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Aquatic Botany 76 (2003) 185–193

**Aquatic
botany**

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Growth and primary production of *Cymodocea nodosa* in a coastal lagoon

Sylvia Agostini^{a,b,*}, Gérard Pergent^c, Bernard Marchand^a

^a Mediterranean Ecosystems Laboratory, University of Corsica, BP 52, 20250 Corte, France

^b Office de l'Environnement de la Corse, Avenue Jean Nicoli, 20250 Corte, France

^c Equip "Écosystèmes Littoraux", University of Corsica, BP 52, 20250 Corte, France

Received 11 June 2002; received in revised form 12 January 2003; accepted 13 January 2003

Abstract

Cymodocea nodosa meadows within the Urbinu lagoon showed unimodal growth during an annual cycle (1998–1999), reaching maximum development in summer, minimal development in winter, and a particularly active phase in spring. The below-ground biomass (446 g dry wt. m⁻²) was higher than the above-ground biomass (332 g dry wt. m⁻²). Leaf production was 2058 g dry wt. m⁻² per year (844 g C m⁻² per year), rhizome production was 412 g dry wt. m⁻² per year (144 g C m⁻² per year) and the production/biomass ratio (P/B) was 3.2 per year. These meadows have high total biomass (778 g dry wt. m⁻²) and vegetative production (2470 g dry wt. m⁻² per year), with the largest total primary production recorded to date. These parameters are higher than those generally observed for the same seagrass species within other Mediterranean lagoonal and marine environments.

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Keywords: Seagrass; Mediterranean lagoon; Density; Biomass; Primary production; *Cymodocea nodosa*

1. Introduction

Although *Cymodocea nodosa* (Ucria) Ascherson is widely distributed throughout the Mediterranean (Den Hartog, 1970), studies on the vegetative development of this seagrass are scarce. The general plant morphology was described by Borner (1864) under the name *Phucagrostis major* Cavolini. Data on the growth and production of *C. nodosa* have been obtained from various areas of the Mediterranean coast: (i) from marine environment by Gessner and Hammer (1960) and Caye and Meinesz (1985; their observations

* Corresponding author. Tel.: +33-4-9545-0075.

E-mail address: agostini@univ-corse.fr (S. Agostini).

revealed seasonality in rhizome growth, but leaf development was poorly assessed) on the French coasts, by Peduzzi and Vukovic (1990) in the Gulf of Trieste (Italy) and by Duarte and Chiscano (1999) in the Mediterranean Sea; (ii) from a lagoonal environment by Pérez (1989) in the Ebro River delta, by Terrados and Ros (1992) in the Mar Menor, Reyes et al. (1995) in El Medano on the Spanish coasts and by Rismondo et al. (1997) in the lagoon of Venice (Italy). To our knowledge, the effect of seasonal changes on the growth and production of *C. nodosa* meadows in lagoons has not been studied so far.

Generally found in the Mediterranean, this protected seagrass is seldom indexed in lagoonal environment in Europe. With a major ecological interest (Ferguson et al., 1980; Phillips, 1984; Denninson et al., 1993; Dawes et al., 1995; Warwick and Clarke, 1996), it develops mainly in an Urbinu Mediterranean lagoon (eastern coast of Corsica; Agostini et al., 2003). The aim of this paper was to closely monitor the development and the vitality of this particular meadow (data on density, biomass and primary production during the annual cycle 1998–1999), to define its behaviour in this lagoonal environment.

2. Materials and methods

2.1. Study area and shoot density

All sampling and in situ measurements were conducted in the Urbinu lagoon, a 135 km² coastal lagoon located off the coast of Corsica in the Northern Mediterranean Sea (9°28'97"E longitude, 42°02'56"N latitude). Its maximum depth is approximately 10 m, water salinity varies between 26 and 44‰ (depending on the season) and water temperature ranges from 6 °C in February to 30 °C in August. At the sampling site, *C. nodosa* grows in dense monospecific beds, at a depth of 1 m. This station was marked with concrete blocks and was considered to be representative of the whole area (Agostini et al., 2003).

Meadow shoot density was estimated in situ, each month during 1998 and 1999 from shoot counts in 10 quadrats (40 cm × 40 cm each). These quadrats were launched at random, from 1 m high.

2.2. Biomass

Sampling was conducted about every month from July 1998 to July 1999 by scuba diving. Four cores were extracted randomly from the meadow using a thin-walled, serrated, stainless steel core tube (15 cm diameter) inserted to a depth of 30 cm (i.e. maximum root length). All plant material was washed with seawater in a 1.5 mm mesh sieve to remove sediments and temporarily stored in labeled plastic bags in a refrigerator (<6 °C) until processing. For biomass determination, leaves, rhizomes and roots were separated and rinsed with tap water to remove the salts. Leaves were dissected following Giraud (1979): (i) stripped from each shoot in distichous order of insertion and (ii) separated into the various categories (adult, intermediate or juvenile leaves). Live roots and rhizomes were separated from dead macro-organic matter, which was excluded from all measurements. Throughout most of

the study period, the leaves had attacked epiphytes which were easily removed by scraping (Kemp et al., 1987). The material was dried at 75 °C to constant weight to determine the dry weight of each fraction.

2.3. Primary production

All primary production estimates were based on vegetative growth only, since sexual production was never detected during this study in the investigated area.

Leaf production (or above-ground production) was measured monthly (from July 1998 to July 1999) in situ (using four permanent quadrats of 40 cm × 40 cm each), by perforating all leaves in a shoot just above the bundle sheath with a needle (Zieman, 1974; Pérez and Romero, 1994). Owing to the constant length of older leaves (Hamburg and Homann, 1986; Peduzzi and Vukovic, 1990), the hole in the outermost, oldest leaf was used as a reference. After 1 month, the shoots were harvested, leaves were classified as “mature” (leaves with hole), “new” (mature leaves without hole) or “young” leaves (shorter than the bundle sheath of mature leaves) and the segments of new growth were removed (including new leaves), rinsed, dried and weighed. Leaf growth was calculated according to the number of new leaves appearing on the marked shoots during the observation period (Jacobs, 1979). Bundles without a clearly identifiable reference leaf were excluded. Seasonal leaf net production (g dry wt. m⁻²) was calculated as the mean leaf production per shoot multiplied by the mean shoot density of the respective season.

Rhizome and root production (or below-ground production) was estimated according to the differences between the maximal and minimal biomass recorded during the year studied, as described by De la Cruz and Hackney (1977), which allowed us to evaluate the total below-ground production and the below-ground production for various tissues (rhizomes and roots).

To estimate the primary production in grams of carbon, *carbon analysis* was carried out on the plant to define the conversion factors of vegetal dry weight into carbon. Various tissues (leaves, rhizomes and roots) were dehydrated in a drying oven (at 60 °C during 48 h), and ground to a fine powder to determine their carbon contents using a CHN autoanalyser (CHN PE 2400 Analyzer, Perkin-Elmer®). We found a conversion factor of 41% for leaves and 35.3% for roots and rhizomes.

3. Results

3.1. Density

Shoot density showed a regular seasonal fluctuation. The mean annual value of density was 1118 shoots m⁻², peaked in summer (1520 shoots m⁻²) and decreased in winter (757 shoots m⁻²; Fig. 1). New shoots appeared faster than they disappeared: within only 3 months (April–June), the cycle passed from its lowest to its highest density, while it needed 9 months (July–March) to achieve the opposite process. Densities recorded in winter presented certain stability with 710.2 shoots m⁻² over January, 738.6 shoots m⁻² in December and 823.9 shoots m⁻² in February.

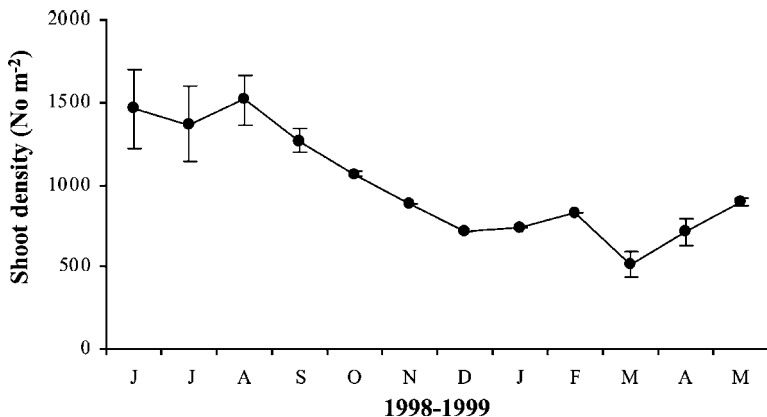


Fig. 1. Annual variation of the *C. nodosa* shoot density (vertical lines indicate standard error of the mean) within the Urbinu lagoon.

3.2. Biomass

The average total biomass of the shoots varied between 431.8 and 1 089.8 g dry wt. m⁻² (from June 1998 to May 1999), with a mean annual value of 777.2 g dry wt. m⁻², according to the season (Kruskal–Wallis test, $P < 0.01$) and the age (Friedman test, $P < 0.01$) of the studied tissue. Values showed a seasonal pattern (Fig. 2), with a maximal mean value in spring–summer, a decrease in late summer and a minimal mean value in winter. The below-ground biomass (445.8 g dry wt. m⁻², including rhizome and root biomass) was generally higher than the above-ground biomass (331.5 g dry wt. m⁻²), except in spring. Moreover, the above-ground and below-ground parts of the plant showed the lowest biomasses

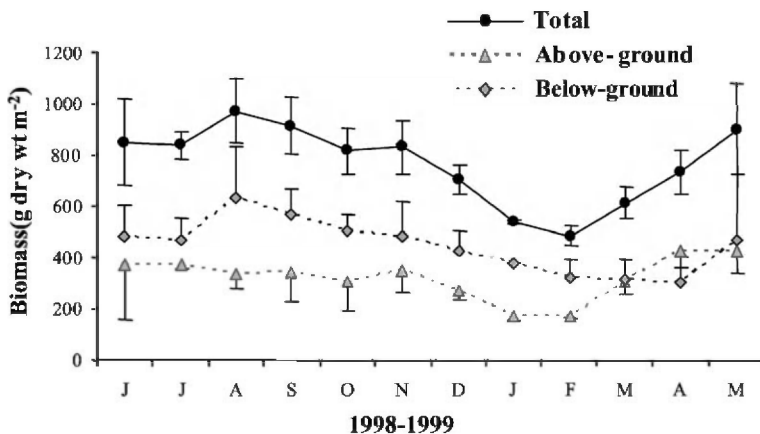
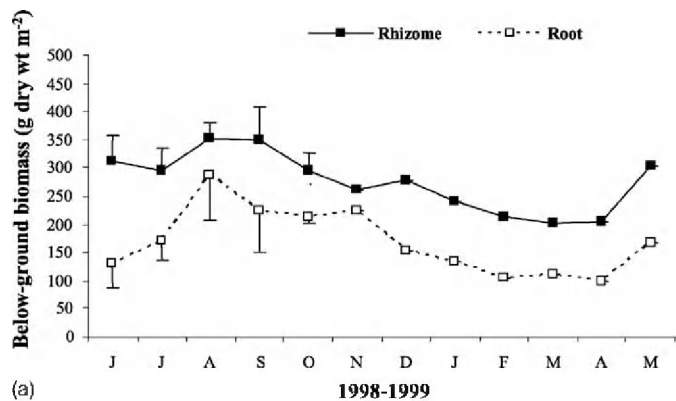
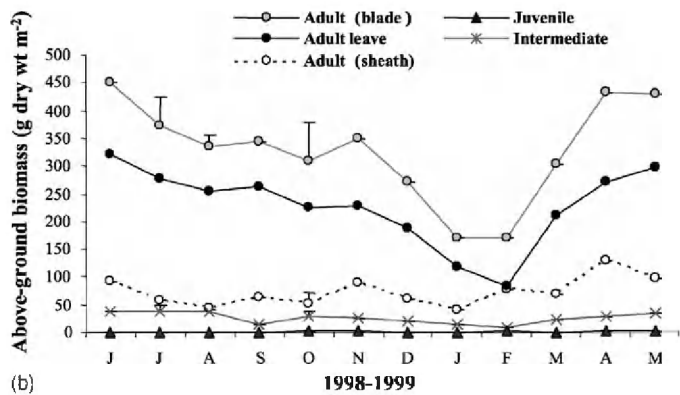


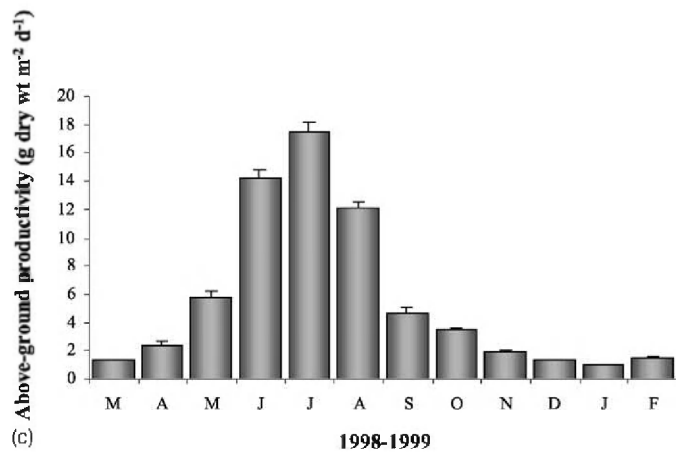
Fig. 2. Mean annual biomass of *C. nodosa* shoots in the Urbinu lagoon.



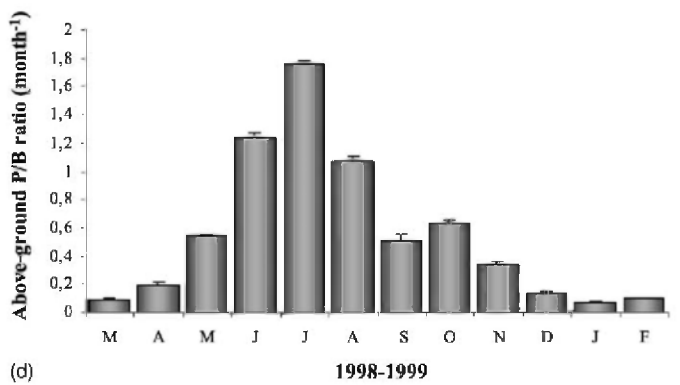
(a)



(b)



(c)



(d)

Fig. 3. (a) Annual variation of the below-ground biomass observed on the Urbinu lagoon; (b) annual variation of the above-ground biomass observed on the Urbinu lagoon; (c) annual variation of mean above-ground primary production of *C. nodosa* shoots in the Urbinu lagoon; (d) annual variation of mean below-ground primary production of *C. nodosa* shoots in the Urbinu lagoon.

Table 1
Below-ground production of *C. nodosa* within the Urbinu lagoon

Tissue	Below-ground production (g dry wt. m ⁻² per year)	P/B ratio (per year)
Rhizomes	169	0.6
Roots	244	1.4
Total tissues	413	1.0

in winter and in spring and the highest biomasses in spring and late summer–beginning of autumn, respectively.

Regarding the below-ground part, the rhizome biomass (280.3 g dry wt. m⁻²) was higher than the root biomass (165.4 g dry wt. m⁻², Fig. 3a). On the above-ground part, the adult leaf biomass showed a mean adult blade biomass value higher than the adult sheath biomass value (231.6 and 72.3 g dry wt. m⁻², respectively), which was in turn greater than the intermediate leaf biomass (26.5 g dry wt. m⁻²). All were higher than the juvenile leaf biomass (1.2 g dry wt. m⁻²), which was negligible during the year of study (Fig. 3b).

3.3. Primary production

The above-ground primary production followed a clearly unimodal seasonal diagram (Fig. 3c), with an annual production of 2057.8 g dry wt. m⁻² per year, corresponding to 843.7 g C m⁻² per year. Productivity abruptly increased between May and June, peaked in July (17.5 g dry wt. m⁻² per day) and decreased to its minimum value in January (1 g dry wt. m⁻² per day).

The results obtained for P/B ratios are presented in Fig. 3d. The turnover was high over the summer period (up to 1.75 per month). The small peak observed in October does not depend on the primary production, but rather suggests a slightly more significant loss of biomass over this period of the year.

The below-ground primary production results are presented in Table 1, and show an average below-ground production of 412 g dry wt. m⁻² per year, which in terms of carbon can be estimated to be 144 g C m⁻² per year.

The total primary production of the *C. nodosa* meadows within the Urbinu lagoon was between 1782.6 and 3157 g dry wt. m⁻² per year, equivalent to 716.7 and 1261.6 g C m⁻² per year.

4. Discussion

The shoot density observed showed a seasonal model identical to that observed for the same seagrass species in marine and lagoonal Mediterranean environments (Peduzzi and Vukovic, 1990; Pérez and Romero, 1994; Reyes et al., 1995): the highest values were recorded in summer and autumn, and the lowest ones in winter and spring. The densities were of the same magnitude as those recorded for other Mediterranean lagoons (Pérez, 1989; Terrados, 1991; Rismondo et al., 1997) and marine environments (Caye and Meinesz, 1985; Vermaat et al., 1993).

The biomass cycle of *C. nodosa* within the Urbinu lagoon showed a unimodal annual model similar to that found by other authors at various locations in the Mediterranean (Peduzzi and Vukovic, 1990; Terrados and Ros, 1992; Pérez and Romero, 1994; Reyes et al., 1995; Rismondo et al., 1997). However, we found an annual average biomass 1.3–1.7 times higher than that generally reported for the same seagrass (Terrados and Ros, 1992; Pérez and Romero, 1994; Reyes et al., 1995; Duarte and Chiscano, 1999). Only Peduzzi and Vukovic (1990) obtained values approaching than ours (between 323 and 1020 g dry wt. m⁻²) in the gulf of Trieste (Italy). As described elsewhere, the biomass of *C. nodosa* varied according to the seasons and tissues studied. The seasonality differed between the above-ground (leaves) and below-ground (rhizomes and roots) biomass: during spring, rhizomes and roots showed minimal production, while leaves were at their maximum. However, the below-ground biomass was higher than the above-ground biomass throughout the year. This difference also depended on the age and functionality of the tissue, with higher biomasses for the oldest tissues (adult leaves) and the reserve organs (rhizomes). Our study revealed that the periods of biomass growth in the various tissues varied throughout the year, with one period of above-ground tissue growth at the end of winter–beginning of spring and a period of below-ground tissue growth at the end of spring–beginning of summer. During an annual cycle, above-ground growth may occur earlier than below-ground growth.

Primary production results can be compared with those found for other *C. nodosa* meadows within the Mediterranean basin. Concerning the above-ground primary production, our data were higher than those reported by Hillman et al. (1989), who found values between 150 and 550 g C m⁻² per year. On average, our values of primary production were higher than those reported in the literature, which range from 160 to 826 g dry wt. m⁻² per year in some lagoons in the Mediterranean basin (Pérez, 1989; Terrados, 1991; Terrados and Ros, 1992; Reyes et al., 1995; Rismondo et al., 1997). However, the annual value of above-ground production in the Urbinu lagoon may be regarded as the highest recorded to date. Indeed, only Reyes et al. (1995) in a Spanish lagoon, and Rismondo et al. (1997) in the lagoon of Venice (Italy) found maximum values of 752 and 826 g dry wt. m⁻² per year, respectively.

The below-ground primary production obtained in our study was higher than that reported in Mediterranean lagoons (Pérez, 1989; Terrados, 1991; Terrados and Ros, 1992; Reyes et al., 1995; Duarte and Chiscano, 1999), which generally ranged from 30 to 78 g dry wt. m⁻² per year. This may be due to the fact that the below-ground production is generally underestimated in the literature (Pérez, 1989; Terrados, 1991; Terrados and Ros, 1992; Reyes et al., 1995; Duarte and Chiscano, 1999), because the estimates available often exclude the root production, which accounts for 15–50% of total production on average (Duarte et al., 1998). Moreover, root production was largely higher than that of rhizomes in the Urbinu lagoon. Only Peduzzi and Vukovic (1990) considered these two tissues, which showed 234 g dry wt. m⁻² per year. However, these lower results may be explained by the influence of depth on primary production, as suggested by these researchers. Indeed, this one decreased with depth, but our sampling was at –1 m, whereas theirs was located at –2 m.

The total primary production of the *C. nodosa* meadow within the Urbinu lagoon is the highest recorded to date, whether we consider the production of the roots or not. Indeed, is higher even if we only take into account rhizomes in the below-ground production. These values are nevertheless equivalent to those measured for other seagrasses like *Zostera*

marina (200–800 g C m⁻² per year; Sand-Jensen, 1975; Wium-Andersen and Borum, 1984) and *Posidonia oceanica* (up to 1000 g C m⁻² per year; Ott, 1980). Our results are consistent with the data of Duarte and Chiscano (1999), who consider an average annual production of seagrasses of 1012 g C m⁻² per year, without taking into account the share of root production.

However, it was also necessary to consider the extent of the meadow in order to determine the total biomass in the environments. In the Urbinu lagoon, *C. nodosa* covered 205.7 ha from a total surface of 714.4 ha. Thus, this lagoon produced on average 5080 t of dry matter and 2035 t of carbon of *C. nodosa* per annum. This is only an estimate, since the production may vary according to the depth (Masini and Manning, 1997).

Acknowledgements

This research work is integrated within the LIFE Program of the Commission of the European Communities and Ministry of Environment: “Conservation of the natural habitats and the vegetable species of Community priority interest of Corsica”. This study was financed by “l’Office de l’Environnement de la Corse” and by “la Collectivité Territoriale de Corse”. We thank Dr. A. Capiomont and Mr. L. Bronzini de Caraffa for their help in the in situ measurements, and Ms. E. Gibbon for useful comments on the manuscript.

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