

## Structure and growth dynamics of *Cymodocea nodosa* meadows\*

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**SUMMARY:** The seasonal changes in the structure and growth dynamics of a *Cymodocea nodosa* meadow off the island of Ischia (Tyrrhenian Sea) were studied from July 1988 to August 1989 using leaf and rhizome marking methods. High levels of leaf production ( $3.1 \text{ g dw m}^{-2} \text{ d}^{-1}$ ) significantly related to water temperature regimes, were observed. The number of new leaves per year (16 leaves  $\text{y}^{-1}$ ), the leaf Plastochrone Interval (23 days) and the life span of the single leaves (from 2 to 6 months) were also calculated. Relevant yearly fluctuations of the leaf canopy, representing about 20% of the total meadow biomass, testify the strong seasonal variability of leaf phenological parameters and shoot density (the latter, between  $925 \pm 323$  and  $1925 \pm 267$  shoots  $\cdot \text{m}^{-2}$ ). On the other hand, a constant and well developed layer of rhizomes and roots is present throughout the year (80% of total biomass), with an annual rhizome elongation of about 30 cm. In spite of the temporal variability of the above-ground compartment ( $\text{CV}=55\%$ ), the below-ground portion represents the conservative compartment of the meadow ( $\text{CV}=7\%$ ). Nevertheless, the remarkable number of seeds present in this meadow (up to  $2112 \text{ m}^{-2}$ ), does not seem to effect the stability of the system through the sexual reproduction. Although similar growth trends have been reported for *C. nodosa* meadows from different geographical areas and habitats (eutrophic zones, confined shallow waters, estuaries), remarkable differences may be found in the highest and lowest values of growth rate. This comparison highlights the ability of this species to grow in different habitats and that growth process seems to be amplified by a high influence of environmental constraints. Moreover, differences from *P. oceanica*, both in the growth rate and reproductive patterns, are identified in order to explain the dynamics of these vegetated systems and their role in the Mediterranean basin.

**Key words:** seagrasses, primary production, phenotypical plasticity, environmental variability, water temperature.

**RESUMEN:** DINÁMICA DE LA ESTRUCTURA Y CRECIMIENTO DE PRADERAS DE *CYMODOCEA NODOSA*. – Se estudiaron los cambios estacionales de la dinámica de la estructura y crecimiento de las praderas de *Cymodocea nodosa* fuera de la Isla de Ischia (Mar Tirreno) desde Julio 1988 a Agosto 1989 utilizando métodos de marcaje de hojas y rizomas. Se observaron elevados niveles de producción de hojas ( $3.1 \text{ g dw m}^{-2} \text{ d}^{-1}$ ) significativamente relacionados con el régimen de temperatura del agua. También se determinó el número de hojas nuevas por año (16 hojas  $\text{y}^{-1}$ ) el intervalo de plastocrono de la hoja (23 días) y el período de vida de las hojas (desde 2 a 6 meses). Las persistentes fluctuaciones anuales de la cobertura de hojas, que representan alrededor del 20% del total de la biomasa de la pradera, confirman la fuerte variabilidad estacional de los parámetros fenológicos de la hoja y la densidad de los tallos (entre  $925 \pm 323$  and  $1925 \pm 267$  tallos  $\cdot \text{m}^{-2}$ ). En cambio, una capa constante y bien desarrollada de rizomas y raíces está presente a lo largo del año (80% de la biomasa total), con una elongación anual del rizoma, alrededor de 30 cm. A pesar de la variabilidad temporal del compartimento de la parte superficial ( $\text{CV} = 55\%$ ), la porción de bajo tierra representa el compartimento conservativo de la pradera ( $\text{CV} = 7\%$ ). Sin embargo, el extraordinario número de semillas presentes en la pradera (hasta  $2112 \text{ m}^{-2}$ ) no parece reforzar la estabilidad del sistema a través de la reproducción sexual. Aunque patrones similares de crecimiento han sido descritos para praderas de *C. nodosa* en diferentes áreas geográficas y hábitats (zonas eutróficas, aguas someras confinadas, estuarios), se pueden encontrar notorias diferencias en los más elevados y más bajos valores de tasas de crecimiento. Esta comparación pone de manifiesto la habilidad de estas especies para crecer en distintos hábitats y que el proceso de crecimiento parece estar amplificado por la

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influencia de las condiciones ambientales. Además se han identificado diferencias con *P. oceánica*, en cuanto tasas de crecimiento y patrones reproductivos con el fin de explicar la dinámica de estos sistemas con vegetación y su papel en la cuenca Mediterránea.

*Palabras clave:* fanerógama marina, producción primaria, plasticidad fenotípica, variabilidad ambiental, temperatura del agua.

## INTRODUCTION

In the Mediterranean basin, seagrass meadows play a crucial role in coastal areas because of their high primary production and their support to the increasing biodiversity (Mazzella *et al.*, 1993) and food web complexity (Mazzella *et al.*, 1992; Buia *et al.*, 2000).

*Cymodocea nodosa* (Ucria) Aschers. is a common seagrass species throughout the Mediterranean and partly in the Mauritania region and the Algarve coasts, colonising also coastal areas of the Canary Islands (Den Hartog, 1970; Reyes *et al.*, 1995). Studies on *C. nodosa* growth in various Mediterranean areas (Terrados and Ros, 1992; Perez and Romero, 1992; Pérez *et al.*, 1994; Reyes *et al.*, 1995; Marbà *et al.*, 1996) have shown that this plant can colonise different types of environment, such as open coastal waters, coastal lagoons and estuaries, and form both monospecific and mixed stands, in association with other seagrasses such as *Posidonia oceanica* (L.) Delile and *Zostera noltii* Hornemann (Buia and Marzocchi, 1995).

Several papers have highlighted relevant differences between *C. nodosa* and *P. oceanica* in their growth strategies, such as the regular, year by year flowering and faster colonisation patterns in *C. nodosa*, vs. the irregular, stochastic flowering and slower growth rates in *P. oceanica* (Buia and Mazzella, 1991; Mazzella *et al.*, 1993; Pergent-Martini and Pergent, 1995; Marbà *et al.*, 1996). All these studies ascribed to *C. nodosa* a higher fitness to environmental variability and, in particular, a more direct response to variations in light, seasonal temperature fluctuations and nutrient load (Caye and Meinesz, 1986; Marbà *et al.*, 1996), providing further support to the classical ecological theory of *C. nodosa* as a coloniser species and *P. oceanica* as a climax species (Molinier and Picard, 1952; Den Hartog, 1970).

The well-known decline of *P. oceanica* meadows in some areas of the Mediterranean (Blanc and Jeudy De Grissac, 1984; Péres, 1984; Pergent-Martini, 1994) has fostered scientific interest in the capacity of *C. nodosa* to replace the former species

in some coastal areas (Tocaceli, 1990). In spite of its different degree of complexity in terms of plant size, meadow architecture and associated animal community (Mazzella *et al.*, 1993; Marbà *et al.*, 1996), *C. nodosa* might also play a comparable, but minor, relevant role as a structuring species (Barbault *et al.*, 1991). Whereas many studies have been carried out on *P. oceanica*, from both structural and functional points of view, less attention has been devoted to *C. nodosa*.

The aim of this research was to characterise the annual growth dynamics of *C. nodosa* and the seasonal changes in the parameters of the meadow structure, in order to evaluate its temporal variability. In addition, a comparison with literature data on meadows from different geographical areas and habitats (eutrophic zones, confined shallow waters, estuaries) was carried out to provide basic knowledge of its adaptive plasticity and successful colonisation in different coastal areas.

## METHODS

The *C. nodosa* meadow was located at Punta San Pietro Bay, on the north-east coast of the island of Ischia (Bay of Naples) (40°44'N, 13°56'E), in correspondence with the artificial reefs which favoured its settlement, thus protecting the meadow from marine currents and wave action. It extended from 0.5 to 5 metres in depth and covered a total area of about 3,400 m<sup>2</sup>; it mixed with patches of *Z. noltii*; they formed, with the trapped sediments, a well-developed rhizosphere of about 30 cm thickness on which the prairie was settled. (Buia *et al.*, 1985). Monthly sampling were taken from July 1988 to August 1989 at 4 m depth; they were performed every two weeks in the spring period, due to the increase in the plant growth rate.

To estimate the dynamic pattern of the meadow, the shoot density of *C. nodosa* and *Z. noltii* was measured in plots of 20x20 cm (4 replicates at each sampling event); 20 shoots of *C. nodosa* were marked monthly 1 cm above the sheath of the oldest leaf (Zieman, 1974) to estimate its leaf production; in the

laboratory, the newly formed tissue was measured by the shift of the marking hole along each leaf.

The plant biomass (above- and below-ground compartments) was furthermore estimated by using a metal cylinder 15 cm in diameter. In the laboratory, shoots, rhizomes and roots were separated; numbers of seeds, flowers, fruits and seedlings in the corers were also recorded.

The number of leaves, and their length and width were measured for each shoot and divided in two age classes: differentiated leaves (with sheath) and undifferentiated leaves (without sheath). In addition, shoots (previously incubated for one hour in 2% acetic acid to remove the epiphytes), rhizomes and roots were then weighed at 60°C until constant weight (Mazzella and Ott, 1984).

Every three months 5 plagiotropic rhizomes were tagged (with a plastic string before the last rhizome node) and they were collected three months later. Their length increase (mm day<sup>-1</sup>) was measured to estimate seasonal rhizome growth.

The number of new leaves produced per year and the leaf Plastochrone Interval (PI) (Duarte, 1991) were also calculated.

The leaf life span was derived from the formulation of a spreadsheet in which each leaf, numbered according to its position in the shoot, was monitored monthly, taking into account both the mean number of leaves for each month and that of new leaves which appeared in the same period.

Some environmental parameters (temperature and irradiance) were tracked monthly, in order to identify physical constraints influencing plant growth. Water temperature was measured at the meadow with a reversing thermometer; quantum irradiance in the Photosynthetically Active Radiation (PAR) band was measured just below the water surface, above and below the leaf canopy, by means of a quantameter (Biospherical Mod.QSI-140B), at noon and in calm surface conditions. The attenuation coefficient of PAR ( $k_{PAR}$ ) was estimated using the following equation:

$$k_{PAR} = \ln(I_0/I_A)/z$$

where  $z$  is depth,  $I_0$  is subsurface irradiance and  $I_A$  is above-canopy irradiance.

Monthly data, collected over the year, were statistically analysed for each variable. The homogeneity of variance was checked by Bartlett's test. When the variance was homogeneous, One-Way ANOVA analysis was used to test the significance of differ-

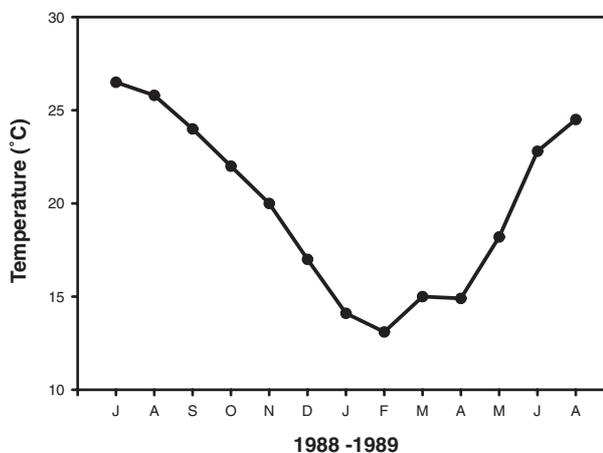


Fig. 1. – The annual trend of water temperature at the depth of the sampling site (-4 m).

ences among samples. The Kruskal-Wallis test was applied when the variance was not homogeneous. Regression analyses were carried out between plant production data and environmental parameters.

## RESULTS

### Environmental parameters

The annual trend of water temperature at the depth of the sampling site (-4 m) showed the typical seasonal variations in the Mediterranean Sea, with the maximum value in July (26.5°) and the minimum in February (13.1°) (Fig. 1).

The attenuation coefficient of Photosynthetically Active Radiation ( $K_{PAR}$ ), calculated for the water column above the canopy, varied from 0.13 (in July) to 0.27 (in November), with an average annual value of  $0.19 \pm 0.042$  (Fig. 2).

Maximum attenuation of PAR was recorded in summer (87.07%), when the leaf canopy was at its peak, illustrating the influence of the canopy structure on light penetration (Fig. 2).

### Meadow structure

The mean annual density of the *C. nodosa* shoots was  $1301 \pm 322$  shoots m<sup>-2</sup>, whereas that of *Z. noltii* was  $305 \pm 197$  shoots m<sup>-2</sup> (Fig. 3). Significant seasonal variations in the number of *C. nodosa* shoots were recorded, with the lowest values in winter ( $925 \pm 323$  shoots m<sup>-2</sup>) and the highest ones in summer ( $1925 \pm 267$  shoots m<sup>-2</sup>).

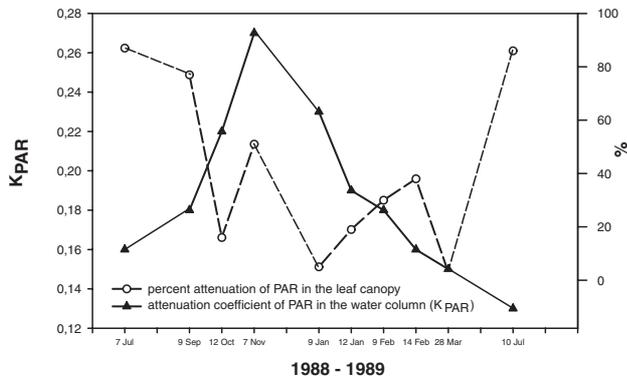


FIG. 2. – The annual trends of the attenuation of coefficient PAR in the water column and of the percent attenuation of PAR in the leaf canopy.

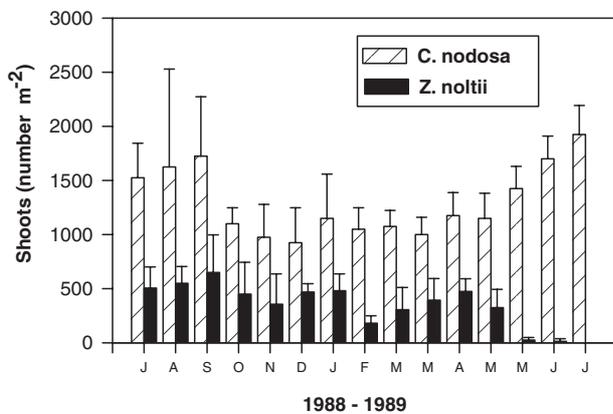


FIG. 3. – Annual variation of shoot density of *C. nodosa* and *Z. noltii* in the mixed bed off San Pietro (Ischia, Gulf of Naples). Two measurements are shown for March and May, due to the increased growth rate during the spring period.

The mean number of *C. nodosa* fruits recorded during the spring-summer season 1988 was  $57 \pm 32$   $m^{-2}$ , while the number of seedlings growing in the next season (1989) after eight months of dormancy was only  $21 \pm 14$   $m^{-2}$ , corresponding to about 37%

TABLE 1. – Fruits, seeds and seedlings densities in the *C. nodosa* meadow of Ischia.

Date	Fruits (number $m^{-2}$ )	Seeds (number $m^{-2}$ )	Seedlings (number $m^{-2}$ )
July 1988	28	824	28
August	57	1222	19
September	85	1042	0
October	57	1070	0
November	0	1326	0
December	0	1061	0
January 1989	0	1752	0
February	0	2112	0
March	0	1468	0
April	0	1439	0
May	0	947	9
June	0	1420	28
July	0	1922	38
August	57	1989	9

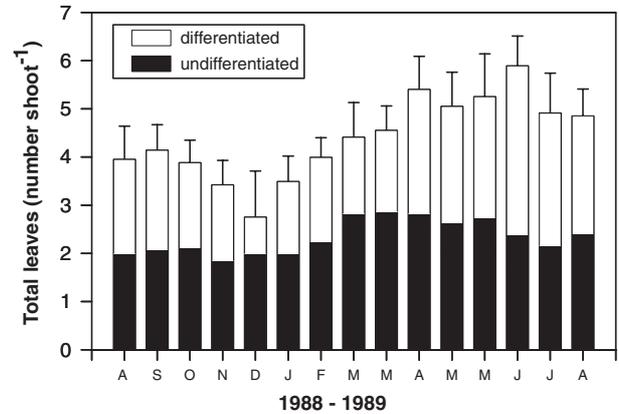


FIG. 4. – Annual pattern of the mean leaf number per shoot of *C. nodosa*, in the different ranks (standard deviations are related to the total mean number of the leaves in the shoot).

(Table 1). The remaining 63% of ungerminated seeds justified the high number of seeds recorded in the sediment all around the year ( $1399 \pm 410$ ).

Comparing the variations in shoot density and the number of seedlings germinated during spring 1989, the contribution of sexual reproduction to the dynamics of this meadow varied between 3.3% (May) and 17% (July).

### Leaf phenology and dynamics

In a year, the total mean number of leaves per shoot was  $4 \pm 0.6$ , showing a seasonal pattern, with the highest values in June ( $6.0 \pm 0.6$ ) and the lowest in December ( $3.0 \pm 0.9$ ) (Fig. 4). The number of the two leaf ranks fluctuated seasonally with the maximum values in spring for the undifferentiated leaves and in summer for the others (Fig. 4).

The monthly mean lengths of both differentiated (sheath included) and undifferentiated leaves showed maximum values in summer ( $40.3 \pm 12.2$  cm and  $17.0 \pm 6.7$  cm respectively), whereas the minimum was recorded in December ( $7.0 \pm 1.3$  cm) for the former, and in March ( $5.8 \pm 0.7$  cm) for the latter (Fig. 5). In addition to the seasonal variability in the leaf dynamics, it was also evident that an inter-annual variability occurred in the maximum length of differentiated leaves, with lower values in the second year (Fig. 5).

The mean width of the differentiated and undifferentiated leaves showed a definite seasonal trend, with maximum values in August ( $3.6 \pm 0.4$  and  $2.9 \pm 0.3$  mm respectively) (Fig. 6). A significant difference was found between the two leaf ranks (K-W test = 31.16;  $P < 0.001$ ).

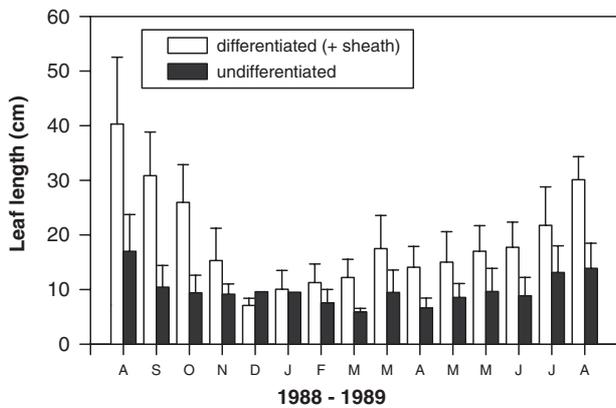


FIG. 5. – Annual trend of the length of the leaves (sheath included)

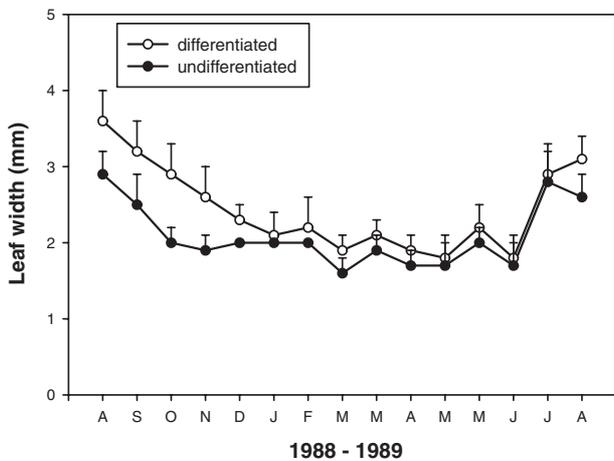


FIG. 6. – Annual trend of the width of leaves in the different ranks.

## Biomass

Total leaf biomass per shoot including sheaths showed a maximum value in August ( $101.4 \pm 0.02$  mg dw shoot<sup>-1</sup>) and a minimum in December ( $25.1 \pm 0.06$  mg dw shoot<sup>-1</sup>) (Fig. 7). In particular, the biomass of new tissue showed maximum values in September ( $54 \pm 0.05$  mg dw shoot<sup>-1</sup>), whereas that of old tissue showed the maximum in August ( $44.5 \pm 0.09$  mg dw shoot<sup>-1</sup>). On the other hand, the biomass values of sheaths were slightly higher in spring than in other seasons ( $32.9 \pm 0.05$  mg dw shoot<sup>-1</sup> in March) (Fig. 7).

A significant seasonal difference of biomass allocated in below- and above-ground compartments was found ( $F = 166.6$ ;  $P < 0.001$ ) (Fig. 8). In spite of the temporal variability of the above-ground compartment ( $CV=55\%$ ), the below-ground portion represented the conservative compartment of the meadow ( $CV=7\%$ ). However, all year round, the below-

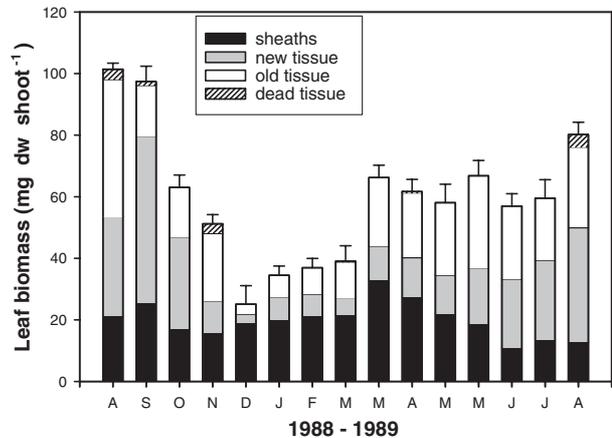


FIG. 7. – Leaf biomass partitioning (standard deviations are related to the total mean leaf biomass).

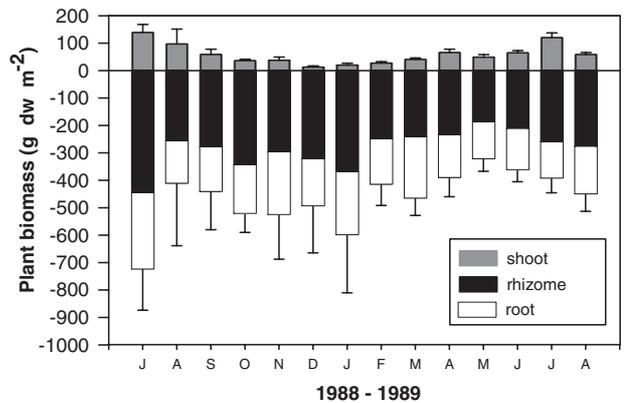


FIG. 8. – Annual variation of above- and below-ground biomass compartments.

ground biomass represented about 80% of total biomass, with the highest values in autumn-winter, in contrast to those of leaf standing crop, reaching its minimum in winter ( $17$  g dw m<sup>-2</sup>) (Fig. 8). In addition, the rhizome-root ratio, quite constant all over the year, was about 61%.

TABLE 2. – Life span of the leaves in the different months.

Month of leaf appearing on the shoot	Mean life span (days)
January	162
February	112
March	103
April	91
May	63
June	104
July	109
August	135
September	123
October	168
November	
December	152

TABLE 3. – Comparison of *C. nodosa* meadows of the Mediterranean Sea.

	GULF OF TRIESTE Peduzzi and Vukovic, 1990			MAR MENOR Terrados and Ros, 1992			ALFACS BAY Perez <i>et al.</i> , 1994	CANARIE Reyes <i>et al.</i> , 1995			ISCHIA present paper		
	min	mean	max	min	mean	max	mean	min	mean	max	min	mean	max
Shoots Density (number m <sup>-2</sup> )	546		2158	1000		1900	1594	934		1928	925		1925
Leaves (number shoot <sup>-1</sup> )		3		2		4	3	2		3	1		4
Leaf Standing Crop (g dw m <sup>-2</sup> )	147		323	5		50	330	55		250	17		159
New Leaves (number month <sup>-1</sup> ) (number year <sup>-1</sup> )		10		0	12	2	1.5 18	1	13	2	1	16	2
Leaf production (g dw m <sup>-2</sup> day <sup>-1</sup> ) (g dw m <sup>-2</sup> year <sup>-1</sup> ) (g C m <sup>-2</sup> day <sup>-1</sup> )	0	473.4	3.4	0.2	164	1.5	1.4	0.9	752	3.6	0.31	412	3.1
Rhizome Production (mm day <sup>-1</sup> ) (g dw m <sup>-2</sup> y <sup>-1</sup> )		33.6		0.05	48	4.65		30	37		0.1		1.9
Leaf Life Span (day)							55				62		167
Plastochrone Interval (day)				32				28			23		

## Production

The life span of single leaves varied between two and six months over the year, according to the period in which they appeared on the shoot (Table 2). The leaves appearing in autumn-winter months had a life span of between 111 and 167 days, as well as by the lowest leaf length; but those appearing in the spring had the shortest life span (62 days) (Table 3). Furthermore, the leaves appearing in summer had a life span of between 103 and 134 days, together with the highest length.

The annual number of leaves produced per shoot was 16, with a monthly maximum production of 2 leaves in the summer time. The mean annual leaf Plastochrone Interval was 23 days.

Total daily leaf elongation was very high in summer (70 mm<sup>2</sup> shoot d<sup>-1</sup>, in August) when compared with that during the rest of the year (Fig. 9). The growth trend of the undifferentiated leaves showed a more rapid decrease in autumn than differentiated ones, whereas they showed an earlier increase in spring.

The daily production of new leaf tissue per square metre showed a unimodal annual trend (Fig. 10). The highest production values were found in summer, with a peak in August (3.1 gDW m<sup>-2</sup> d<sup>-1</sup>),

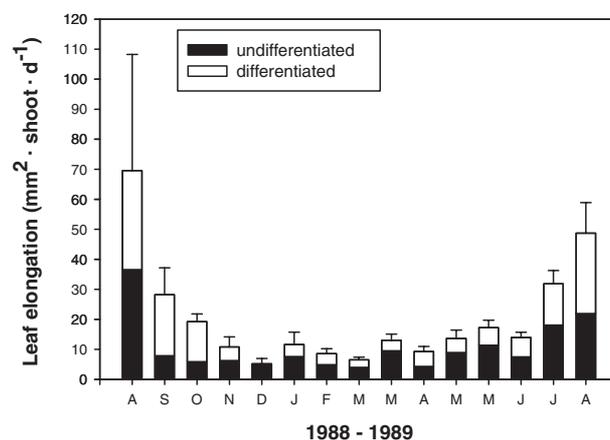


FIG. 9. – Annual pattern of daily leaf growth for leaves of different age class (standard deviations are related to the total mean leaf elongation).

followed by a rapid decrease in autumn; the lowest values were recorded in winter (0.1 g dw m<sup>-2</sup> d<sup>-1</sup>), with a gradually increasing trend in spring (Fig. 10).

New leaf tissue production per shoot was significantly correlated to differentiated leaf elongation ( $R^2 = 77.9$ ;  $P < 0.001$ ) and to its mean lengths ( $R^2 = 73.9$ ;  $P < 0.001$ ).

Significant correlations were found between monthly leaf production per shoot and environmental parameters: seasonal temperature ( $R^2 = 76.4$ ;  $P <$

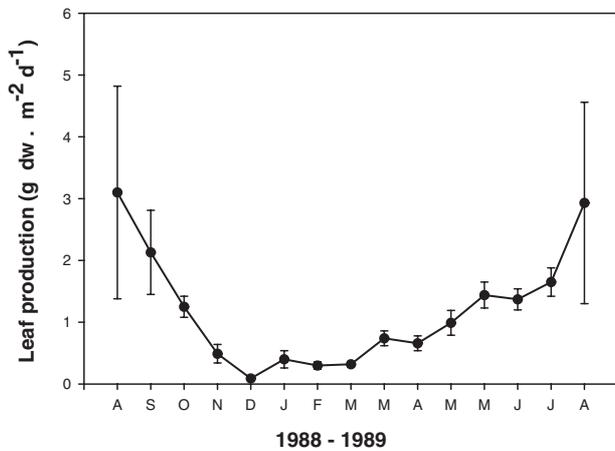


FIG. 10. – Annual pattern of daily leaf production.

0.001) and percent attenuation of PAR in the leaf canopy ( $R^2= 58.9$ ;  $P=0.02$ )

As regards the daily rhizome production, the lowest rates were shown in winter (0.10 mm d<sup>-1</sup> and 0.2 mg d<sup>-1</sup>) and the highest in summer (1.85 mm d<sup>-1</sup> and 2.49 mg d<sup>-1</sup>) (Fig. 11). Their mean values were respectively 0.89 mm d<sup>-1</sup>, and 1.05 mg d<sup>-1</sup> with an annual growth rate of 32.5 cm and 381.3 mg rhizome apex<sup>-1</sup>.

## DISCUSSION

The present work identified high levels of primary production in a *C. nodosa* meadow off the island of Ischia and wide temporal variations in its growth dynamics. The marked differences recorded in both shoot density and primary production explain the peculiar changes found in meadow structure and in plant biomass throughout the year.

Shoot density ranges widely within one order of magnitude from winter to summer values, mostly depending on the annual rate of vegetative propagation. On the other hand, seed germination, even recurring annually in *C. nodosa* meadows (Buia and Mazzella, 1991; Mazzella *et al.*, 1993; Terrados, 1993), does not seem to contribute significantly to the successful recruitment of new shoots in the dynamic process of this meadow, as testified by the high number of ungerminated seeds and by the low percentage of new shoots obtained by sexual reproduction.

What conditions the leaf canopy is the wide seasonal variation in phenological parameters (number of leaves, leaf length, leaf width and biomass), with peaks in summer and very low growth rates in winter.

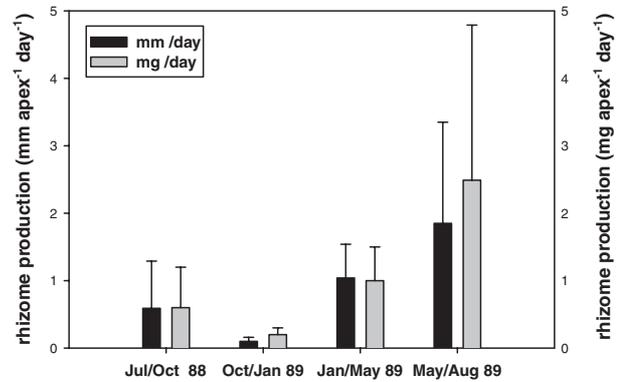


FIG. 11. – Annual pattern of daily rhizome production.

The below-ground system looks more stable when compared to the leaf canopy. Biomass partitioning clearly shows the highest allocations in rhizomes and roots all year round. The rhizomes and root standing crop do not show any variability; nevertheless, relevant differences are observed in the summer-winter comparison of rhizome growth rates. Indeed, the fast rhizome elongation rate and increase in shoot density during spring-summer and the maintenance of similar rhizome biomass could indicate a fast replacement of rhizome biomass during some periods of the year. Therefore, in spite of the high temporal variability of its leaf canopy, the *C. nodosa* meadow is characterised by a well-developed layer of rhizomes and roots, which represents the true conservative compartment of this system.

The low number of seedlings related to the conspicuous number of seeds recorded throughout the year has just been recorded by different authors, testifying the role of vegetative propagation in the dynamics of seagrass systems, without distinction among seagrass species (Duarte and Sand-Jensen, 1990; Olesen, 1999). The high quantity of seeds present in the sediment does not seem to contribute large seed banks, even though they are much larger than in other places; on the contrary, it could be related to the presence of the well developed rhizosphere, that can play an important role in trapping seeds, avoiding their transport by water movements outside the prairie. Furthermore, the quantity of seeds is not due to differences in seed dormancy, as in Ischia populations are of 8 months (Pirc *et al.*, 1985) which is similar to those reported by other authors (Caye and Meinesz, 1986; Reyes *et al.*, 1995).

The seasonal patterns in shoot features show significant correlations with the environmental levels and parameters. In particular, positive correlations

between temperature, light and growth dynamics of *C. nodosa* have also been found by other authors (Perez and Romero 1992; Marbà *et al.*, 1996). Our results lead to the hypothesis that in *C. nodosa*, more than in other seagrasses, primary production can be largely modulated by local environmental conditions, as well as by flowering and germination (Buia and Mazzella, 1991).

All these data are consistent with studies carried out on *C. nodosa* meadows of other geographical areas, both in open coastal waters (Mediterranean, Atlantic; in Peduzzi and Vukovic, 1990; Reyes *et al.*, 1995) and in confined meadows (coastal lagoons or estuaries) (in Terrados and Ros, 1992; Perez *et al.*, 1994), under different environmental conditions (oligotrophic waters, estuaries, eutrophic zones) (Table 3).

Although similar trends are detectable among various Mediterranean sites, differences can be found in the maximum and/or minimum values of several plant parameters (Table 3). The greatest differences between different sites are related to leaf standing crop (L.S.C.) and leaf primary production, whereas shoot density and leaf number per shoot show the smallest differences (Table 3). The highest level of leaf production is recorded in the *C. nodosa* meadow of the Canary Islands ( $752 \text{ g dw m}^{-2} \text{ y}^{-1}$ ) and the lowest in the Mar Menor ( $164 \text{ g dw m}^{-2} \text{ y}^{-1}$ ), where the L.S.C. is also very low (between 5 and  $50 \text{ g dw m}^{-2}$ ). It is worth noting that at the Canary Islands site, the annual range of water temperature is smaller ( $18.5\text{--}24.5^\circ\text{C}$ ; in Reyes *et al.*, 1995) when compared to that recorded in the Mar Menor ( $12\text{--}30^\circ\text{C}$ ; in Terrados and Ros, 1992). Therefore, these differences in leaf production would be due to the length of the growing season, according to the latitude (Duarte, 1989). In the Canary Islands *C. nodosa* probably grows at fast rates for longer periods than it does in the northern Mediterranean.

Factors other than water temperature and light may certainly affect the growth and structure of *C. nodosa* meadows (i.e. nutrient load, water hydrodynamic force and competition with other seagrass species). The very high values of L.S.C. and new leaves per year recorded in Alfacs Bay (Ebro Delta, Spain) (Table 3) could be directly related to the high concentrations of nutrients (N and P) found in this estuarine area (Perez *et al.*, 1994).

The variation of all these meadow parameters can be seen as a phenotypical plasticity of this plant, which responds differently to environmental constraints.

It is impossible, at the moment, to assess to what extent this phenotypical variability is supported by

genotypic differences. In fact, the only studies carried out up to now on this topic illustrate a high genetic variability in *C. nodosa* populations settled in Mediterranean marine coastal areas (Ischia, Procaccini and Mazzella, 1996) but, on the other hand, a high genetic homogeneity in the North Atlantic lagoon (Ria Formosa, Alberto *et al.*, 2001). Studies will be necessary to analyse the role exerted by local conditions (geographic isolation) in determining the degree of gene flow. High genetic diversity in the Ischia population may be explained, at least in part, by the germination success, as compared to other data (Hemminga and Duarte, 2000).

When *C. nodosa* and *P. oceanica* are compared in their structural, phenological and growth parameters, differences in their strategy can be identified. If we compare leaf growth of *C. nodosa* with that of *P. oceanica*, the higher value of specific growth rate of the former is accompanied by shorter leaf life span (up to 4.7%; between 2 and 6 months) against those of the latter (1.5%; between 6 and 10 months) (Mazzella *et al.*, 1993, Zupo *et al.*, 1997). The short life span could be a factor which can explain the wide seasonality of the leaf canopy of *C. nodosa*. In particular, temperature and light represent modulating factors of the growth pattern at different temporal scales, seasonal in *P. oceanica* and monthly in *C. nodosa*, which is consistent with their different metabolic growth rate.

In both species, below-ground portions account for the highest biomass throughout the year, even if the dynamics is higher in *C. nodosa*. The differences between these two species are reflected in strategies of structuring capacity with respect to the system. *P. oceanica* appears to be a biomass storer in which a key role is played by storage compartments located in the below-ground portions, whereas in *C. nodosa* a more even partitioning of resources occurs between above and below compartments (Guidetti *et al.*, 2001)

To conclude, all growth features identified in this plant lead to the opinion that *C. nodosa* is a plastic species with a high capacity to adapt to environmental variability. This phenotypical plasticity plays a crucial role in the colonisation of new substrates and it may explain how *C. nodosa* refills the areas where environmental conditions are unfavourable for *P. oceanica* (Pergent-Martini, 1994). In these environments, at smaller scale, *C. nodosa* may play the same role of a structural species that is characteristic of *P. oceanica* in the whole Mediterranean basin.

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