

Allometric scaling of seagrass form and productivity

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ABSTRACT: The implications of differences in plant size for seagrass productivity were examined based on an extensive compilation of data on architecture and growth of seagrass species. The analysis revealed strong allometric relationships between the size of different components, particularly a close scaling of the size of leaves, shoots, and fruits to rhizome diameter, as well as strong relationships between shoot size and the dynamics (e.g. turnover rate, plastochrone interval, and longevity) of seagrass leaves and rhizomes of different species. The decrease in rhizome elongation rates and leaf turnover rates with increasing seagrass size demonstrates the importance of architecture for seagrass productivity, and also provides explanations for the different ecological roles of small, colonizing species, and large, climax seagrass species. In addition, these results demonstrate that while habitat conditions have important influences on seagrass productivity, differences in size may explain the vast range of turnover times, plastochrone intervals, and module longevities, encountered among seagrass species.

INTRODUCTION

Seagrasses are characterized by a relative taxonomic and architectural uniformity, and are represented by few (about 50 species distributed in 12 genera) species (Den Hartog 1970, Stevenson 1988). Seagrasses grow by the reiteration of modules (rhizome internodes, leaf clusters, and roots; cf. Tomlinson 1974). Yet, the biomass and turnover rates of different seagrass species differ by orders of magnitude (cf. Stevenson 1988).

Attempts to explain differences in seagrass biomass and production and, thus, their importance in shallow sandy ecosystems, have focused primarily on the influence of habitat conditions, particularly temperature and light (cf. Hillman et al. 1989) and, more recently, nutrient availability (Short 1987, Short et al. 1990, Perez et al. 1991). However, fast-growing, colonizing species are often small (e.g. *Halophila* spp.), whereas slow-growing, 'climax' species are often large (e.g. *Enhalus acoroides* and *Posidonia* spp.; cf. Den Hartog 1977, Hillman et al. 1989), suggesting that differences in plant size may help to explain productivity differences among seagrass species.

Here I used an extensive compilation of data on architecture and growth of different seagrass species to examine the implications of differences in module size to account for differences in productivity among seagrass

species. To achieve this goal I first examined the (interspecific) allometric relationships among the size of different seagrass modules, and then assessed the implications of differences in module size for seagrass dynamics.

METHODS

I searched the literature for data on seagrass module size (rhizome diameter and internodal length, shoot weight, leaf area, and fruit size) and dynamics [longevity, plastochrone intervals (i.e. the time elapsed between production of consecutive modules), and growth; Table 1]. I also report data for *Ruppia maritima* L., an angiosperm species similar in architecture to seagrasses and also abundant in coastal zones throughout the world. I used average values when possible, and when data were given as ranges, I used the arithmetic and geometric midpoint for ranges smaller and greater than an order of magnitude, respectively. Because the architecture and dynamics of individual seagrass populations may reflect habitat conditions rather than characteristic values for the species, the variables in the data set compiled were averaged by species, and these average values were then used to represent the architecture and productivity of each seagrass species in the analyses. Thus, the units ana-

Table 1. Sources of data on architectural and dynamic characteristics of different seagrass species, and on *Ruppia maritima*, an angiosperm species abundant in coastal areas

Species	Source	Species	Source
<i>Amphibolis antarctica</i>	Den Hartog (1970) Walker & McComb (1988) Clarke & Kirkman (1989) Hillman et al. (1989) Walker (1989)	<i>Phyllospadix iwatensis</i>	Den Hartog (1970)
<i>Amphibolis griffithii</i>	Den Hartog (1970) Hillman et al. (1989)	<i>Phyllospadix japonicus</i>	Den Hartog (1970)
<i>Cymodocea angostata</i>	Den Hartog (1970)	<i>Phyllospadix serrulatus</i>	Den Hartog (1970)
<i>Cymodocea nodosa</i>	Den Hartog (1970) Cayé & Meinesz (1985) Perez (1989) Peduzzi & Vukovics (1990) Duarte (unpubl. results)	<i>Phyllospadix torreyi</i>	Den Hartog (1970) Stewart (1989)
<i>Cymodocea rotundata</i>	Ogden & Ogden (1982) Brouns (1987)	<i>Phyllospadix scouleri</i>	Den Hartog (1970)
<i>Cymodocea rotundifolia</i>	Den Hartog (1970)	<i>Posidonia australis</i>	Den Hartog (1970) Larkum (1976) Kirkman & Reid (1979) West & Larkum (1979) Silverstein et al. (1986) Walker & McComb (1988) Clarke & Kirkman (1989) Hillman et al. (1989) West et al. (1989) West (1990)
<i>Cymodocea serrulata</i>	Den Hartog (1970) Ogden & Ogden (1982) Brouns (1987)	<i>Posidonia oceanica</i>	Den Hartog (1970) Ott (1979) Ott (1980) Bedhomme (1981) Thelin & Bouderesque (1983) Bay (1984) Bouderesque et al. (1984) Pirc (1984) Wittmann (1984) Buia et al. (1985) Romero-Martinengo (1985) Pergent & Pergent-Martini (1990) Semround et al. (1990) Duarte (unpubl. results)
<i>Enhalus acoroides</i>	Den Hartog (1970) Johnstone (1979) Ogden & Ogden (1982) Brouns & Heijs (1986) Estacion & Fortes (1988)	<i>Posidonia ostenfeldii</i>	Den Hartog (1970)
<i>Halodule beaudettei</i>	Den Hartog (1970)	<i>Ruppia maritima</i>	Bigley & Harrison (1986)
<i>Halodule bermudensis</i>	Den Hartog (1970)	<i>Syringodium filiforme</i>	Den Hartog (1970) Ogden & Ogden (1982) Fry (1983) Barber & Beherens (1985) Eleuterius (1987) Williams (1987) Fry & Virnstein (1988)
<i>Halodule pinifolia</i>	Den Hartog (1970)	<i>Syringodium isoetifolium</i>	Den Hartog (1970) Brouns (1987) Clarke & Kirkman (1989)
<i>Halodule uninervis</i>	Den Hartog (1970) Ogden & Ogden (1982) Brouns (1987)	<i>Thalassia hemprichii</i>	Den Hartog (1970) Ogden & Ogden (1982) Brouns (1985) Brouns (1987)
<i>Halodule wrightii</i>	Den Hartog (1970) Vinstein (1982) Eleuterius (1987)	<i>Thalassia testudinum</i>	Tomlinson & Vargo (1966) Den Hartog (1970) Patriquin (1973) Taylor et al. (1973) Buesa (1974) Zieman (1975) Zieman et al. (1984) Barber & Beherens (1985) Iverson & Bittaker (1986) Eleuterius (1987) Williams (1987) Dawes & Tomasko (1988)
<i>Halophila baillonis</i>	Den Hartog (1970)		
<i>Halophila beccarii</i>	Den Hartog (1970)		
<i>Halophila decipiens</i>	Den Hartog (1970) Gil-Rodriguez & Cruz-Simó (1982) Josselyn et al. (1986) Kenworthy et al. (1989)		
<i>Halophila engelmanni</i>	Den Hartog (1970)		
<i>Halophila hawaiiiana</i>	Herbert (1986)		
<i>Halophila ovalis</i>	Den Hartog (1970) Ogden & Ogden (1982) Brouns (1987) Clarke & Kirkman (1989) Hillman et al. (1989)		
<i>Halophila ovata</i>	Den Hartog (1970)		
<i>Halophila spinulosa</i>	Den Hartog (1970)		
<i>Halophila stipulacea</i>	Den Hartog (1970) Hulings (1979) Wahbeh (1984)		
<i>Heterozostera tasmanica</i>	Den Hartog (1970) Bulthuis (1983) Bulthuis & Woelkerling (1983) Phillips et al. (1983) Clarke & Kirkman (1989) Hillman et al. (1989)		

Table 1 (continued)

Species	Source	Species	Source
<i>Thalassia testudinum</i>	Williams (1988) Tomasko & Dawes (1989) Tomasko & Dawes (1990) Duarte (unpubl. results)	<i>Zostera marina</i>	Jacobs (1979) Mukai et al. (1979) Aioi (1980) Bak (1980) Nienhuis & De Bree (1980) Jacobs (1984) Robertson & Mann (1984) Thorne-Miller & Harlin (1984) Dennison & Alberte (1985) Kentula & McIntire (1986) Ibarra-Obando & Huerta-Tamayo (1987) Gambi (1988) Roman & Able (1988) Umebayashi (1988) Gambi et al. (1990) Pedersen (1990)
<i>Thalassodendron ciliatum</i>	Den Hartog (1970) Lipkin (1988)	<i>Zostera mucronata</i>	Den Hartog (1970)
<i>Thalassodendron pachyrhizum</i>	Den Hartog (1970) Kirkman & Cook (1987)	<i>Zostera muelleri</i>	Den Hartog (1970) Clough & Attiwell (1980) Kerr & Strother (1989)
<i>Zostera americana</i>	Den Hartog (1970)	<i>Zostera noltii</i>	Den Hartog (1970) Jacobs et al. (1983a, b) Vermaat et al. (1987)
<i>Zostera asiatica</i>	Den Hartog (1970)	<i>Zostera novazelandica</i>	Den Hartog (1970)
<i>Zostera caespitosa</i>	Den Hartog (1970)		
<i>Zostera capensis</i>	Den Hartog (1970)		
<i>Zostera capricorni</i>	Den Hartog (1970) Larkum et al. (1984) Kirkman & Cook (1982) Hillman et al. (1989) West et al. (1989)		
<i>Zostera caulescens</i>	Den Hartog (1970)		
<i>Zostera japonica</i>	Den Hartog (1970) Bigley & Harrison (1986)		
<i>Zostera marina</i>	Keller & Harris (1966) Den Hartog (1970) Sand-Jensen (1975) Backman & Barilotti (1976)		

lyzed were seagrass species and not seagrass stands. Relationships among these variables were then described using reduced major axis regression analyses (Till 1974) to prevent bias in regression coefficients derived from error in the independent and dependent variables (LaBarbera 1989). The allometric relationships between the size of plant parts and between plant size and dynamics were described by fitting the equation

$$Y = aX^b$$

which has been used extensively to describe allometric relationships between organismal parts, and to scale plant growth to size (Huxley 1932, LaBarbera 1989). The strength of the relationships obtained was described by the coefficient of determination (R^2), and their precision was described by the standard error of the regression estimate.

The importance of among- versus within-species variability in seagrass architecture and dynamics was assessed by comparing the among- and within-species coefficient of variation for those variables where sufficient information was available to calculate both. Within-species variability reflects both differences among populations of individual seagrass species and seasonal variability in the properties examined, since average annual values were not available for all species.

RESULTS

Seagrass species differ widely in module size (Table 2), among-species variability being much greater than that within species, except for differences in the number of leaves per shoot (or leaf cluster) and, to a lesser extent, the length of rhizome internodes, where within-species variability was comparable to among-species differences (Table 2). The dynamic properties of seagrasses also ranged widely among species, except for leaf elongation rates, where variability within species was quite considerable and comparable to that among species (Table 2).

Allometric relationships between seagrass modules

The sizes of leaves, shoots, and fruits of different seagrass species were strongly related to the diameter of their rhizomes (Eqs. 1 to 3 in Table 3; Fig. 1). The rate of increase in size with increasing rhizome diameter was greatest for fruit volume (slope = 2.91), intermediate for shoot weight (slope = 2.57), and smallest for leaf size (slope = 2.17; Table 3). The number of shoots produced per rhizome internode, which influences the spacing in between shoots, was also strongly, positively related to rhizome diameter ($r = 0.78$, $p < 0.001$), indicating that shoots of seagrass species with thick diameters are

Table 2. Average values of architectural and dynamic properties of different seagrass species. Architectural: RD, rhizome diameter (mm); RIL, rhizome internodal length (cm); NL, no. of leaves shoot⁻¹; LS, leaf surface (cm²); FS, fruit size (mm³); SW, shoot weight (mg DW shoot⁻¹). Dynamic: SE, shoot elongation rate (cm shoot⁻¹ d⁻¹); LE, leaf elongation rate (mm leaf⁻¹ d⁻¹); RE, rhizome horizontal elongation rate (cm yr⁻¹); LSY, leaf production rate (leaves shoot⁻¹ yr⁻¹); RLY, rhizome internodal production rate (rhizome internodes yr⁻¹); SRI, shoots per rhizome internode; SPI, shoot plastochrone interval (d shoot⁻¹); LPI, leaf plastochrone interval (d leaf⁻¹); RPI, rhizome plastochrone interval (days per rhizome internode); L Age, leaf longevity (d); S Age, shoot longevity (yr); LPB, leaf turnover rate (yr⁻¹); RPB, rhizome turnover rate (yr⁻¹). Also shown are the among-species average and coefficient of variation (CV) and the average within-species CV

Species	Architectural properties										Dynamic properties									
	RD	RIL	NL	LS	FS	SW	SE	LE	RE	LSY	RLY	SRI	SPI	LPI	RPI	L Age	S Age	LPB	RPB	
<i>Amphibolis antarctica</i>	3.0	0.63		2.52					35.0		55.4	0.13	52.7		6.6			3.94		
<i>Amphibolis griffithii</i>	2.0	0.63		2.03														2.77		
<i>Cymodocea angostata</i>		1.75	3	7.88	113.1															
<i>Cymodocea nodosa</i>	3.0	2.59	3.8	9.00	48.0	82.8	1.3	2.6	82.6	11.1	28.5	0.56	22.9	32.9	12.8	45.0	2.40	3.48	0.14	
<i>Cymodocea rotundata</i>	2.0	4.40	3.04	3.30	60.0	23.4		2.5	411.0	34.2	93.6	0.39	10.0	10.7	3.9		1.80	11.68	3.23	
<i>Cymodocea rotundifolia</i>	2.0	2.75	7	3.30	60.0															
<i>Cymodocea serrulata</i>	2.0	3.97	4.04	6.82	43.7	38.8		1.9	216.0	32.6	54.6	0.32	21.2	11.2	6.7		1.98	12.05	6.08	
<i>Enhalus acoroides</i>	15.0	0.10	3.48	100.78	75398.4	436.0	2.0	9.4	0.9	8.6	8.6			42.4	42.4		5.37		0.23	
<i>Halodule beaudettei</i>	1.4	1.96	3	1.25								0.71								
<i>Halodule bermudensis</i>		2.25		0.41																
<i>Halodule pinifolia</i>	1.5	2.00		1.13	4.9															
<i>Halodule uninervis</i>	1.0	2.36	2.23	1.07	5.7	9.4			136.5	31.7	57.9	0.80	7.9	11.5	6.3	0.19	13.87		0.99	
<i>Halodule wrightii</i>		1.62	3.2	1.16	2.8	6.4	2.5	7.7	365.0		219.0				1.7		3.00	17.19		
<i>Halophila baillonis</i>		2.25	6	0.68	8.2															
<i>Halophila beccarii</i>		1.50		0.14		2.4						1.00								
<i>Halophila decipiens</i>	0.8	2.62	2	0.89	3.0	2.3			215.0	200.5	82.0	1.00	4.5	1.8	4.5	8.6		32.36		
<i>Halophila engelmanni</i>		3.00	4	0.90																
<i>Halophila hawaiiiana</i>	1.2	1.50	2	0.38		6.8				189.6	94.8			1.9	3.9			24.82		
<i>Halophila ovalis</i>	1.5	3.50	2	3.12	22.4	0.9			574.0	328.0	164.0	1.00	2.2	1.1	2.2	12.4	0.20	20.85		
<i>Halophila ovata</i>	0.8	2.00	2	0.42	14.1															
<i>Halophila spinulosa</i>		3.00		0.63																
<i>Halophila stipulacea</i>	1.3	2.50	5	2.84	65.5	15.1	1.8	2.2		45.1		0.56		8.1		74.0	5.62			
<i>Heterozostera tasmanica</i>	1.5	1.50	7.7	2.13	19.2	107.8	1.1		150.0	30.5				12.0		73.3	5.04			
<i>Phyllospadix iwataensis</i>	5.0	0.45		36.25	42.1															
<i>Phyllospadix japonicus</i>	3.5	0.40		10.94	33.4															
<i>Phyllospadix serrulatus</i>	5.0	0.65		10.50				3.0	25.6											
<i>Phyllospadix torreyi</i>	5.0	0.85		18.75	15.1															
<i>Phyllospadix scouleri</i>	6.5	0.35		31.25	56.3															
<i>Posidonia australis</i>	7.0	0.75	3.5	64.87	662.0	1347.0	0.8	3.1	4.2	7.7	16.4	0.09	213.0	47.2	22.3	302.8	11.98	3.86	0.09	
<i>Posidonia oceanica</i>	10.0	0.35	6.06	82.82	523.6	731.0	0.8	3.1	4.2	7.7	16.4	0.09	213.0	47.2	22.3	302.8	11.98	1.87	0.09	
<i>Posidonia ostenfeldii</i>	3.5	1.50		15.75	486.7															
<i>Ruppia maritima</i>		1.00			60.3								2.7				0.14			
<i>Syringodium filiforme</i>	2.7	1.60	2	3.20	27.3	30.4	2.5	6.3	134.0	16.6	70.0	1.00	5.2	22.0	5.2	45.0	2.00	13.70		
<i>Syringodium isoetifolium</i>	1.3	2.50	3	2.17	6.9	14.5	1.3		75.0	11.0	58.0	0.71	7.7	33.2	6.3	52.0	1.46	10.95	1.53	
<i>Thalassia hemprichii</i>	4.0	0.60	3.2	18.75	4712.4	73.0		6.3	87.6	34.3	146.0	0.07	38.5	10.6	2.5			18.34	0.54	
<i>Thalassia testudinum</i>	7.3	3.19	3.34	18.22	3607.0	264.0	3.1	3.3	151.5	23.3	47.3	0.09	24.7	15.6	7.7	40.0	7.00	7.73		
<i>Thalassodendron ciliatum</i>	6.0	2.25	7.5	14.40	605.0							0.22								
<i>Thalassodendron pachyrhizum</i>	5.0	4.00	7	9.78				1.7		11.1			300.0	33.0				6.57		

Table 2 (continued)

Species	Architectural properties										Dynamic properties									
	RD	RIL	NL	LS	FS	SW	SE	LE	RE	LSY	RIY	SRI	SPI	LPI	RPI	L Age	S Age	LPB	RPB	
<i>Zostera americana</i>	0.8	0.73	4	1.65	6.0															
<i>Zostera asiatica</i>	5.5	2.00	5	195.00	99.5															
<i>Zostera caespitosa</i>		0.50	4	31.50	18.0															
<i>Zostera capensis</i>	1.3	1.02	5	1.42	6.0															
<i>Zostera capricorni</i>	1.4	1.26	6	6.73	3.1	91.3	1.9	28.1	28.1	28.1	13.0	13.0	13.0	13.0	56.0	56.0	6.83	6.83		
<i>Zostera caulescens</i>	3.5	1.75	4	48.00	33.5															
<i>Zostera japonica</i>	1.3	1.09	4	1.28	4.2	272.5	3.2	7.8	40.9	27.9	22.9	0.38	42.3	13.1	16.0	51.4	1.52	11.17	2.19	
<i>Zostera marina</i>	3.5	1.78	4.2	34.65	18.0												0.18			
<i>Zostera mucronata</i>	1.0	1.26	5	0.83																
<i>Zostera muelleri</i>	1.0	1.11	6	1.68	5.5		0.5	23.4	23.4	23.4	15.6	2.8	3.4	3.4	52.0	52.0	12.57	16.42		
<i>Zostera noltii</i>	1.3	1.18	3.7	1.15	2.8	6.5		126.7	107.0	107.0	3.4	2.8	3.4	3.4						
<i>Zostera novazelandica</i>	1.0	0.77	6	0.84	10.6															
Average	3.2	1.7	4.2	16.63	2331	183	1.8	4.2	149	60.1	71.9	0.53	47.4	17.0	10.3	67.7	2.6	11.2	1.67	
Among-species CV	89	61	38	202	531	176	50	62	102	139	77	66	178	80	102	113	128	68	117	
Within-species CV	23	46	30	49	56	21	52	86	17	26	33	33	31	35	21	33	33	33	17	

separated by more rhizome internodes than those of seagrasses with thin rhizomes. Rhizome diameter, however, characterizes the size of rhizome modules (i.e. rhizome internodes) only partially, for rhizome internodal length varied by a factor of 40-fold among species (Table 2). However, the relationships between leaf and shoot size and the size of rhizome internodes were considerably weaker than those to rhizome diameter, for there was a weak, but significant trend for rhizome internodal length to be shorter in seagrass species with thick rhizomes ($r = -0.42$, $p < 0.01$).

Allometric scaling of seagrass dynamics

The hypothesis of size-dependence of seagrass dynamics was confirmed by the analyses, as demonstrated by the 1/2 power scaling of the average time elapsed between emergence of consecutive leaves, shoots, and rhizome internodes (i.e. plastochrone intervals) to shoot weight (Eqs. 4 to 6 in Table 3; Fig. 2). Fast rates of leaf emergence in small seagrasses should result in rapid leaf turnover, as supported by the tendency of leaf turnover rates to decrease as (shoot size)^{-1/2} (Eq. 7 in Table 3; Fig. 3).

Because plastochrone intervals reflect the 'biological age' of plants (Lamoreaux et al. 1978, Ritterbusch 1990), the long plastochrone intervals characteristic of modules of large seagrasses (Fig. 2) suggest that these may live longer than modules of small seagrasses. This contention was also confirmed by the tendency of leaf and shoot longevity to increase with increasing shoot size ($r = 0.65$ and 0.56 respectively, $p < 0.01$). Scaling of shoot longevity to seagrass size was, however, stronger when plant size was represented by rhizome diameter (Eq. 8 in Table 3; Fig. 4) than when shoot size was used to represent seagrass size, probably because shoot size is subject to greater variability than rhizome diameter (Table 2). The plastochrone intervals (P.I.) and turnover rates (P/B: production/biomass, yr⁻¹) of different seagrass modules were also strongly related to each other ($r_{\log \text{ leaf P.I. vs } \log \text{ rhizome P.I.}} = 0.72$, $r_{\log \text{ leaf P/B vs rhizome P/B}} = 0.74$, $p < 0.001$; Fig. 5). Thus, species with fast leaf turnover rates and short plastochrone intervals also tend to have rapid rhizome turnover rates and short plastochrone intervals (Fig. 5), thereby reflecting a fundamental similarity in seagrass growth patterns. However, these relationships were not homogeneous, and seagrass species with fast rhizome turnover rates do not show any increase in leaf turnover rates with further increments in rhizome turnover rates (Fig. 5).

The elongation rate of seagrass leaves and shoots did not show any consistent pattern across species, and were poorly related ($p > 0.01$) to the size of either rhizomes or shoots. However, the horizontal elongation

Table 3. Relationships between seagrass architecture and seagrass dynamics described by regression equations of the form $Y = aX^b$. N represents the number of observations (i.e. seagrass species) included in the analysis. The strength of the relationships is characterized by the coefficient of determination (R^2), their precision by the standard error of the (log-transformed) regression estimates ($SE_{\log est.}$), and the uncertainty about the regression slope is described by the standard error of the slope (SE_{slope}). Units for architectural and dynamic properties as in Table 2. P.I.: plastochrone interval; P/B: production/biomass

Eq.	Y	X	a	b	R ²	N	SE _{slope}	SE _{log est.}
(1)	Leaf size	Rhizome diameter	-0.18	2.17	0.80	41	0.33	0.31
(2)	Shoot weight	Rhizome diameter	0.72	2.57	0.68	20	0.31	0.49
(3)	Fruit size	Rhizome diameter	0.56	2.91	0.61	33	0.32	0.63
(4)	Leaf P.I.	Shoot weight	0.21	0.52	0.63	18	0.09	0.28
(5)	Shoot P.I.	Shoot weight	0.02	0.73	0.65	14	0.11	0.33
(6)	Rhizome P.I.	Shoot weight	1.22	0.44	0.63	18	0.09	0.28
(7)	Leaf P/B	Shoot weight	1.52	-0.36	0.58	20	0.05	0.20
(8)	Shoot longevity	Rhizome diameter	-0.62	1.85	0.72	11	0.32	0.32
(9)	Rhizome elongation	Rhizome diameter	2.03	-0.47	0.59	18	0.30	0.45
(10)	Rhizome elongation	Internodal length	1.63	1.57	0.76	19	0.19	0.34

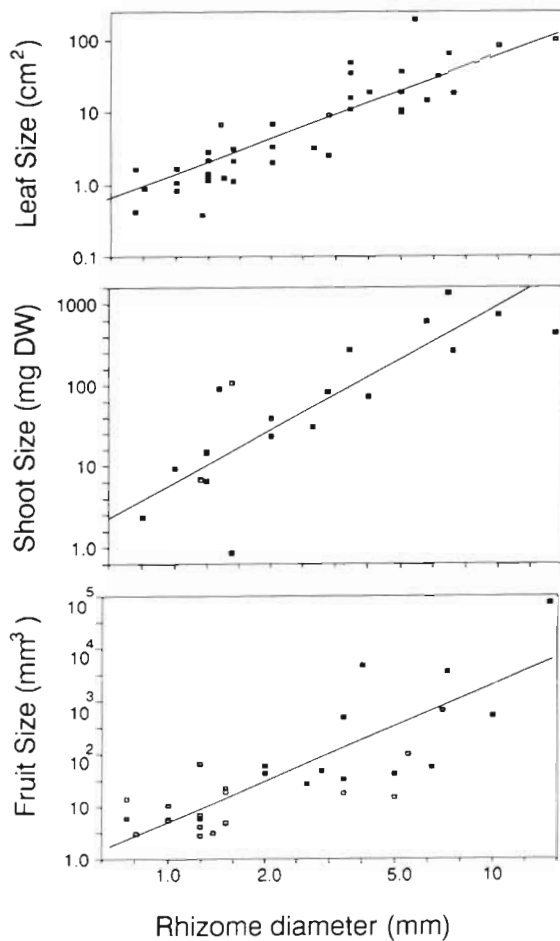


Fig. 1 Relationships between leaf size, shoot size (DW: dry wt), fruit size, and rhizome diameter. Each data point represents the average values obtained for a different seagrass species

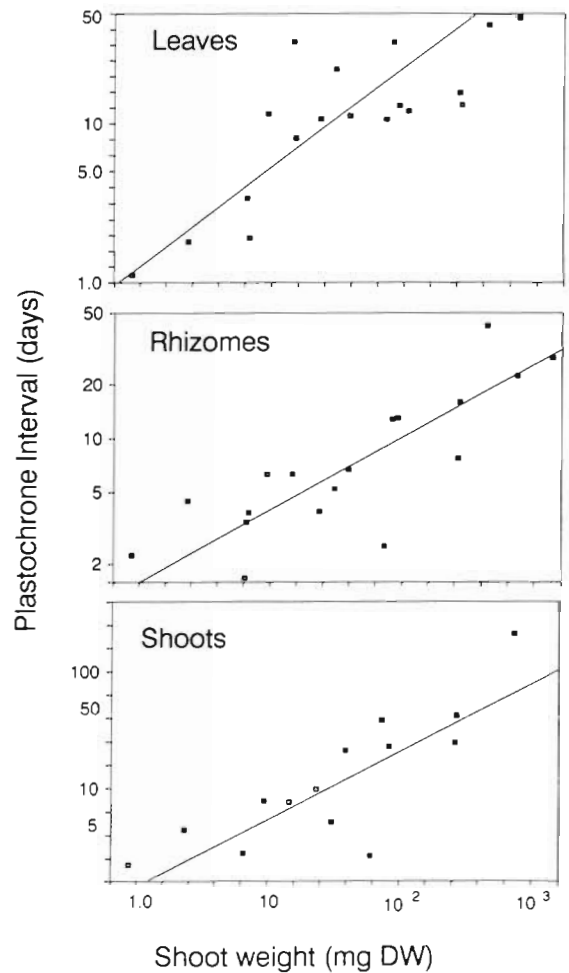


Fig. 2 Relationships between leaf, rhizome, and shoot plastochrone intervals (i.e. time elapsed between the appearance of 2 consecutive modules), and shoot weight

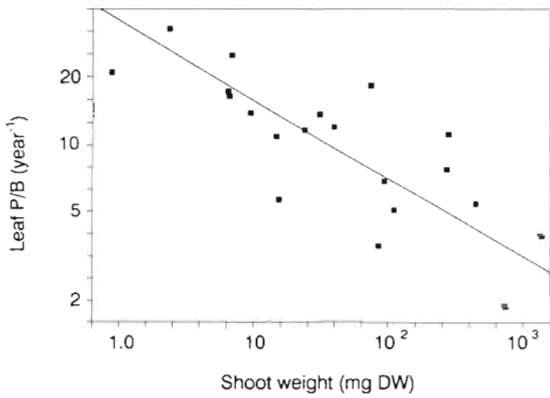


Fig. 3. Relationships between leaf turnover rate (P/B: production/biomass, yr⁻¹) and shoot weight

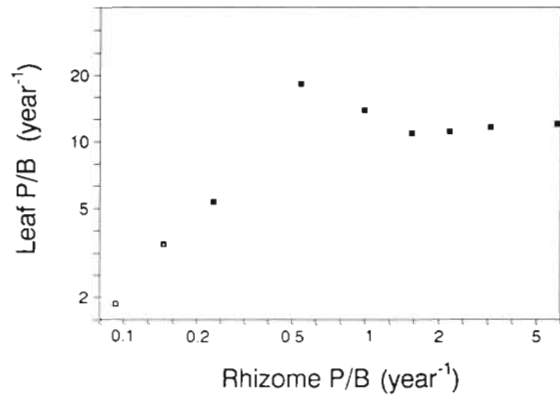
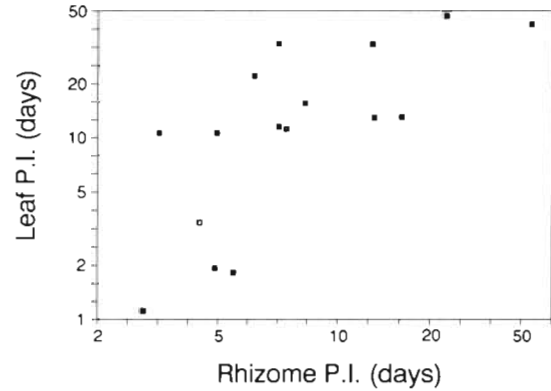


Fig. 5. Relationships between plastochrone intervals (P.I.) and turnover rates (P/B: production/biomass, yr⁻¹) of seagrass leaves and rhizomes

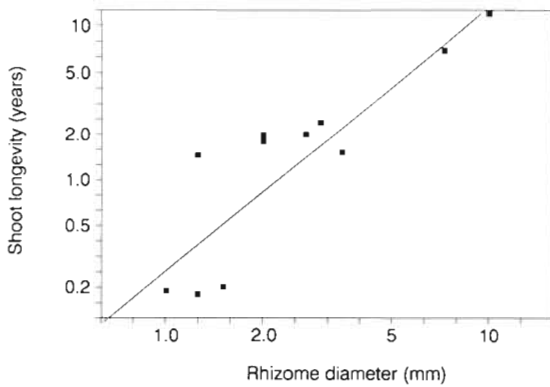


Fig. 4. Relationships between shoot longevity and rhizome diameter

rates of seagrass rhizomes were strongly related to the size of seagrass modules, and decreased with increasing rhizome diameter (Eq. 9 in Table 3; Fig. 6), but increased with increasing internodal length (Eq. 10 in Table 3; Fig. 6). Thus, a regression model including both rhizome diameter and internodal length,

$$\begin{aligned} \log \text{Rhizome elongation (cm yr}^{-1}\text{)} = & \\ & 1.93 - 0.62 \log \text{Rhizome diameter (mm)} + \\ & 1.14 \log \text{Internodal length (cm)} \\ (R^2 = 0.84, N = 18, SE_{\text{slope}} = 0.26 \text{ and } 0.22; \\ & SE_{\log \text{ est.}} = 0.28), \end{aligned}$$

accounted for most of the variability in rhizome elongation rates among seagrass species.

DISCUSSION

The data compiled here show that, because of their limited architectural repertoire, size differences (Table 2) play an important role in accounting for productivity

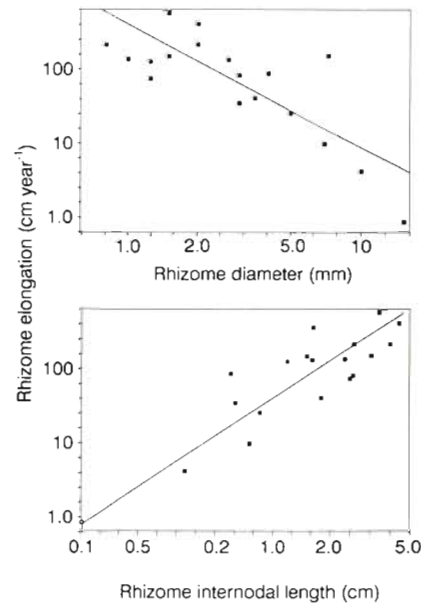


Fig. 6. Relationship between rhizome horizontal elongation rates and rhizome diameter and internodal length

differences among seagrass species. Yet, within-species variability in some properties was found to be similar in magnitude to that among species. For instance, within-species variability in rhizome internodal length and number of leaves per shoot was similar in magnitude to among species variability, for both these properties are subject to strong seasonal variability, both showing minimum values in winter and peak values in mid-summer (e.g. Cayé & Meinesz 1985, Kentula & McIntire 1986, Duarte & Sand-Jensen 1990). Similarly, leaf elongation rates, which are strongly seasonal and show considerable variability among populations of a given species (Zieman 1975, Thorhaug & Roessler 1977, Bulthuis & Woelkerling 1983), also varied almost as much within as among species (Table 2). Seasonal and habitat-dependence are also evident in other properties of seagrass, notably shoot and leaf size, leaf turnover rates and plastochrone intervals (e.g. Sand-Jensen 1975). Yet, among-species variability in these properties is larger than that within species (Table 2).

The strong relationships found among the sizes of different seagrass parts (Fig. 1, Table 3) provide evidence of the architectural similarity of seagrass species. These relationships, however, revealed differences in the relative increase in size of different seagrass components (Table 3). Rhizome diameter was found to be an appropriate factor for scaling the size of different seagrass modules, since the size of leaves, shoots, and fruits increased with increasing rhizome diameter among different species (Eqs. 1 to 3 in Table 3). In addition, within-species variation in rhizome size was found to be smaller than that in leaf or shoot size (Table 2), further demonstrating the use of rhizome diameter as a robust and useful descriptor of the architecture of seagrass species.

Rhizome diameter (D) represents, in a pipe model of seagrass architecture (cf. Shinozaki et al. 1964), the width of the channels for substance transfer, which has a great influence on the volume rate of flow (Q) along the channel (i.e. $Q \approx D^4$, Hagen-Poiseuille law; Bird et al. 1980). Thus, thick rhizomes should allow for a better integration among distant modules than in species with thinner rhizomes. Consequently, species with thick rhizomes should be able to gather the resources necessary to produce new shoots, leaves, and fruits from modules further apart than in species with thinner rhizomes, which should be more dependent on the resources available locally. The greater integration allowed by thick rhizomes, however, is achieved at the expense of a reduced potential for rhizome extension, and, thus, a limited colonizing capacity. Further, if seagrasses are likened to trees laid on their sides, as other rhizomatous plants have been (cf. Watt 1940, Harper 1977), the allometric rela-

tionships of seagrass parts to rhizome diameter described here would be equivalent to those relating the size of terrestrial plants to stem diameter (e.g. Kittredge 1944, White 1981).

Differences in seagrass size had, as postulated, important implications for seagrass dynamics, for large seagrass species had slower turnover rates of leaves and rhizomes, and exhibited longer time lapses between the appearance of different modules (i.e. plastochrone intervals; Fig. 2), and longer-living leaves and shoots than did smaller species. Further, the -0.36 scaling of leaf P/B ratios to shoot size (Eq. 7 in Table 3; Fig. 3) is similar to that described in the past for other field populations (Banse & Mosher 1980). Although differences in leaf turnover and plastochrone intervals in leaves and rhizomes were found to be correlated, these relationships were not linear, for leaf turnover increases more slowly than rhizome turnover (Fig. 5). This implies that rapid rhizome turnover rates are achieved at the expense of reduced leaf turnover rates, and, consequently, a shift of resource allocation from leaf to rhizome growth.

Large seagrass species compensate their slower growth and turnover through extended life spans (Eq. 8 in Table 3; Fig. 4). Thus, large, long-living seagrasses are more productive – when productivity is scaled to their biological time (i.e. life span) – than are more ephemeral seagrasses, as demonstrated by significant positive correlations of the total production of leaves, rhizome internodes, and shoots during the life-span of a single shoot to shoot longevity ($r = 0.78, 0.55$ and 0.79 respectively, $p < 0.001$). Further, shoots of some of the larger seagrass species develop flowers very rarely; for instance, shoots of *Posidonia oceanica* have been reported to flower, on average, once every 6 to > 50 yr (Pergent & Pergent-Martini 1990). However, these apparently small reproductive efforts may become, when computed over the extended shoot life spans of large seagrasses (Table 2), quite considerable. Moreover, since the total number of shoots and rhizome internodes produced along a rhizome axis during the life span of a shoot are also greater in the more longevous seagrass species, the reproductive effort of individual genets, which may appear small in natural time, may be quite phenomenal if computed during their life span, which is the relevant time frame for examining population dynamics.

The strong relationships between seagrass dynamics and size demonstrate the importance of architecture for seagrass productivity, and also provide explanations for the different ecological roles of small and large seagrass species. Small species are able to display the fast rhizome elongation rates and leaf turnover necessary to colonize new environments (Den Hartog 1977, Hillman et al. 1989). In contrast, large seagrass species

are more longevous and their thicker rhizomes allow for a greater integration among modules, which permits the efficient use of resources necessary for the maintenance of long-lasting seagrass meadows in unproductive environments.

Size-differences among seagrass species, which constrain their ecological role, also determine the type of environments they may occupy. Small seagrass species may occupy frequently disturbed habitats, for they have the potential (e.g. fast rhizome elongation rates) to develop extensive populations and produce substantial amounts of organic carbon during the short time intervals between disturbances. Large seagrass species, however, require stable environments, which probably become even more stable when supporting a continuous seagrass cover, to develop similarly extensive and productive populations.

In summary, the results obtained demonstrate the importance of seagrass size as a constraint on the productivity and ecological strategies displayed by different seagrass species. These results also demonstrate that while habitat conditions, particularly light, temperature, and nutrients, play an important role in controlling seagrass productivity (e.g. Hillman et al. 1989), differences in the species composition of seagrass populations alone may involve order-of-magnitude differences in productivity, depending on architectural differences among the species involved. Thus, the allometric relationships described here may provide, in the future, a basis for the prediction of species succession patterns and seagrass productivity from simple architectural characteristics of local floras.

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LITERATURE CITED

- Aioi, K. (1980). Seasonal changes in the standing crop of the eelgrass (*Zostera marina* L.) in Odawa Bay, central Japan. *Aquat. Bot.* 8: 343–354
- Backman, T. W., Barilotti, D. C. (1976). Irradiance reduction: effects on standing crops of the eelgrass *Zostera marina* in a coastal lagoon. *Mar. Biol.* 34: 33–40
- Bak, H. P. (1980). Age populations and biometrics in eelgrass, *Zostera marina* L. *Ophelia* 19: 155–162
- Banase, K., Mosher, S. (1980). Adult body mass and annual production/biomass relationships of field populations. *Ecol. Monogr.* 50: 355–479
- Barber, B. J., Beherens, P. J. (1985). Effects of elevated temperature on seasonal *in situ* leaf productivity of *Thalassia testudinum* Banks ex König and *Syringodium filiforme* Kützinger. *Aquat. Bot.* 22: 61–69
- Bay, D. (1984). A field study of the growth dynamics and productivity of *Posidonia oceanica* (L.) Delile in Calvi Bay, Corsica. *Aquat. Bot.* 20: 43–64
- Behdome, A. L. (1981). Phénologie et production des feuilles de *Posidonia oceanica* (Linnaeus) Delile dans la Baie de Port-Cross: probeles methodologiques. M.Sc. thesis. Université d'Aix-Marseille II
- Bigley, R. E., Harrison, P. G. (1986). Shoot demography and morphology of *Zostera japonica* and *Ruppia maritima* from British Columbia, Canada. *Aquat. Bot.* 24: 69–82
- Bird, R. B., Stewart, W. E., Lightfoot, E. N. (1980). Transport phenomena. Wiley, New York
- Bouderesque, C. F., Jeudy de Grissac, A., Meinesz, A. (1984). Relation entre la sédimentation et l'allongement des rhizomes orthotropes de *Posidonia oceanica* dans la Baie D'Elbu (Corse). In: Boudouresque, C. F., Jeudy de Grissac, A., Olivier, J. (eds.) *Int. Workshop Posidonia beds*. GIS Posidonie, Marseille, p. 185–191
- Brouns, J. J. W. M. (1985). A comparison of the annual production and biomass in three monospecific stands of the seagrass *Thalassia hemprichii* (Ehrenb.) Achers. *Aquat. Bot.* 23: 149–175
- Brouns, J. J. W. M. (1987). Growth patterns of some Indo-West-Pacific seagrasses. *Aquat. Bot.* 28: 39–61
- Brouns, J. J. W. M., Heijs, F. M. L. (1986). Production and biomass of the seagrass *Enhalus acoroides* (L. f.) Royle and its epiphytes. *Aquat. Bot.* 25: 21–45
- Buesa, R. (1974). Population and biological data on turtle grass (*Thalassia testudinum* König, 1805) on the Northwestern Cuban Shelf. *Aquaculture* 4: 207–226
- Buia, M. C., Cormaci, M., Furnari, G., Mazella, L. (1985). Osservazioni sulla struttura delle praterie di *Posidonia oceanica* (L.) Delile di Capo Passero (Siracusa) e studio della macroflora epifita delle foglie. *Boll. Accad. Gioenia Sci. nat.* 18: 463–484
- Bulthuis, D. A. (1983). Effects of *in situ* light reduction on density and growth of the seagrass *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog in Western Port, Victoria, Australia. *J. exp. mar. Biol. Ecol.* 67: 910–103
- Bulthuis, D. A., Woelkerling, Wm. J. (1983). Seasonal variation in standing crop, density, and leaf growth rate of the seagrass, *Heterozostera tasmanica*, in Western Port and Port Phillips Bay, Victoria, Australia. *Aquat. Bot.* 16: 111–136
- Cayé, G., Meinesz, A. (1985). Observations on the vegetative development, flowering and seeding of *Cymodocea nodosa* (Ucria) Ascherson on the Mediterranean coasts of France. *Aquat. Bot.* 22: 277–289
- Clarke, S. M., Kirkman, H. (1989). Seagrass dynamics. In: Larkum, A. W. D., McComb, A. J., Shepherd, S. A. (eds.) *Biology of seagrasses. A treatise on the biology of seagrasses with special reference to the Australian region*. Elsevier, Amsterdam, p. 304–345
- Clough, B. F., Attiwell, P. M. (1980). Primary production of *Zostera muelleri* Irmisch. ex Aschers. in Western Port Bay (Victoria, Australia). *Aquat. Bot.* 9: 1–13
- Dawes, C. J., Tomasko, D. A. (1988). Depth distribution of *Thalassia testudinum* in two meadows on the west coast of Florida; a difference in effect of light availability. *P.S.Z.N.I. Mar. Ecol.* 9: 123–130
- Den Hartog, C. (1970). *The seagrasses of the world*. North Holland Publ., Amsterdam
- Den Hartog, C. (1977). Structure, function and classification in seagrass communities. In: McRoy, C. P., Helfferich, C. (eds.) *Seagrass ecosystems: a scientific perspective*. Marcel Dekker, New York, p. 89–121
- Dennison, W. C., Alberte, R. S. (1985). Role of daily light

- period in the depth distribution of *Zostera marina* (eelgrass). Mar. Ecol. Prog. Ser. 25: 51–61
- Duarte, C. M., Sand-Jensen, K. (1990). Seagrass colonization: biomass development and shoot demography in *Cymodocea nodosa* patches. Mar. Ecol. Prog. Ser. 67: 97–103
- Eleuterius, L. N. (1987). Seagrass ecology along the coasts of Alabama, Louisiana, and Mississippi. In: Durako, M. J., Phillips, R. C., Lewis, R. R., III (eds.) Proc. Symp. subtropical-tropical seagrasses in the southeastern United States. Fla. mar. Res. Publ. 42: 11–20
- Estacion, J. S., Fortes, M. D. (1988). Growth rates and primary production of *Enhalus acoroides* (L. f.) Royle from Lag-It North Bais Bay, The Philippines. Aquat. Bot. 29: 347–356
- Fry, B. (1983). Leaf growth in the seagrass *Syringodium filiforme* Kutz. Aquat. Bot. 16: 361–368
- Fry, B., Virnstein, R. W. (1988). Leaf production and export of the seagrass *Syringodium filiforme* Kutz. in Indian River lagoon, Florida. Aquat. Bot. 30: 261–266
- Gambi, M. C. (1988). Flowering in a *Zostera marina* bed off San Juan Island (Washington, USA) during winter. Aquat. Bot. 30: 267–272
- Gambi, M. C., Nowell, A. R. M., Jumars, P. A. (1990). Flume observations on flow dynamics in *Zostera marina* (eelgrass) beds. Mar. Ecol. Prog. Ser. 61: 159–169
- Gil-Rodríguez, M. C., Cruz-Simó, M. C. (1982). *Halophila decipiens* Ostenfeld (Hydrocharitaceae), una fanerogama marina nueva para el Atlántico oriental. Vieraea 11: 207–216
- Harper, J. L. (1977). Population biology of plants. Academic Press, London
- Herbert, D. A. (1986). The growth dynamics of *Halophila hawaiiiana*. Aquat. Bot. 23: 351–360
- Hillman, K., Walker, D. I., Larkum, A. W. D., McComb, A. J. (1989). Productivity and nutrient limitation. In: Larkum, A. W. D., McComb, A. J., Shepherd, S. A. (eds.) Biology of seagrasses. A treatise on the biology of seagrasses with special reference to the Australian region. Elsevier, Amsterdam, p. 635–685
- Hulings, N. C. (1979). The ecology, biometry and biomass of the seagrass *Halophila stipulacea* along the Jordanian coast of the Gulf of Aqaba. Botanica mar. 22: 425–430
- Huxley, J. S. (1932). Problems of relative growth. Methuen & Co., London
- Ibarra-Obando, S. E., Huerta-Tamayo, R. (1987). Blade production of *Zostera marina* L. during the summer-autumn period on the Pacific Coast of Mexico. Aquat. Bot. 28: 301–315
- Iverson, R. L., Bittaker, H. F. (1986). Seagrass distribution and abundance in eastern Gulf of Mexico coastal waters. Estuar. coast. Shelf Sci. 22: 577–602
- Jacobs, R. P. W. M. (1979). Distribution and aspects of the production and biomass of eelgrass, *Zostera marina* L. at Roscoff, France. Aquat. Bot. 7: 151–172
- Jacobs, R. P. W. M. (1984). Biomass potential of eelgrass (*Zostera marina* L.). CRC critical Rev. Plant Sci. 2: 49–80
- Jacobs, R. P. W. M., Hegger, H. H., Ras-Willems, A. (1983a). Seasonal variations in the structure of a *Zostera* community on tidal flats in the SW Netherlands, with special reference to the benthic fauna. Proc. K. ned. Akad. Wet. (Sect. C) 86: 347–357
- Jacobs, R. P. W. M., Noten, T. M. P. A., Claassen, E. (1983b). Population and growth characteristics of the seagrass *Zostera noltii* Hornem. in the Dutch Wadden Sea. Proc. Int. Symp. on Aquatic Macrophytes, Nijmegen, The Netherlands. Catholic Univ., Nijmegen, p. 95–100
- Johnstone, I. M. (1979). Papua New Guinea seagrasses and aspects of the biology and growth of *Enhalus acoroides* (L.f.) Royle. Aquat. Bot. 7: 197–208
- Josselyn, M., Fonseca, M., Niesen, T., Larson, R. (1986). Biomass, production and decomposition of a deep water seagrass, *Halophila decipiens* Ostenf. Aquat. Bot. 25: 47–61
- Keller, M., Harris, S. W. (1966). The growth of eelgrass in relation to tidal depth. J. Wildl. Mgmt 30: 280–285
- Kentula, M. E., McIntire, C. D. (1986). The autoecology and production dynamics of eelgrass (*Zostera marina* L.) in Netarts Bay, Oregon. Estuaries 9: 188–199
- Kenworthy, W. J., Currin, C. A., Fonseca, M. S., Smith, G. (1989). Production, decomposition, and heterotrophic utilization of the seagrass *Halophila decipiens* in a submarine canyon. Mar. Ecol. Prog. Ser. 51: 277–290
- Kerr, E. A., Strother, S. (1989). Seasonal changes in leaf growth rate of *Zostera muelleri* Irmisch ex Aschers. in South-Eastern Australia. Aquat. Bot. 33: 131–140
- Kirkman, H., Cook, I. H. (1982). Biomass and growth of *Zostera capricorni* Aschers. in Port Hacking, N.S.W., Australia. Aquat. Bot. 12: 57–67
- Kirkman, H., Cook, I. H. (1987). Distribution and leaf growth of *Thalassodendron pachyrhizum* Den Hartog in Southern Western Australia. Aquat. Bot. 27: 257–266
- Kirkman, H., Reid, D. D. (1979). A study of the role of the seagrass *Posidonia australis* in the carbon budget of an estuary. Aquat. Bot. 7: 173–183
- Kittredge, J. (1944). Estimation of the amount of foliage of trees and shrubs. J. For. 42: 905–912
- LaBarbera, N. (1989). Analyzing body size as a factor in ecology and evolution. A. Rev. Ecol. Syst. 20: 97–117
- Lamoreaux, R. J., Chaney, W. R., Brown, K. M. (1978). The plastochrone index: a review after two decades of use. Am. J. Bot. 65: 586–593
- Larkum, A. W. D. (1976). Ecology of Botany Bay. I. Growth of *Posidonia australis* (Brown) Hook. f. in Botany Bay and other Bays of the Sidney Basin. Aust. J. mar. Freshwat. Res. 27: 117–127
- Larkum, A. W. D., Collett, L. C., Williams, R. J. (1984). The standing stock, growth, and shoot production of *Zostera capricorni* Aschers. in Botany Bay, New South Wales, Australia. Aquat. Bot. 19: 307–327
- Lipkin, Y. (1988). *Thalassodendretum ciliati* in Sinai (Northern Red Sea) with special reference to quantitative aspects. Aquat. Bot. 31: 125–139
- Mukai, H., Aioi, K., Koike, I., Iizumi, J., Ohtsu, M., Hattori, A. (1979). Growth and organic production of eelgrass (*Zostera marina* L.) in temperate waters of the Pacific coast of Japan. I. Growth analysis in spring–summer. Aquat. Bot. 7: 47–56
- Nienhuis, P. H., De Bree, B. H. H. (1980). Production and growth dynamics of eelgrass (*Zostera marina*) in brackish Lake Grevelingen (The Netherlands). Neth. J. Sea Res. 14: 102–118
- Ogden, J. C., Ogden, N. B. (1982). A preliminary study of two representative seagrass communities in Palau, Western Caroline Islands (Micronesia). Aquat. Bot. 12: 229–244
- Ott, J. A. (1979). Persistence of a seasonal growth rhythm in *Posidonia oceanica* (L.) Delile under constant conditions of temperature and illumination. Mar. Biol. Lett. 1: 99–104
- Ott, J. A. (1980). Growth and production in *Posidonia oceanica* (L.) Delile. P.S.Z.N.I. Mar. Ecol. 1: 47–64
- Patriquin, D. (1973). Estimation of growth rate, production and age of the marine angiosperm *Thalassia testudinum* König. Canb. J. Sci. 13: 111–123
- Pedersen, M. F. (1990). Production dynamics of eelgrass (*Zostera marina* L.). M.Sc. thesis, University of Copenhagen

- Peduzzi, P., Vuković, A. (1990). Primary production of *Cymodocea nodosa* in the Gulf of Trieste (Northern Adriatic Sea): a comparison of methods. *Mar. Ecol. Prog. Ser.* 64: 197–207
- Perez, M. (1989). Fanerógamas marinas en sistemas estuáricos: producción, factores limitantes, y algunos aspectos del ciclo de nutrientes. Ph.D. thesis, Universidad de Barcelona
- Perez, M., Romero, J., Duarte, C. M., Sand-Jensen, K. (1991). Phosphorus limitation of *Cymodocea nodosa* growth. *Mar. Biol.* 109: 129–133
- Pergent, G., Pergent-Martini, C. (1990). Some applications of lepidochronological analysis in the seagrass *Posidonia oceanica*. *Botanica mar* 33: 299–310
- Phillips, R. C., Santelices, B., Bravo, R., McRoy, C. P. (1983). *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog in Chile. *Aquat. Bot.* 15: 195–200
- Pirc, H. (1984). Depth-adaptation in *Posidonia oceanica* (L.) Delile. In: Boudouresque, C. F., Jeudy de Grissac, A., Olivier, J. (eds.) *Int. Workshop Posidonia beds*. GIS Posidonie, Marseille, p. 227–234
- Ritterbusch, A. (1990). The measurement of biological age in plant modular systems. *Acta biotheor* 38: 113–124
- Robertson, A. I., Mann, K. H. (1984). Disturbance by ice and life-history adaptations of the seagrass *Zostera marina*. *Mar. Biol.* 80: 131–141
- Roman, C. T., Able, K. M. (1988). Production ecology of eelgrass (*Zostera marina* L.) in a Cape Cod salt marsh-estuarine system. *Aquat. Bot.* 32: 353–363
- Romero-Martinengo, J. (1985). Estudio ecológico de las fanerógamas de la costa Catalana: producción primaria de *Posidonia oceanica* (L.) Delile en las Islas Medes. Ph.D. thesis, Universidad de Barcelona
- Sand-Jensen, K. (1975). Biomass, net production and growth dynamics in an eelgrass (*Zostera marina* L.) population in Vellerup Vig, Denmark. *Ophelia* 14: 185–201
- Semroud, R., Mezegrane, S., Soltane, L. (1990). Etude lepidochronologique de *Posidonia oceanica* dans la région d'Alger (Algérie): données préliminaires. *Rapp. Comm. int. Étude Mer Médit.* 32 (B-I): 15
- Shinozaki, K., Yoda, K., Hozumi, K., Kira, T. (1964). A quantitative analysis of plant form – the pipe model theory. 1 Basis analyses. *Jap. J. Ecol.* 14: 97–105
- Short, F. T. (1987). Effects of sediment nutrients on eelgrasses: literature review and mesocosms experiment. *Aquat. Bot.* 27: 41–57
- Short, F. T., Dennison, W. C., Capone, D. G. (1990). Phosphorus-limited growth of the tropical seagrass *Syringodium filiforme* in carbonate sediments. *Mar. Ecol. Prog. Ser.* 62: 169–174
- Silverstein, K., Chiffings, A. W., McComb, A. J. (1986). The loss of seagrass in Cockburn Sound, Western Australia. III. The effect of epiphytes on productivity of *Posidonia australis* Hook F. *Aquat. Bot.* 24: 355–371
- Stevenson, J. C. (1988). Comparative ecology of submerged grass beds in freshwater, estuarine, and marine environments. *Limnol. Oceanogr.* 33: 867–893
- Stewart, J. G. (1989). Maintenance of a balanced, shifting boundary between the seagrass *Phyllospadix* and algal turf. *Aquat. Bot.* 33: 223–241
- Taylor, J. L., Saloman, C. H., Prest, K. W. Jr (1973). Harvest and regrowth of turtle grass (*Thalassia testudinum*) in Tampa Bay, Florida. *Fish. Bull. U.S.* 71: 145–148
- Thelin, I., Boudouresque, C. F. (1983). Longevité des feuilles de *Posidonia oceanica* dans un herbier superficiel de la Baie de Port-Cross (Var, France). *Rapp. Comm. int. Étude Mer Médit.* 28: 115–116
- Thorhaug, A., Roessler, M. A. (1977). Seagrass community dynamics in a subtropical estuarine lagoon. *Aquaculture* 12: 253–277
- Thorne-Miller, B., Harlin, M. M. (1984). The production of *Zostera marina* L. and other submerged macrophytes in a coastal lagoon in Rhode Island, USA. *Botanica mar* 27: 539–546
- Till, R. (1974). *Statistical methods for the earth scientist*. An introduction. Macmillan, New York
- Tomasko, D. A., Dawes, C. J. (1989). Evidence for physiological integration between shaded and unshaded short shoots of *Thalassia testudinum*. *Mar. Ecol. Prog. Ser.* 54: 299–305
- Tomasko, D. A., Dawes, C. J. (1990). Influences of season and water depth on the clonal biology of the seagrass *Thalassia testudinum*. *Mar. Biol.* 105: 345–351
- Tomlinson, P. B. (1974). Vegetative morphology and meristem dependence. The foundation of productivity in seagrasses. *Aquaculture* 4: 107–130
- Tomlinson, P. B., Vargo, G. A. (1966). On the morphology and anatomy of turtle grass, *Thalassia testudinum* (Hydrocharitaceae). 1 Vegetative morphology. *Bull. mar. Sci.* 16: 748–761
- Umebayashi, O. (1988). Individual leaf growth of vegetative shoots of eelgrass, *Zostera marina*. *Bull. Tokai reg. Fish. Res. Lab.* 125: 1–13
- Vermaat, J. E., Hootsman, M. J. M., Nienhuis, P. H. (1987). Seasonal dynamics and leaf growth of *Zostera noltii* Hornem., a perennial intertidal seagrass. *Aquat. Bot.* 28: 287–299
- Virstein, R. W. (1982). Leaf growth of the seagrass *Halodule wrightii* photographically measured *in situ*. *Aquat. Bot.* 12: 209–218
- Wahbeh, M. I. (1984). The growth and production of the leaves of the seagrass *Halophila stipulacea* (Forsk.) Aschers. from Aqaba, Jordan. *Aquat. Bot.* 20: 33–41
- Walker, D. I. (1989). Regional studies – Seagrass in Shark Bay, the foundations of an ecosystem. In: Larkum, A. W. D., McComb, A. J., Shepherd, S. A. (eds.) *Biology of seagrasses. A treatise on the biology of seagrasses with special reference to the Australian region*. Elsevier, Amsterdam, p. 182–210
- Walker, D. I., McComb, A. J. (1988). Seasonal variation in the production, biomass, and nutrient status of *Amphibolis antarctica* (Labill.) Sonder ex Aschers. and *Posidonia australis* Hook. F. in Shark Bay, Western Australia. *Aquat. Bot.* 31: 259–275
- Watt, A. S. (1940). Contributions to the ecology of bracken (*Pteridium aquilinum*). 1. The rhizome. *New Phytol.* 39: 401–422
- West, R. J. (1990). Depth-related structural and morphological variations in an Australian *Posidonia* seagrass bed. *Aquat. Bot.* 36: 153–166
- West, R. J., Larkum, A. W. D. (1979). Leaf productivity of the seagrass, *Posidonia australis*, in Eastern Australian waters. *Aquat. Bot.* 7: 57–65
- West, R. J., Larkum, A. W. D., King, R. J. (1989). Regional studies – Seagrasses of South-Eastern Australia. In: Larkum, A. W. D., McComb, A. J., Shepherd, S. A. (eds.) *Biology of seagrasses. A treatise on the biology of seagrasses with special reference to the Australian region*. Elsevier, Amsterdam, p. 230–260
- White, J. (1981). The allometric interpretation of the self-thinning rule. *J. theor. Biol.* 89: 475–500
- Williams, S. L. (1987). Competition between the seagrasses *Thalassia testudinum* and *Syringodium filiforme* in a Caribbean lagoon. *Mar. Ecol. Prog. Ser.* 35: 91–98

Williams, S. L. (1988). *Thalassia testudinum* productivity and grazing by green turtles in a highly disturbed seagrass bed. *Mar. Biol.* 98: 447–455

Wittmann, K. J. (1984). Temporal and morphological variations of growth in a natural stand of *Posidonia oceanica* (L.) Delile. *P.S.Z.N.I. Mar. Ecol.* 5: 301–316

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Zieman, J. C. (1975). Seasonal variation of turtle grass, *Thalassia testudinum* König, with reference to temperature and salinity effects. *Aquat. Bot.* 1: 107–123

Zieman, J. C., Fourqurean, J. W., Iverson, R. L. (1984). Distribution, abundance, and productivity of seagrasses and macroalgae in Florida Bay. *Bull. mar. Sci.* 44: 292–311

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