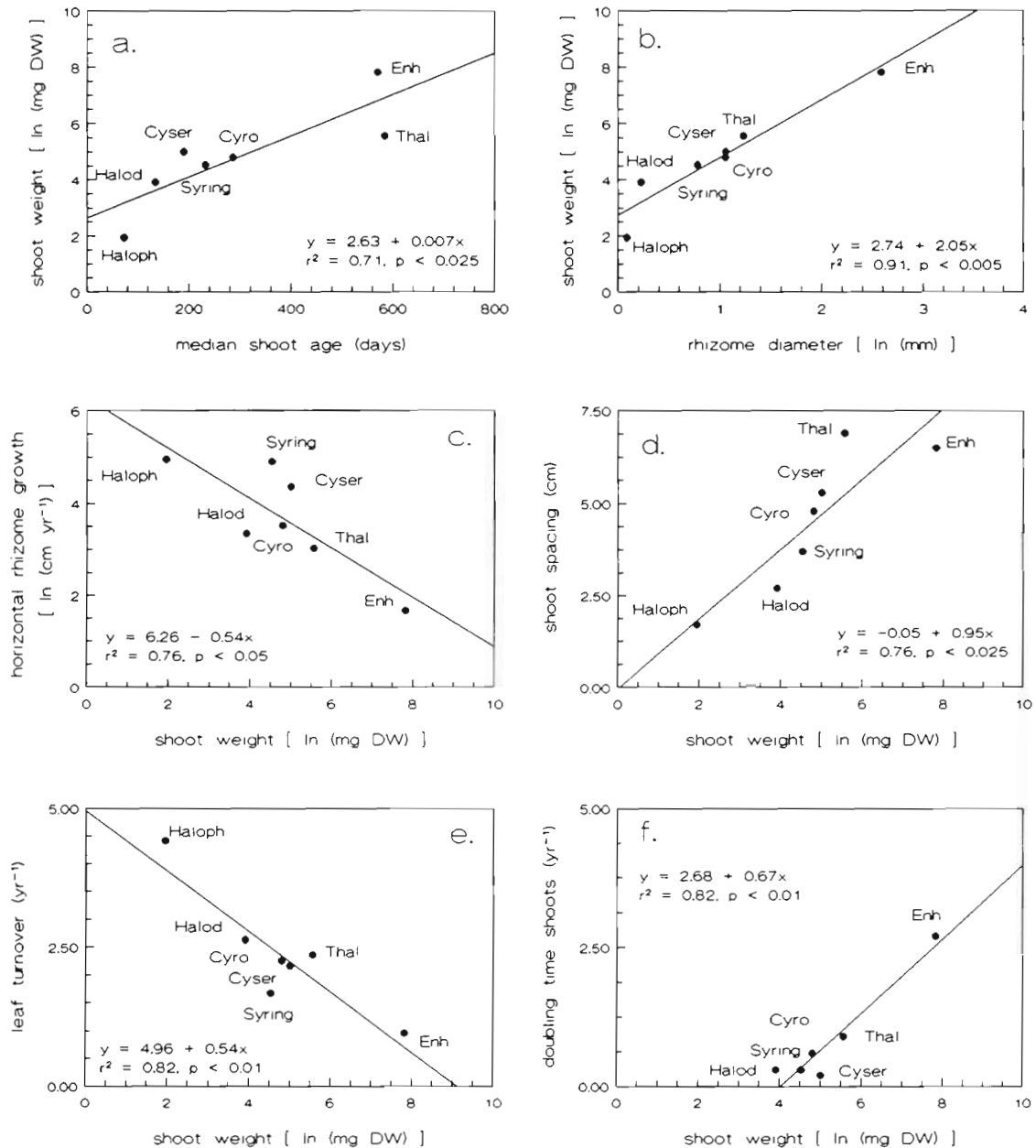


Fig. 5. Allometric scatterplots for the different seagrass species of the mixed meadow at Bolinao, and fitted regression equations, for: (a) shoot weight vs median shoot age, (b) shoot weight vs rhizome diameter, (c) rhizome elongation rate vs shoot weight, (d) shoot spacing vs shoot weight, (e) leaf turnover [calculated as (leaf crops shoot⁻¹ yr⁻¹)/(leaves shoot⁻¹)] vs shoot weight, and (f) shoot recruitment [expressed as doubling time, (m²)/R, from Table 3] vs shoot weight. Where natural-log transformations were used this is denoted with ln. Cyro: *Cymodocea rotundata*; Cyser: *C. serrulata*; Enh: *Enhalus acoroides*; Halod: *Halodule uninervis*; Haloph: *Halophila ovalis*; Syring: *Syringodium isoetifolium*; Thal: *Thalassia hemprichii*

ter and shoot age ($r^2 = 0.71$, $p < 0.025$; not shown). Accordingly, shoot weight and rhizome diameter were closely correlated (Fig. 5b), and both can be used to scale the size range encountered here. Vertical shoot growth was not correlated significantly with shoot size ($p > 0.10$), whereas for horizontal growth there was a significant negative correlation (Fig. 5c). Larger shoots were spaced out at significantly longer intervals along

the rhizome (Fig. 5d). Leaf turnover was correlated negatively, and shoot population doubling-time positively, with shoot weight (Fig. 5e, f). Hence, compared across species in this mixed bed, growth declined with size, as reflected in lower horizontal rhizome growth and shoot as well as leaf turnover.

The mean annual shoot density of the different species present ranged from 10 (*Cymodocea serrulata*) to

548 shoots m^{-2} (*Thalassia hemprichii*). The main leaf canopy was made up largely of *C. rotundata* and *T. hemprichii* (mean leaf height 15 to 20 cm; adding leaf length to vertical stem length in Table 1), together responsible for an LAI of $2.1 m^2 m^{-2}$ out of the total of $3.0 m^2 m^{-2}$ (Table 4). Above this level scattered tufts (with an average of 2 shoots in a cluster) of *Enhalus acoroides* extended to a height of some 60 cm (LAI of 0.8). The leaves of the smallest *Halophila ovalis* remained below 5 cm height and formed a sparse understory. The main leaf canopies were maintained by a considerable shoot flux (annually recruited shoots/mean shoot density = 0.6 in *E. acoroides* and *T. hemprichii* and 1.5 in *C. rotundata*; Tables 3 & 4) and by leaf turnover (Table 2). The total biomass (excluding roots) of the meadow was $624 g DW m^{-2}$, of which 45% was represented by horizontal rhizomes (Table 4). Aboveground biomass was dominated by the leafy shoots of *T. hemprichii* (72%); belowground, the massive rhizomes of *Enhalus acoroides* dominated (65%). Combining the estimated biomass with leaves produced per year and vertical and horizontal growth, the annual productivity was calculated to be $2140 g$

$DW m^{-2} yr^{-1}$ (roots excluded; Table 4), of which 91% was leaves that were largely produced by *T. hemprichii* (77%).

DISCUSSION

The species forming the mixed meadow at Bolinao span the broadest possible range in size, from the tiny *Halophila ovalis* to the largest seagrass species in the world, *Enhalus acoroides* (Duarte 1991a). Confirming our hypothesis, allometric scaling across the species present was found to be significant in several respects: shoot recruitment, leaf turnover and horizontal rhizome elongation and branching rates were less for species with older and larger shoots (Fig. 5). The smaller, short-lived species are thus best equipped to colonize new areas through rhizome expansion, or to wander from gap to gap (Sousa 1984) within established beds ('guerilla' strategy; see review by Harper 1976). Yet, the presently observed horizontal rates are lower than previously reported for the same species (e.g. *Cymodocea serrulata*: $340 cm yr^{-1}$; Brouns 1987a), suggesting

Table 4. Shoot and rhizome apex density, leaf area index (LAI, $m^2 m^{-2}$, single-sided), stand biomass and annual production of the seagrass species present in the mixed meadow at Bolinao (Luzon, The Philippines). Biomass as well as annual productivity excludes roots; na: not applicable; -: data were not collected

	<i>Cymodocea rotundata</i>	<i>Cymodocea serrulata</i>	<i>Enhalus acoroides</i>	<i>Halophila ovalis</i>	<i>Halodule uninervis</i>	<i>Syringodium isoetifolium</i>	<i>Thalassia hemprichii</i>	Totals
Density, no. m^{-2}								
Shoot density	171 ± 22	10 ± 5	21 ± 3	16 ± 10	47 ± 12	109 ± 18	548 ± 21	
Rhizome apex density ^a	17	1	na	na	9	-	58	
LAI	0.63	0.03	0.76	0.02	0.01	0.09	1.45	2.99
Biomass, g DW m^{-2}								
Aboveground (leaves + vertical internodes)	22.9	2.4	53.0	0.1	4.5	12.5	250.2	345.6
Rhizomes	16.2	0.3	180.2	0.1	2.8	1.8	77.3	278.7
Total biomass	39.1	2.7	233.3	0.2	7.3	14.3	327.5	624.3
Annual productivity, g DW $m^{-2} yr^{-1}$ (% of total)								
Leaves	199.0 (97.4)	13.0 (87.2)	139.1 (64.5)	9.5 (70.9)	32.8 (78.5)	53.6	1511.5 (94.8)	1958.5 (91.4)
Vertical internodes	2.2 (1.1)	1.6 (10.7)	0	0	5.4 (12.9)	3.6	61.0 (3.8)	73.8 (3.4)
Rhizomes	3.2 (1.5)	0.3 (2.0)	76.5 (35.5)	3.9 (29.1)	3.6 (8.6)	-	22.8 (1.4)	110.2 (5.1)
Total above-ground	201.2	14.6	139.1	9.5	38.2	57.2	1572.5	2032.3
Total above- and below-ground	204.3	14.9	215.6	13.4	41.8	(57.2)	1595.2	2142.4
^a In <i>E. acoroides</i> and <i>H. ovalis</i> , rhizome apex density is shoot density								

that rhizome growth declines in stable meadows as compared to expanding monospecific patch fronts. In contrast, *Thalassia hemprichii* and *E. acoroides* have longer-lived and larger shoots which allow them to occupy space more permanently, and accumulate and retain resources for extended periods of time. Hence, the smaller species are arrested in a permanent state of colonisation, or 'pioneer' role, imposed by this high shoot mortality rate and the need for fast, continuous rhizome growth to provide the required shoot flux. Also, we speculate that the shorter-lived species have relatively long-lived seeds (McMillan 1991), as is commonly observed in terrestrial plants (Harper 1977).

Shoot recruitment and mortality were relatively well balanced for most species; only *Thalassia hemprichii* and *Cymodocea rotundata* had a distinct positive net recruitment (Table 3), suggesting that on average they had expanded their share in the mixed meadow during the preceding 4 to 6 yr. The range of recruitment and mortality rates was comparable to values found in temperate as well as tropical seagrass beds (recruitment 0.3 to 4.3 yr⁻¹, mortality 0.7 to 3.5 yr⁻¹; Vermaat et al. 1987, Duarte & Sand-Jensen 1990, Gallegos et al. 1993, 1994, Harrison 1993, Olesen & Sand-Jensen 1994).

Biomass and annual productivity of this mixed meadow were relatively high (Duarte 1989) but comparable to values reported for tropical meadows (Brouns 1987b, Gallegos et al. 1993). Meadow biomass was quantitatively dominated by the long-lived 'climax' species, *Thalassia hemprichii* and *Enhalus acoroides* (52 and 37%, respectively, of which 24 and 77% were rhizomes; Table 4), as has been observed in other mixed meadows in SE Asia (Brouns 1987b, Nienhuis et al. 1989, Tomasko et al. 1993). Co-dominance of *E. acoroides* in terms of biomass, however, did not result in a similarly important contribution to annual productivity: only 10%, compared to the 74% contribution by *T. hemprichii*. This difference can be explained by the lower horizontal rhizome growth as well as leaf turnover in *E. acoroides*, coupled with its larger shoot size (Fig. 5), but also by its considerable reproductive effort: in other seagrass species less than 10% of the shoots flower annually, but in *E. acoroides* each shoot typically produces several large flowers and fruits per year (Gallegos et al. 1992, J.S. Uri et al. unpubl.), which may represent a considerable loss of resources.

The co-dominant *Enhalus acoroides* is unlikely to be subjected to significant interference by the other species, because its leaf surface is raised above that of the others and its rhizomes send their roots deeper into the sediments (Fortes et al. unpubl.). The leaf canopy (LAI of 0.8 m² m⁻²) formed by *E. acoroides*, on the other hand, will not cause significant shading of the smaller species. The similarly sized species that form the main

canopy (i.e. *Thalassia hemprichii*, *Cymodocea rotundata*, *C. serrulata* and *Syringodium isoetifolium*), however, may compete for both light and nutrients, because leaves as well as roots (Fortes et al. unpubl.) are positioned at similar levels in the water column and sediment, respectively (cf. Williams 1987). Shading is likely to be most acute for *Halophila ovalis*, which has its leaves almost on the sediment. This species must compensate for its unfavourable light climate by having low light requirements, which is reflected in the greater depths it can inhabit compared to other seagrasses (Duarte 1991b).

Vertical growth, which was found to be a size-independent trait, may be important in the competition for light, since considerable vertical elongation, as observed in *Cymodocea serrulata* (13.1 ± 1.8 cm yr⁻¹), will position the leaves higher up in the canopy as compared to the much lower elongation rates of *C. rotundata* (1.5 ± 0.1 cm yr⁻¹). This, however, may also be achieved by adjusting leaf lengths; hence differences in vertical shoot growth are probably more important for surviving under conditions of high sedimentation rates (Marbà et al. 1994a, b). Since the mean vertical elongation rates in *Thalassia hemprichii* found here are comparable to rates found for the Caribbean *Thalassia testudinum* Banks ex Koenig in low-sedimentation areas (Marbà et al. 1994a), we speculate that sedimentation rates in the Bolinao reef lagoon are relatively low.

Previous analyses of the role of different seagrass species in SE Asian meadows (Birch & Birch 1984, Brouns 1987a, Nienhuis et al. 1989) identified *Enhalus acoroides* and *Thalassia hemprichii* as 'constant' species and *Cymodocea rotundata*, *Halodule uninervis* and *Halophila ovalis* as 'pioneering' species. Our data on size and associated growth rates, as well as population dynamics, provide a quantitative explanation for this classification, demonstrating the significance of seagrass size as a predictor of the role of the different species in the mixed seagrass meadows that dominate SE Asian coastal waters.

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