

Growth patterns of Western Mediterranean seagrasses: species-specific responses to seasonal forcing

Núria Marbà*, Just Cebrián, Susana Enríquez, Carlos M. Duarte

Centre d'Estudis Avançats de Blanes, CSIC, Camí de Santa Bàrbara s/n, E-17300 Blanes (Girona), Spain

ABSTRACT: The seasonal growth pattern of the 4 seagrass species occurring in the NW Mediterranean (i.e. *Cymodocea nodosa*, *Zostera noltii*, *Z. marina*, *Posidonia oceanica*) was studied in populations growing in the same locality (Cala Jonquet, Girona, NE Spain), and thus experiencing the same seasonal (i.e. temperature and light) forcing, to evaluate the contribution of species-specific responses to seagrass growth seasonality. *C. nodosa*, *Z. noltii*, and *Z. marina* showed comparable growth patterns as indicated by significant correlations of growth across species (cross correlation, $r > 0.54$, $p < 0.05$). This result provided evidence of a similarity in the response of these species to seasonal forcing. The seasonal pattern of *P. oceanica* resembled that of the other species in shoot weight, shoot elongation, and ramet recruitment, whereas it differed in internode weight and rhizome elongation. Despite some similarities in seasonal growth patterns, the patterns were lagged by 1 to 2 mo across species, and the magnitude of seasonal growth fluctuations was species-dependent. Species-specific responses of seagrasses to climate forcing should be related to differences in the capacity of the plants to store resources and to the extent of ramet integration among species, both processes being closely related to plant size. Large seagrasses (e.g. *P. oceanica*), with thick and long-living rhizomes, should be able to store more photoassimilates and to transport them over longer distances than small plants (e.g. *C. nodosa*), with thinner and shorter-living rhizomes. Large species should, therefore, be able to grow more independently of environmental conditions than small ones. Moreover, *C. nodosa* showed the greatest response to temperature fluctuations whereas *Z. marina* growth was strongly coupled to seasonal light conditions, indicating different plant sensitivity to climate fluctuations among species. This study confirms the great variability in seagrass seasonality possible under similar seasonal forcing, and demonstrates that seagrass seasonality has both an extrinsic component, dependent on seasonal forcing of light and temperature, and an intrinsic component. The intrinsic component of seagrass seasonality likely involves a differential capacity of the species to regulate the internal resource economy which may buffer, or amplify, the external seasonal forcing.

KEY WORDS: *Posidonia oceanica* · *Cymodocea nodosa* · *Zostera marina* · *Zostera noltii* · Seasonality · Module size · Module appearance rate · Module growth · Ramet recruitment · Flowering

INTRODUCTION

Seagrass biomass exhibits high seasonal fluctuations in temperate waters (Duarte 1989). The strong seasonality of temperate seagrass growth has been demonstrated to be coupled to seasonal forcing through

correlations between plant growth and seasonal variations in light and temperature (e.g. Sand-Jensen 1975, Zieman 1975, Jacobs et al. 1982, Phillips et al. 1983, Wium-Andersen & Borum 1984, Kentula & McIntire 1986, Terrados 1991, Pérez & Romero 1992, Olesen & Sand-Jensen 1994a, Alcoverro et al. 1995). The hypothesis that seasonal variation in seagrass growth exclusively derives from seasonal changes in irradiance and temperature implies that species growing together should exhibit parallel seasonal growth

*Present address: Centre for Estuarine and Coastal Ecology, NIOO, Vierstraat 28, 4401 EA Yerseke, The Netherlands.
E-mail: marba@nioo.nl

dynamics. Yet, seagrass responses to seasonal forcing may also incorporate species-specific effects. These effects may result from different physiological plant responses to light and temperature conditions (Evans et al. 1986), as well as from other intrinsic factors such as the ability to allocate resources to reproduction, leaves or belowground modules, or the differential ability of the species to store and use resources (Ashmun et al. 1982, Pitelka & Ashmun 1985), which may partially uncouple plant growth from environmental conditions (Pirc 1985). Further, seagrass seasonal responses may be set by internal clocks, rather than reflect direct physiological effects of environmental conditions, rendering seasonal dynamics relatively independent of interannual environmental variability. For instance, there is evidence that the large seagrass *Posidonia oceanica* is able to maintain its seasonal pattern of leaf production for 2 yr even when growing under constant light, temperature and day length (Ott 1979). Despite the possibility of species-specific effects on seagrass growth seasonality this aspect remains untested, perhaps because temperate seagrass stands, unlike those in the tropics, are mostly monospecific.

There are 4 seagrass species growing in the Western Mediterranean. *Posidonia oceanica* (L.) Delile and, in sheltered bays, *Cymodocea nodosa* (Ucria) Aschers. are dominant. *Zostera noltii* Hornem. occurs in shallow, protected bays and lagoons, and *Z. marina* L. is restricted to brackish lagoons and some sheltered coves (den Hartog 1970). The growth seasonality of *P. oceanica* (Ott 1980, Cayé & Rossignol 1983, Bay 1984, Wittman 1984, Romero 1985, Buia et al. 1992, Alcov-erro et al. 1995) and *C. nodosa* (Pérez 1989, Peduzzi & Vukovic 1990, Terrados & Ros 1992) has been described for plants growing in different locations in the Mediterranean region. Seasonality of *Z. marina* and *Z. noltii* growth has been observed in populations in the Atlantic Ocean (Sand-Jensen 1975, Jacobs 1979, Nienhuis & De Bree 1980, Robertson & Man 1984, Thorne-Miller & Harlin 1984, Wium-Andersen & Borum 1984, Orth & Moore 1986, Vermaat et al. 1987, Roman & Able 1988, Pedersen & Borum 1993, Pérez-Llorens & Niell 1993, Olesen & Sand-Jensen 1994a) and other seas (e.g. the Pacific; Backman & Barilotti 1976, Aioi 1980, Mukai et al. 1980, Kentula & McIntire 1986, Ibarra-Obando 1989, Thom 1990), but it has never been examined in the Mediterranean Sea, except for a description of seasonal changes in *Z. noltii* biomass (Pérez 1989). The discovery of a location in the NW Mediterranean where all 4 species grow together (Cala Jonquet, NE Spain, 42° 18.26' N, 3° 18.11' E) offered an opportunity to test for the species-specific aspects of seagrass growth seasonality.

Here we examine seasonal fluctuations in the growth of all seagrass species occurring in the NW

Mediterranean (*Cymodocea nodosa*, *Zostera noltii*, *Z. marina*, *Posidonia oceanica*) by analysing seasonal variation in the weight, formation rate and growth of modules (i.e. leaf, flower, rhizome internode, root; White 1979) and ramets in the same location (Cala Jonquet). This similarity in seasonal conditions allowed us to quantify the importance of intrinsic factors (e.g. plant sensitivity to seasonal conditions, and ability to allocate, store and use resources) on seagrass growth seasonality. Moreover, we provide here a first account of the dynamics of seasonal growth of *Z. noltii* and *Z. marina* in the Mediterranean.

METHODS

The growth of *Cymodocea nodosa*, *Zostera noltii*, *Z. marina* and *Posidonia oceanica* was studied in Cala Jonquet, a protected cove where all 4 seagrass species present in the NW Mediterranean coast occur (Fig. 1). *P. oceanica* grows from 2 m to often around 16 m depth, forming a continuous monospecific meadow. *C. nodosa* and *Z. noltii* develop a mixed meadow in the shallow (<1.5 m) part of the cove, where changes in the sea level sporadically expose the shallow margins of the seagrass meadow. *Z. marina* grows in 2 small patches in the shallow part of the cove (Fig. 1). All species were sampled at the depth of maximal shoot density. This depth was 4 m for *P. oceanica* and 1 m for all other species. Nutrient concentrations in the water were relatively low (annual average 1.1 $\mu\text{mol l}^{-1}$ of nitrate, 1.4 $\mu\text{mol l}^{-1}$ of ammonium and 0.3 $\mu\text{mol l}^{-1}$ of phosphate), and they did not fluctuate seasonally (Vidondo & Duarte 1995).

We sampled, at monthly intervals between September 1991 and June 1993, the *Cymodocea nodosa*, *Zostera noltii* and *Posidonia oceanica* populations. *P. oceanica* was sampled every other month during 1993. The finding of 2 *Z. marina* patches in April 1992 allowed monthly sampling of this species to be conducted until August 1993. During each visit, we marked 10 apices of the horizontal rhizomes of each species by placing a plastic tag around the last horizontal rhizome internode produced and marking the adjacent leaf sheaths. We marked the adjacent leaf sheaths by punching a hole through the leaves, at the level of their leaf sheaths, with a hypodermic needle (Pérez et al. 1991). Because *P. oceanica* and *C. nodosa* have horizontal and vertical rhizomes (i.e. short shoots; Tomlinson 1974) that grow at different rates (Duarte et al. 1994), the latter producing most of the leaves, we also marked 10 to 15 vertical rhizomes of these species by marking the leaves as described above. We then collected the plant material marked during the previous visit and more than 100 supplementary ramets of

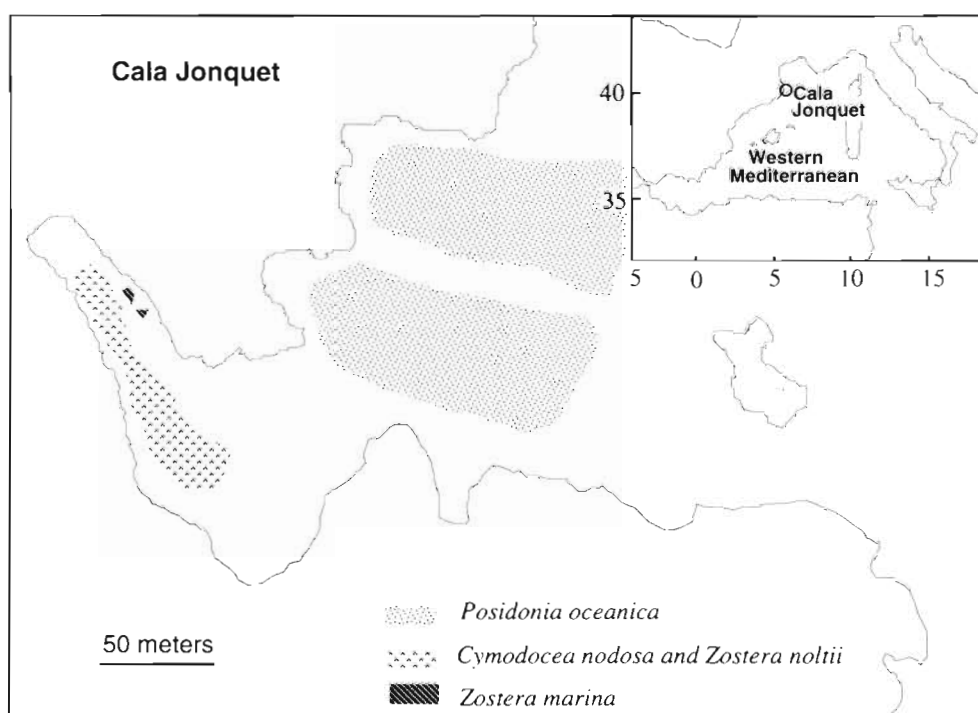


Fig. 1 Location of the sea-grass populations studied

C. nodosa and *Z. noltii* within three 20 cm diameter cores, and we harvested, individually, about 50 supplementary ramets of *P. oceanica* and *Z. marina*. In the laboratory, we recorded the number of new modules (leaf, flower, rhizome internode, root) and ramets that appeared during the marking period, and the length of new growth of the marked plant material (leaves and rhizomes). We measured, after overnight desiccation at 85°C, dry weight of leaf clusters (hereafter referred to as shoots) and of new rhizome internodes of all species, and that of the new roots produced on the tagged rhizomes of *C. nodosa*, *Z. noltii* and *Z. marina*. We recorded the fraction of flowering ramets of each species in the supplementary ramets collected, and weighed a sample of dried inflorescences. These measurements allowed examination of annual changes in module size, in the rate of module and ramet appearance, and in module growth.

New leaves were identified by unmarked young leaves, and new horizontal rhizome internodes, new ramets and new roots were identified as those which developed between the horizontal rhizome apex and the plastic tag. The rate of appearance of leaves per shoot, and, similarly, the rate of appearance of horizontal rhizome internodes and ramets per rhizome apex, were calculated as

$$\text{Rate of appearance of leaves} = \frac{\text{No. of new leaves in a shoot}}{T}$$

where T was the number of days in the marking pe-

riod. Leaf, rhizome, and root growth were estimated as

$$\text{Leaf elongation rate} = \frac{(\text{Length of new leaves} + \text{Elongation of old leaves}) \text{ produced per shoot}}{T}$$

$$\text{Rhizome elongation rate} = \frac{\text{Length of horizontal rhizome produced by an apex}}{T} \text{ and}$$

$$\text{Root production rate} = \frac{\text{Weight of new roots produced by an apex}}{T}$$

These measurements underestimate leaf elongation rate of *Cymodocea nodosa*, and *Zostera* spp. during peak growth, when >1 leaf was lost. They underestimate, by about 10%, rhizome elongation rate of *C. nodosa* and *Z. noltii* in July, and of *Z. marina* in September, when there was some growth of the youngest rhizome internode after it was produced. Root growth is also underestimated because the measurements do not account for growth of old roots, nor for root production on vertical rhizomes of *C. nodosa*.

Daily incident irradiance was obtained from a station 21 km south of the study site (Experimental Research Station Mas Badia, St. Pere Pescador). Surface water temperature was measured weekly at a location 27 km south of the study site (L'Estartit; J. Pascual unpubl. data). We cumulated the daily incident irradiance data over each month, whereas we used the monthly average water temperature.

We used the coefficient of variation to represent the extent of the variability of module size and dynamics

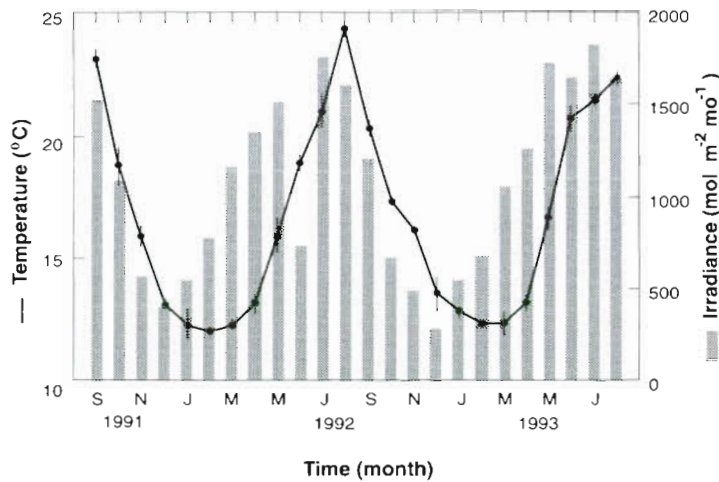


Fig. 2. Monthly variation in surface sea temperature (—♦—) and cumulative solar irradiance per month (bars) during the study period in the NW Mediterranean

over the year. The plant response to seasonal forcing, described by solar irradiance and water temperature, was examined using cross correlation analysis to allow for lagged responses between seasonal changes and

plant dynamics. The strength of the coupling between seasonal changes and plant response was represented by the coefficient of determination (R^2 , i.e. the percent of annual variance in module size and dynamics statistically accounted for by variation in temperature or irradiance). Cross correlation analysis was also used to examine the similarity of the seasonal growth patterns across species.

RESULTS

The irradiance received at the water surface ranged from 269 mol photons $m^{-2} mo^{-1}$ in December to 1824 mol photons $m^{-2} mo^{-1}$ in July (Fig. 2). Irradiance fluctuations were similar in 1992 and 1993, but very low irradiance occurred in June 1992, due to a long storm period (Fig. 2). This anomaly, however, was not reflected in the water temperature, which produced a smooth annual pattern, with a minimum of 12°C, in February and a maximum of 23.2°C, in September (Fig. 2). Water temperature lagged changes in irradiance by about 1 mo (cross correlation, lag = 1 mo,

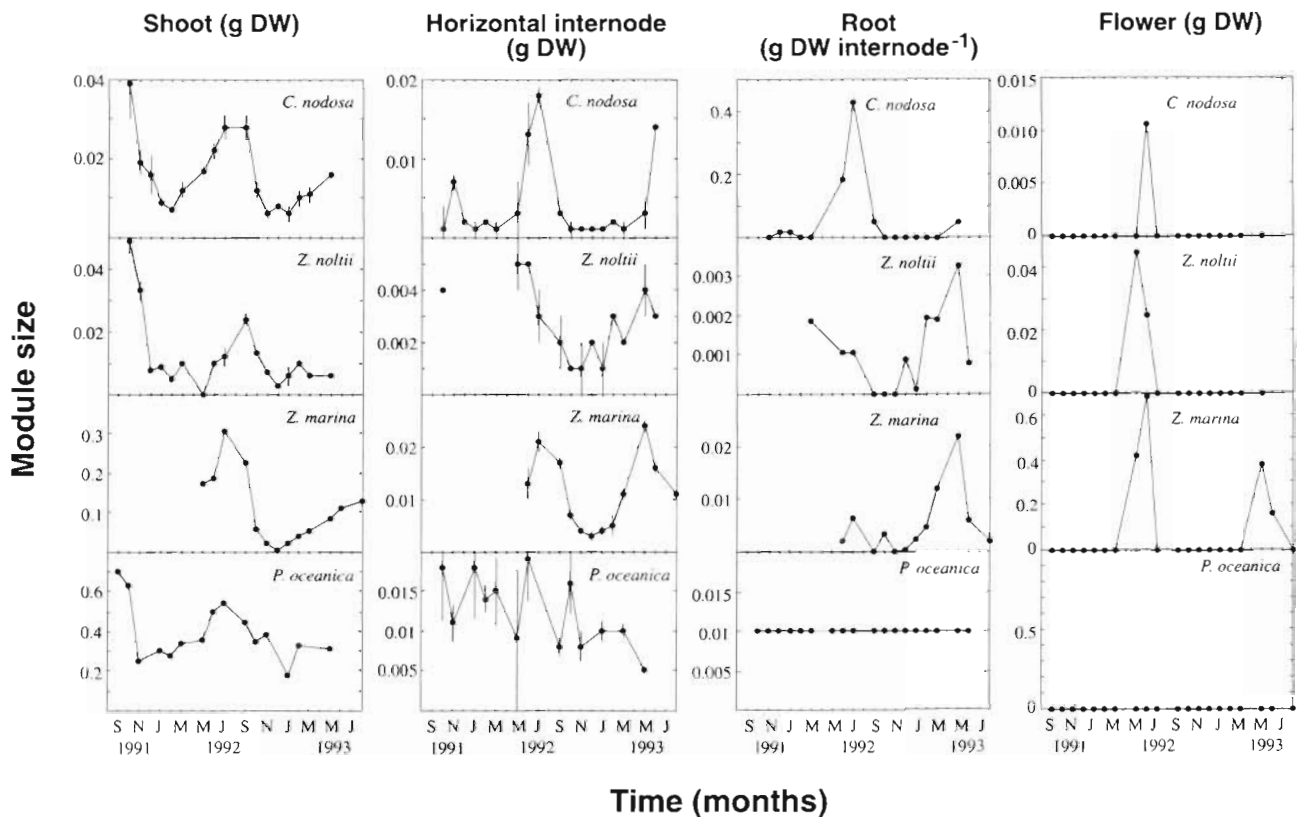


Fig. 3. Seasonal changes in seagrass module size. Bars represent the standard error of the mean; no bars drawn for pooled measurements (i.e. at least 10 modules weighted together)

$r = 0.87$, $p < 0.05$). Water transparency was higher in spring–summer than in winter, but it always exceeded >9 m depth (J. Pascual unpubl. data).

All seagrass species growing in Cala Jonquet flowered between May and June, except for *Posidonia oceanica*, which did not flower during the study period. *Zostera marina* produced the largest inflorescences (0.39 g DW) and in considerable abundance during the flowering period (19% of shoots flowered per year). *C. nodosa* produced small inflorescences (i.e. 0.029 g dry weight, DW) but flowered profusely (23% of the shoots flowered per year), and flowering of *Z. noltii* (0.072 g DW inflorescence⁻¹) was scarce (1% of the shoots flowered per year). Though we did not find any inflorescences of *P. oceanica*, we identified inflorescence peduncles (cf. Pergent et al. 1989) on its shoots (0.01 peduncles shoot⁻¹), indicative of flowering events in past years.

The weight of the vegetative modules produced by these seagrasses varied greatly over the year (Figs. 3 & 4). *Posidonia oceanica* was the largest species, with the largest shoots and roots, though horizontal internodes were small. *Zostera marina* was also large, but its roots were much smaller than those of *Cymodocea nodosa*. The shoots of *Z. marina* were smaller in this nutrient-poor Mediterranean Bay than those normally reported for the Atlantic populations (e.g. McRoy 1966, Phillips 1972, Lalumière et al. 1994), whereas the reverse applied to *Z. noltii*, which grew subtidally here but mostly occupies the intertidal zone in the Atlantic region (e.g. Vermaat et al. 1987, Pérez-Llorens 1991).

The lowest annual variability in module size was observed in *Posidonia oceanica* (Fig. 4). *Zostera* spp. showed the widest fluctuations in the size of seagrass shoots, whereas the annual variability in the size of belowground modules (i.e. horizontal rhizome internodes and roots) was greatest in *Cymodocea nodosa* (Fig. 4). The size of the vertical rhizome internodes of *P. oceanica* and *C. nodosa* also changed during the year with much greater changes in *C. nodosa* (CV = 56.5%) than in *P. oceanica* (CV = 6.5%).

All species experienced similar annual fluctuations in shoot weight, and *Cymodocea nodosa* and *Zostera marina* shared similar patterns in horizontal internodal

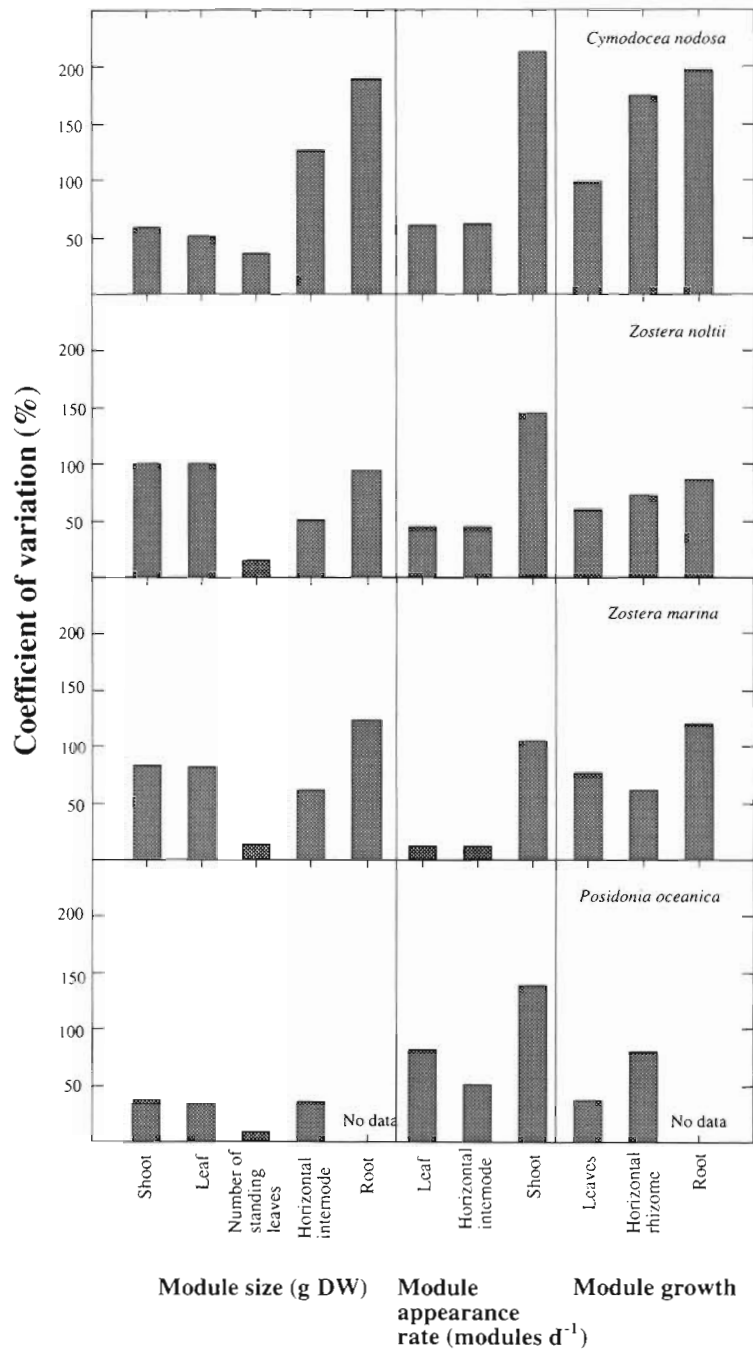


Fig. 4. Magnitude of annual fluctuations in module size, appearance rate and growth for the 4 seagrass species studied

weight as well (Table 1). The plants carried the largest shoots, and produced the heaviest rhizome internodes, in summer and the smallest and lightest ones in winter, although for *Z. noltii* this pattern was delayed (relative to shoots of *Z. marina*) by 1 mo (Fig. 3, Table 1). *C. nodosa* root weight showed seasonal changes, with the largest roots in summer (Fig. 3), the time of greatest nutrient demands (S. Enríquez et al. unpubl. results).

Table 1. *Cymodocea nodosa*, *Zostera marina*, *Z. noltii* and *Posidonia oceanica*. Cross correlation analysis of seasonal patterns between seagrass species in the NW Mediterranean. Negative and positive lags indicate the extent to which the seasonal pattern of the first species is delayed or advanced, respectively, relative to that of the second; lag: time in months for maximal correlation; r: Pearson coefficient (after log transformation, when necessary); ns: non-significant correlation ($p > 0.05$); nd: no data

Variable	<i>C. nodosa</i> - <i>Z. noltii</i>	<i>C. nodosa</i> - <i>Z. marina</i>	<i>P. oceanica</i> - <i>C. nodosa</i>	<i>Z. noltii</i> - <i>Z. marina</i>	<i>P. oceanica</i> - <i>Z. noltii</i>	<i>P. oceanica</i> - <i>Z. marina</i>
Shoot size (g DW)						
Lag	0	0	0	-1	0	0
r	0.762	0.544	0.667	0.319 ns	0.430 ns	0.380 ns
SE	0.242	0.236	0.236	0.250	0.236	0.229
Horizontal internode size (g DW)						
Lag	-1	0	-1	1	0	0
r	0.381 ns	0.540	0.270 ns	0.430 ns	0.420 ns	0.641 ns
SE	0.243	0.236	0.250	0.243	0.243	0.236
Root size (g DW internode⁻¹)						
Lag	3	-2	nd	0	nd	nd
r	-0.528 ns	0.836 ns		0.816 ns		
SE	0.277	0.258		0.277		
Horizontal internode appearance rate [internodes (horizontal rhizome)⁻¹ d⁻¹]						
Lag	0	0	-2	0	-3	0
r	0.468 ns	0.561	0.377 ns	0.186 ns	0.368 ns	0.226 ns
SE	0.236	0.236	0.258	0.236	0.267	0.236
Leaf appearance rate (leaves shoot⁻¹ d⁻¹)						
Lag	0	0	-2	0	-2	-2
r	0.541	0.349 ns	0.647	0.186 ns	0.374 ns	0.231 ns
SE	0.243	0.236	0.289	0.236	0.289	0.277
Ramet recruitment [ramets (horizontal rhizome)⁻¹ d⁻¹]						
Lag	-1	0	2	1	-1	0
r	0.389 ns	0.531	0.324	0.616	0.531	0.278 ns
SE	0.243	0.236	0.258	0.243	0.250	0.236
Leaf elongation rate (cm shoot⁻¹ d⁻¹)						
Lag	1	0	1	-1	2	1
r	0.792	0.765	0.560	0.704	0.574 ns	0.649
SE	0.250	0.243	0.277	0.250	0.289	0.267
Rhizome elongation rate [cm (horizontal rhizome)⁻¹ d⁻¹]						
Lag	-1	0	-2	1	-3	-2
r	0.821	0.615	0.247 ns	0.473 ns	0.325 ns	0.620
SE	0.243	0.236	0.258	0.243	0.267	0.250
Root production [g DW (horizontal rhizome)⁻¹ d⁻¹]						
Lag	-1	-1	nd	0	nd	nd
r	0.655	0.435 ns		0.776		
SE	0.258	0.250		0.277		

This increase of *C. nodosa* root weight might reflect phosphorus limitation of plant growth in summer, since there is evidence that phosphorus-limited *C. nodosa* allocates more biomass to root development to increase the capacity of roots to acquire phosphorus from the sediment (Pérez et al. 1995). The largest roots in *Z. noltii* and *Z. marina* were observed in spring (Fig. 3).

The overall similarity in the seasonal fluctuations of module size for all 4 species suggests that they might respond to similar factors, such as seasonal changes in water temperature and irradiance. Variability in water temperature explained most ($R^2 > 50\%$; Fig. 5) of the annual variability of seagrass shoot weight for all species, except for *Zostera noltii* ($R^2 = 0.24$; Fig. 5). The

seasonal changes in the size of horizontal rhizome internodes were partially attributable ($>40\%$) to seasonal variability in temperature (*Cymodocea nodosa*; Fig. 5) and light (*Z. marina*; Fig. 6). Changes in vertical internode length were independent of seasonal variability in temperature and irradiance (cross correlation, $p > 0.5$), suggesting that other non-seasonal environmental factors (e.g. sediment dynamics) may influence their size (cf. Marbà & Duarte 1994, Marbà et al. 1994). Root size was correlated with temperature only for *C. nodosa*.

The rate of module reiteration in these seagrass populations fluctuated over the year (CV from 13 to 213%; Figs. 4 & 7). The greatest seasonal variability in leaf

appearance rate was observed in *Posidonia oceanica*. The amplitude of seasonal fluctuations in the production of new horizontal internodes was similar among species, apart from *Zostera marina* (Figs. 4 & 7). All species, except *Z. marina*, followed similar patterns of leaf formation rate (Table 1), with maximum rates of leaf formation attained in September (Fig. 7). *Z. marina* produced new leaves and new horizontal internodes at a remarkably constant (and high) rate over the year (Figs. 4 & 7), particularly when compared with *Z. marina* populations growing in the Atlantic (Sand-Jensen 1975, Wium-Andersen & Borum 1984, Olesen & Sand-Jensen 1994a), and it did not show any seasonal trend. Ramet recruitment showed large seasonal fluctuations ($CV > 100\%$, Figs. 4 & 7) and revealed the existence of a single cohort (i.e. a single period of ramet recruitment) per year, in spring or early summer, in all species except for *Z. noltii*. *Z. noltii* appeared to produce several cohorts from spring to autumn. Ramet recruitment patterns were significantly correlated, but lagged 1 or 2 mo, among species (Table 1).

The similar patterns of leaf formation rate among the species were associated ($> 50\%$ of the variance) with fluctuations in temperature and irradiance (Figs. 5 & 6). This correlation was strongest for the larger species (*Posidonia oceanica* and *Cymodocea nodosa*) than for the small *Zostera noltii* (Figs. 5 & 6). Seasonal variability in temperature accounted for the seasonality in the rate of horizontal internode formation of *C. nodosa* and *Z. noltii* (Figs. 5 & 6). Ramet recruitment was strongly associated with seasonal variation in temperature and irradiance only for *C. nodosa* and *Z. marina* (Figs. 5 & 6). Ramet recruitment was coupled ($r = 0.60, 0.67$ and $0.89, p < 0.05$, for *P. oceanica*, *Z. marina* and *C. nodosa*, respectively) to the rate of appearance of horizontal internodes, with a lag of 4 mo between maximal rates of appearance of horizontal internodes and shoot recruitment in *P. oceanica*. This delay in *P. oceanica* ramet recruitment, relative to horizontal rhizome appearance, could derive from the difficulty in identifying new ramets when they start to develop (i.e. < 2 leaves or, on average, 3.8 mo old).

Seagrass growth of all 4 seagrass species varied over the year (Fig. 8). The extent of seasonal variation in

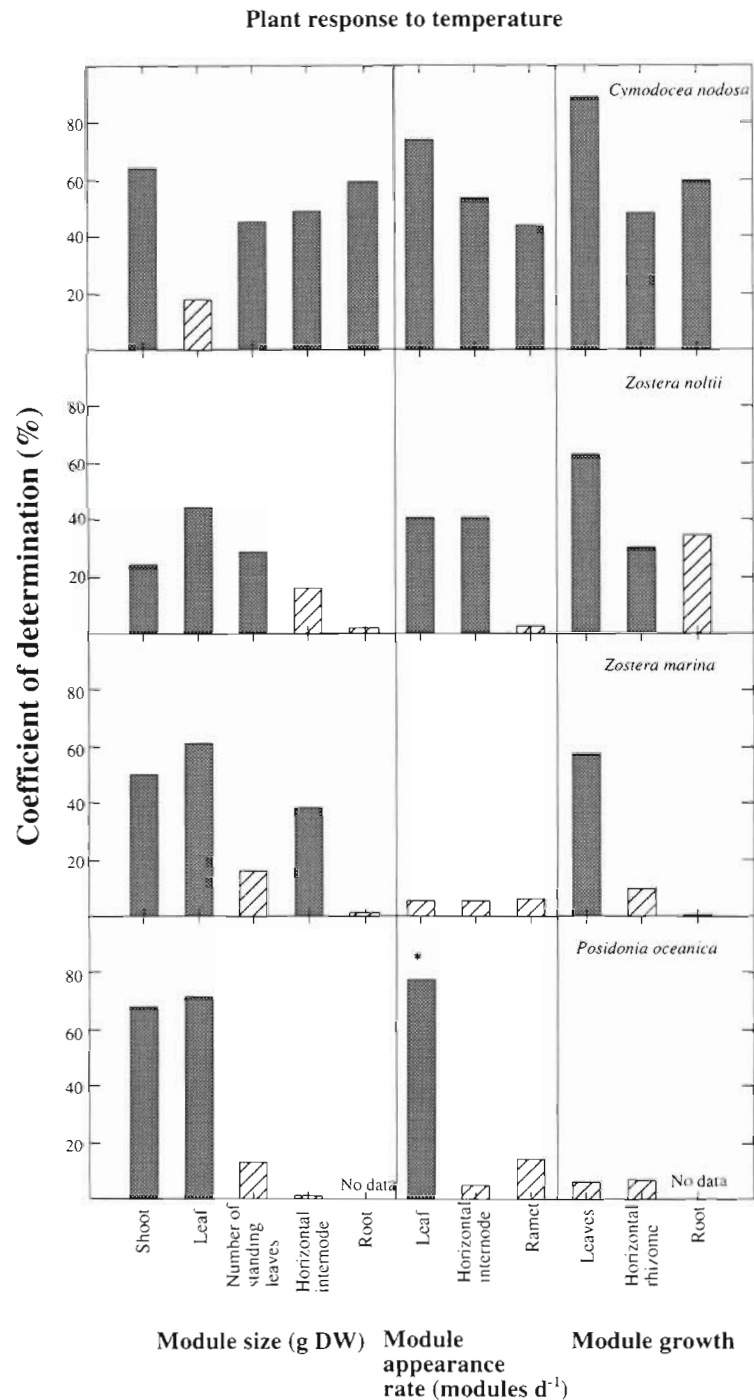


Fig. 5. Coefficients of determination for the relationships of seagrass module size, appearance rate, and growth [units for leaf growth are $\text{cm shoot}^{-1} \text{d}^{-1}$, for rhizome growth $\text{cm (horizontal rhizome apex)}^{-1} \text{d}^{-1}$, and for root growth $\text{g DW (horizontal rhizome apex)}^{-1} \text{d}^{-1}$] to water temperature conditions. Shaded bars indicate significant relationships ($p < 0.05$), hatched bars indicate non-significant ($p > 0.05$) relationships. *Relationship lagged by 2 mo

seagrass growth was greatest in belowground modules (horizontal rhizomes and roots) as compared to leaves (Fig. 4). The allocation of growth to aboveground or

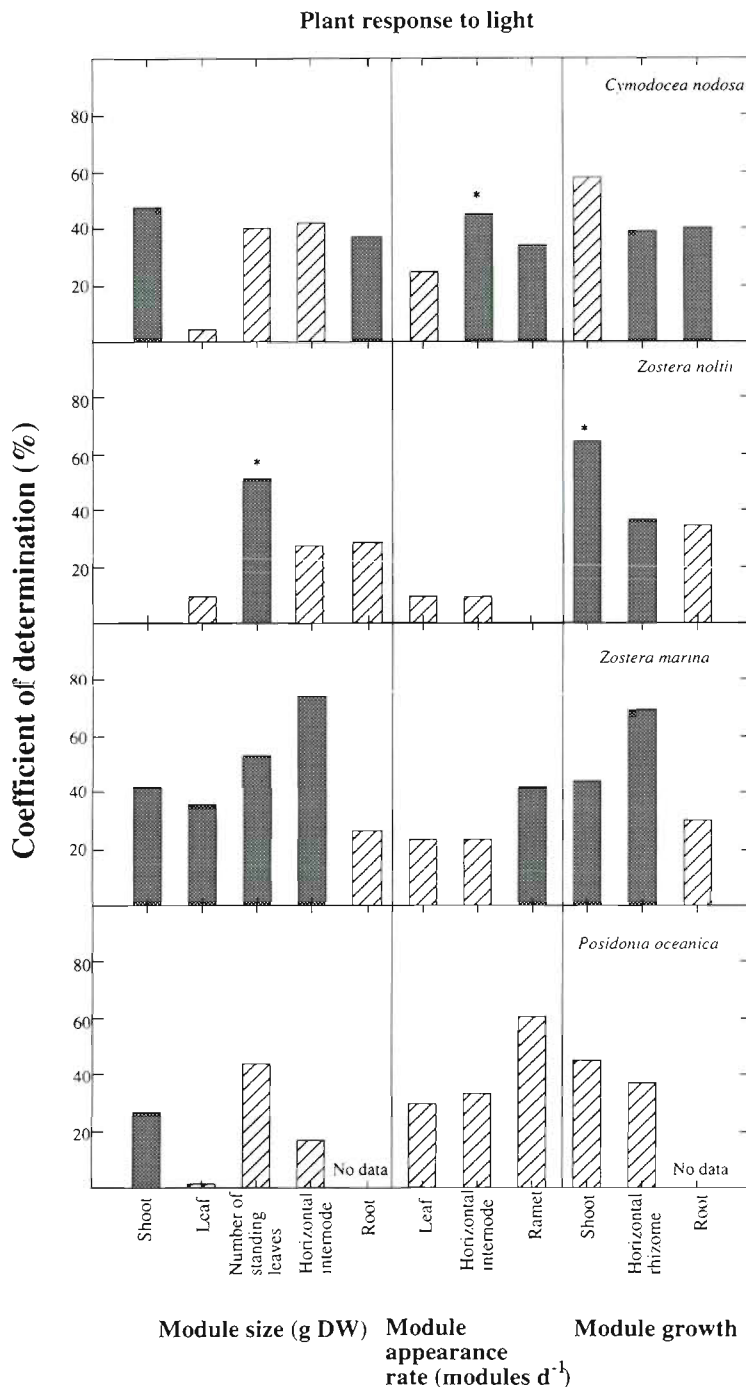


Fig. 6. Coefficients of determination for the relationships between seagrass module size, appearance rate and growth [units for leaf growth are $\text{cm shoot}^{-1} \text{d}^{-1}$, for rhizome growth $\text{cm (horizontal rhizome apex)}^{-1} \text{d}^{-1}$, and for root growth $\text{g DW (horizontal rhizome apex)}^{-1} \text{d}^{-1}$] and surface irradiance. Shaded bars indicate significant relationships ($p < 0.05$), hatched bars indicate non-significant ($p > 0.05$) relationships. *Relationship lagged by 1 mo

belowground modules was species-specific, with *Zostera marina* showing the greatest leaf growth, and *Cymodocea nodosa* the highest rhizome and root

growth rates (Fig. 8). *Posidonia oceanica* experienced the smallest variability in plant growth (Figs. 4 & 8). Seasonal variation in the leaf elongation rate in the shoots of all species followed the same pattern (Table 1), with the maximum growth occurring in summer and the minimum in winter (Fig. 8, Table 1), but delayed by 1 mo in *Z. noltii*. A similar pattern was observed in the horizontal rhizome elongation of *C. nodosa*, *Z. noltii* and *Z. marina*, though maximum elongation of *Z. noltii* occurred 1 mo earlier than in *C. nodosa* and *Z. marina* (Fig. 8, Table 1). Variability in rhizome elongation also induced changes in root production, with a similar seasonal pattern in these 3 species. Maximum rhizome elongation and root production were also reached 1 mo earlier in *Z. noltii* (Table 1). The rhizome elongation rate of *P. oceanica* was maximal during fall and minimal in spring (Fig. 8).

The patterns observed in seagrass growth, except that in *Posidonia oceanica*, closely correlated ($r > 0.70$, $p < 0.05$) with seasonal fluctuations in climate conditions. However, seagrass growth in one species (i.e. *Cymodocea nodosa*) was mainly correlated with temperature fluctuations, while others (i.e. *Zostera noltii* and *Z. marina*; Figs. 5 & 6) tracked the light variability more closely. Seasonality in root production was observed only in *C. nodosa* and it was strongly (60% of the variance) correlated to temperature (Fig. 5). The absence of substantial correlations between annual growth of *P. oceanica* and external forcing (i.e. light and temperature) suggests that the seasonality of this species is strongly constrained by internal factors.

DISCUSSION

The results demonstrate distinct seasonal growth patterns among the 4 seagrass species that occur in the NW Mediterranean, and the importance of species-specific responses to seasonal forcing. The significant correlations between the seasonal growth patterns of the different species (Table 1) demonstrate that environmental forcing imposes a general, and similar, trend of growth seasonality in species growing at the same site. Yet, the seasonal growth peaks displayed by seagrasses

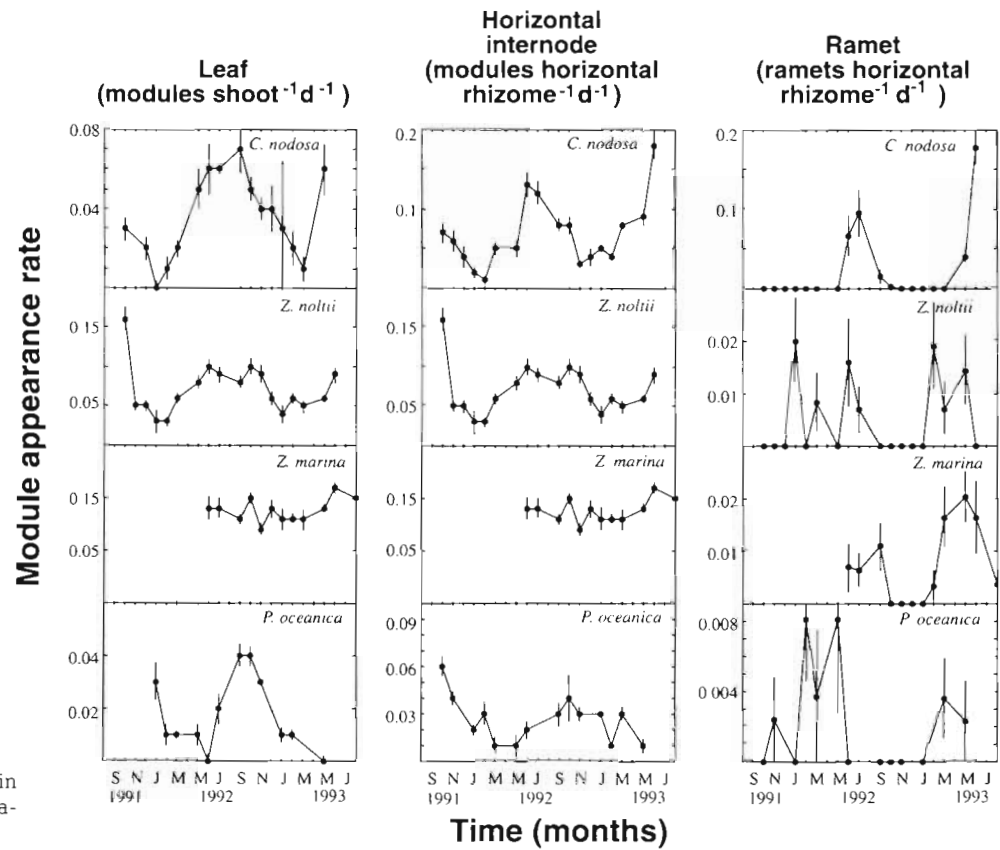


Fig. 7 Seasonal changes in the rate of appearance of seagrass modules

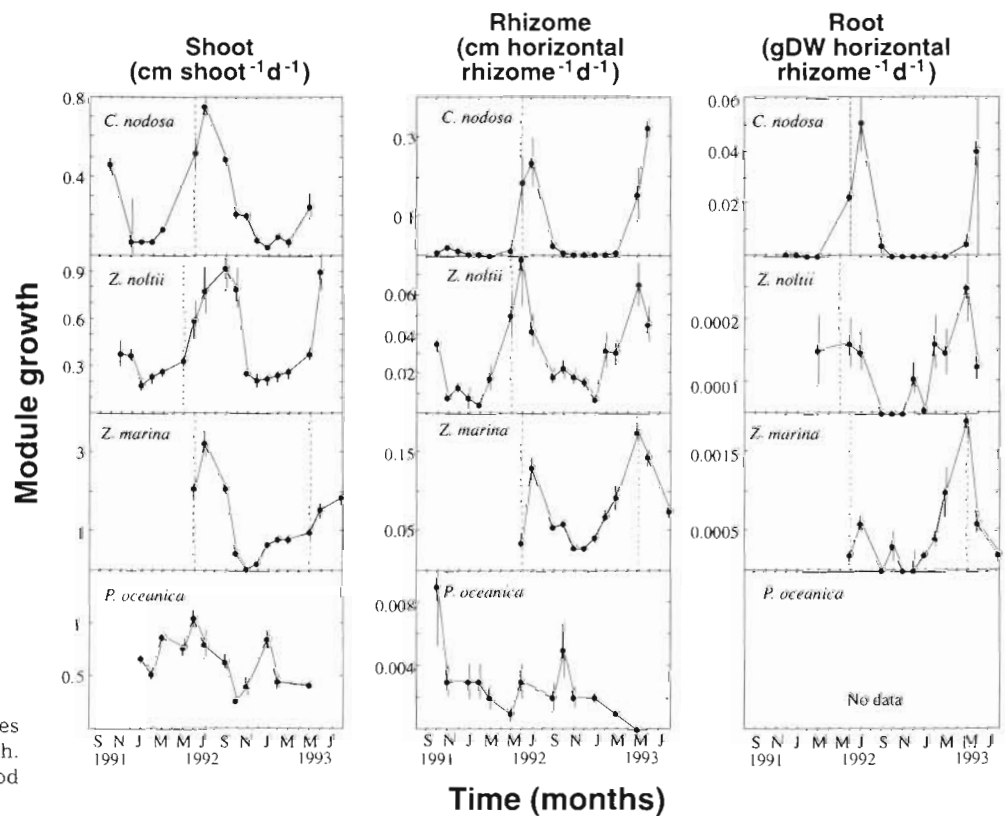


Fig. 8. Seasonal changes in seagrass module growth. Dashed lines indicate period of maximal flowering

differed by 1 to 2 mo when compared across species (Table 1). This finding, and the great species differences in the amplitude of seasonal growth fluctuations (Fig. 4), reveal an important intrinsic component of seagrass growth seasonality. Hence, climatic seasonality should largely determine the annual variability in seagrass seasonal growth dynamics, but the timing and the magnitude of plant responses should be species-dependent. The existence of species-specific responses of seagrasses to changes in seasonal forcing has been also observed in *Zostera marina* and *Ruppia maritima* coexisting in Chesapeake Bay, USA, where they displayed different physiological responses to changes in temperature and light (Evans et al. 1986). In addition, there is a local component of seagrass seasonality, not attributable to species-specific responses, which derives from local variability in resource availability (nutrients and dissolved inorganic carbon) and other local conditions (e.g. redox potential; Alcoverro et al. 1995).

The species most sensitive to seasonal fluctuations was *Cymodocea nodosa*. *C. nodosa* module size and growth were strongly coupled to climatic conditions, particularly temperature, while *Posidonia oceanica* was the species least responsive to seasonal fluctuations (Figs. 5 & 6). Hence, the growth pattern of *P. oceanica* was relatively independent of environmental conditions when compared to those of the other species examined, albeit it grew under slightly more uniform annual light and temperature conditions, due to the greater depth, than the other species. The seasonal growth patterns of *C. nodosa*, *P. oceanica*, and *Zostera noltii* were primarily associated with temperature changes while that of *Z. marina* was best related to the average irradiance (Figs. 5 & 6). The differential association of the seagrass species with light or temperature contributes to the moderate differences in their seasonal development. The specific sensitivity of seagrass growth to light and temperature observed here is in agreement with those observed for populations growing in other localities, supporting the idea of species-specific responses to seasonal light and temperature fluctuations. For instance, leaf growth seasonality in other *Z. marina* populations has been attributed to annual variability in insolation (Sand-Jensen 1975, Sand-Jensen & Borum 1983, Wium-Andersen & Borum 1984), and aboveground biomass seasonality in other *C. nodosa* Mediterranean meadows to fluctuations in temperature (e.g. Terrados 1991). Studies in other *P. oceanica* meadows also revealed little seasonality in plant growth (e.g. Wittman 1984, Buia et al. 1992), albeit somewhat related to temperature fluctuations (Pirc 1985, Romero 1985, Alcoverro et al. 1995). The strong sensitivity of *C. nodosa*, the species showing the greatest seasonal-

ity in module size and dynamics, to temperature may reflect the tropical origin of the genus *Cymodocea* compared to the temperate origin of the other taxa (cf. Phillips & Meñez 1988). The uniform growth of *Z. marina*, as indicated by quasi-constant (CV = 12.6%) leaf and rhizome plastochron intervals, contrasts with the large seasonality in these properties reported for stands in other geographic regions, and may reflect the less variable, warmer temperatures and higher irradiances received in the NW Mediterranean when compared to north temperate seas.

Seagrass response to climate changes may be constrained by the rate of addition of modules. The length of the plastochron interval (i.e. the time elapsed between the formation of 2 consecutive modules; Erickson & Michelini 1957), which is strongly species-specific (Duarte 1991), would limit the capacity of plants to respond to environmental variability. The short plastochron intervals (e.g. leaf plastochron interval = 14 d) of small seagrasses (e.g. *Zostera noltii*) allows a faster plant response to seasonal fluctuations than the long module plastochron intervals (e.g. leaf plastochron interval = 58 d) of large seagrasses (*Posidonia oceanica*). Similarly, the seasonality in module plastochron intervals exhibited by these seagrasses and other species growing elsewhere (e.g. West & Larkum 1979, Barber 1985, Brouns 1985) would lead to faster plant responses to climate changes in summer than in winter. The very long plastochron intervals of large seagrasses should effectively buffer seasonal environmental variability, leading to the limited seasonality observed for *P. oceanica* growth, and may uncouple seasonal growth patterns from environmental forcing.

The species-specific seasonal responses observed must reflect differences in the capacity to store resources and the extent of ramet integration among species, both processes being closely related to plant size. Seagrasses synthesise carbohydrates in excess during suitable high-light periods, and these are stored as starch in the rhizomes (e.g. Pirc 1985, Dawes & Guiry 1992) to be used later under low-light conditions (e.g. Ralph et al. 1992). The dynamics of this carbohydrate pool has been extensively demonstrated for clonal terrestrial plants, such as *Phragmites australis* (Granéli et al. 1992), *Rumex alpinus* (Klimes et al. 1993), *Clitonia borealis* (Ashmun et al. 1982) and *Fragaria chiloensis* (Alpert & Mooney 1986). The storage capacity of clonal plants is higher for large plants with thick and long-lived rhizomes than for small ones with thin and short-lived rhizomes (Ashmun et al. 1982). In addition, neighbour ramets within the clone can be integrated (Sarukhán & Harper 1973) allowing some ramets to use the resources stored by others (cf. Pitelka & Ashmun

1985, Libes & Boudouresque 1987, Tomasko & Dawes 1989). The capacity for clonal integration, which can vary with season and water depth (Tomasko & Dawes 1990), depends on the distance that resources must travel and on rhizome longevity (Pitelka & Ashmun 1985). Large plants have longer-lived rhizomes (Duarte 1991) and shorter rhizome internodes than small plants, and when rhizome connections persist during, at least, the life span of the shoots, they are able to transport photoassimilates further apart than small plants (Pitelka & Ashmun 1985). Hence, *Posidonia oceanica*, with thick (10 mm diameter, Duarte 1991) and long-lived (>12 yr, Duarte 1991) rhizomes, should be able to store and transport enough carbohydrates to allow the plant to support a growth pattern relatively independent of environmental conditions. *Cymodocea nodosa*, with thinner (3 mm, Duarte 1991) and perennial rhizomes (2.4 yr, Duarte 1991), should be able to store in its rhizomes the carbohydrates produced in excess during summer. These stored resources would increase (i.e. amplify) plant growth when the conditions for growth become favourable (in the spring). Similarly, the rhizomes of *Zostera marina* (3.5 mm, Duarte 1991) live for 1.5 yr (Duarte 1991) and should also allow for some storage of resources to amplify the plant response to seasonal variability under favourable growth conditions, as has been demonstrated for reeds (*Phragmites australis*, Granéli et al. 1992). Conversely, the thin (1.3 mm, Duarte 1991) and short-lived (<1 yr) rhizomes of *Z. noltii* should have a very limited storage of resources from one year to another. Growth of *Z. noltii*, therefore, should be coupled to seasonal or short-term time-scale resource variability, but it should not be able to amplify its response using stored resources. This postulated relationship between seagrass architecture and plant storage capacity closely agrees with the decreasing carbohydrate contents reported from *P. oceanica*, to *Z. marina*, *C. nodosa*, and *Z. noltii* rhizomes (Pirc 1985, 1989, Dawes & Guiry 1992).

Allocation of resources to sexual reproduction, indicated here by flowering, could also influence the seasonal growth patterns observed. The decline in seagrass leaf, rhizome and root growth occurs about 1 mo after flowering (cross correlation, $r > 0.6$ in all species; Fig. 8), when the plants are fruiting and temperature and irradiance are still rising (Fig. 2). This suggests production of flowers and fruits might involve a shift of resource allocation, probably nutrients from vegetative to reproductive structures resulting in a decrease in plant growth. However, seagrass inflorescences are green and they could supply some, or most, of the carbohydrate demand created by seed production (Harper 1977). The role of flowering and sexual reproduction as a factor causing seagrass seasonality has been

suggested for tropical seagrasses (e.g. Zieman 1975, Gallegos et al. 1992).

The different influence of seasonality on seagrass leaf or rhizome growth across species has important implications for the seasonal biomass development of seagrass meadows. Large seagrasses (*Posidonia oceanica*) experience seasonal fluctuations in shoot growth while smaller ones (*Cymodocea nodosa*, *Zostera marina* and *Z. noltii*) exhibit seasonal variability both in shoot and rhizome growth. Rhizome growth is closely related with shoot recruitment, because new shoots are produced at regular intervals along the rhizome (Tomlinson 1974, Duarte 1991). Thus, fluctuations in rhizome growth involve fluctuations in shoot density. This suggests the existence of species-specific differences in the seasonal dynamics of seagrass meadows which appear to reflect the basic architecture of seagrass species. Seasonal fluctuations in the aboveground biomass of small seagrasses should reflect changes in both shoot size and shoot density, whereas it should mainly reflect changes in shoot size in larger species. This hypothesis has been tested for *Z. marina*, a relatively large seagrass, where seasonal changes in standing biomass are mainly derived from changes in shoot size rather than in shoot density when the meadow has not been highly disturbed during winter or early spring (Olesen & Sand-Jensen 1994b). Because the cost of building rhizomes increases as the square of their diameter (Duarte 1991), small species with thin rhizomes can elongate their rhizomes and produce a substantial number of shoots every year at a much lower cost than large species with thick rhizomes, for which a seasonality of biomass based on changes in shoot density would be too resource-demanding to be sustainable. The limited contribution of changes in shoot density (i.e. rhizome growth) to the seasonality of biomass of species with thick rhizomes postulated here is also in agreement with the long plastochrone intervals (Fig. 7) and life span of their shoots (Duarte 1991). Thus, the relative importance of seasonal changes in shoot or rhizome growth of different seagrass species may be intimately linked to their basic architecture.

In summary, these results demonstrate that seagrass seasonality in temperate areas derives from both extrinsic forcing (e.g. light and temperature), and intrinsic components (e.g. resource allocation, reproduction). The extrinsic forcing, mainly constrained by the latitudinal position of seagrass communities, would impose a common seasonal pattern on sympatric species. However, the intrinsic component of seagrass seasonality, which is intimately linked to seagrass size, involves species-specific differences in their capacity to regulate the internal resource economy which may buffer, or amplify, the external seasonal forcing

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