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Seasonal growth of *Codium bursa*, a slow-growing Mediterranean macroalga: *in situ* experimental evidence of nutrient limitation

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ABSTRACT: The seasonal growth of *Codium bursa* J. Agardh was examined in relation to ambient and internal nutrient concentrations to elucidate whether the low tissue nutrient concentrations observed are an intrinsic feature of this species or reflect nutrient-limited growth. Growth rates were rather low (mean ± SE: 2.2 ± 0.4 × 10^{-3} d^{-1}; doubling time = 1.24 ± 0.1 yr), and were significantly correlated to seasonal changes in ambient and internal nutrient concentrations, suggesting nutrient, probably P, limitation. This suggestion is supported by the rather high atomic tissue C/P ratios (1712), compared to C/N ratios (31.8) observed in summer. This was confirmed by experimentally injecting nutrients into the internal lumen of the plants *in situ*, which resulted in a doubling of growth rate, photosynthetic efficiency, and a reduction in light compensation irradiance (39.6 and 29.9 µmol photons m^{-2} s^{-1} in control and fertilised specimens, respectively). These results provide, along with the strong correlation between growth rate and ambient and internal phosphorus concentrations, clear evidence of a tight nutrient (likely phosphorus), rather than light or temperature, control of *C. bursa* growth rates. Hence, even inherently slow-growing organisms in the oligotrophic Mediterranean may be resource limited.

KEY WORDS: Slow-growing macroalga · Growth · Nutrient limitation

INTRODUCTION

Slow-growing macroalgae are important components of oligotrophic coastal environments (Duarte 1995). They dominate there because their slow growth rate results in low nutrient requirements, and because, by being thick and long-lived, they minimise losses (Duarte 1995). Because of their growth strategy, slow-growing macroalgae are paradigms of 'stress-tolerant' plants (Grime 1974). Stress-tolerant plants are considered to be relatively independent of resource availability, with their production being limited by their own intrinsic growth, rather than resource supply (e.g. Chapin 1988). Conversely, slow-growing macroalgae have thick thalli and, therefore, low surface-to-volume ratios, which should impose a low nutrient uptake capacity (Hein et al. 1995). As a consequence, slow-growing macroalgae show low nutrient concentrations (Duarte 1995), and may experience nutrient limitation, despite their low nutrient demand.

Codium bursa J. Agardh., a balloon-like Mediterranean macroalga, has been recently shown to rank amongst the slowest-growing plants yet studied (Geertz-Hansen et al. 1994). *C. bursa* supports extremely low photosynthetic rates and grows very slowly, but develops considerable biomass and reaches large sizes (>20 cm in diameter), indicating that they must experience few losses (Geertz-Hansen et al. 1994). Yet, we observed unusually low phosphorus concentrations in the tissues of *C. bursa* (average C/P = 1472 ± 64; cf. Geertz-Hansen et al. 1994), suggesting that it may be phosphorus limited despite its low growth and nutrient demands. Phosphorus has been shown to limit the growth of phytoplankton (Estrada 1979, Krom et al. 1991), and seagrasses (Pérez et al. 1991, 1994) in the Mediterranean, and it may well be that this also applies to the slowest growing plants there (i.e. *C. bursa*). Demonstration of nutrient limitation in *C. bursa* would challenge the notion that intrinsically slow-growing, stress-tolerant plants are relatively independent of resource availability (Grime 1974, Chapin 1988).

Examination of the seasonal growth pattern of this species in relation to ambient nutrient concentrations

could help ascertain whether the low nutrient concentration observed is an intrinsic feature of this species. Correlations between seasonal growth and ambient nutrient concentrations would suggest nutrient limitation, which must then be confirmed by experimental evidence. Here we follow this approach to test the importance of nutrients for the growth of *Codium bursa*, one of the slowest-growing macroalgal species. We first examine seasonal growth patterns, and their relation to ambient and internal nutrient concentrations. The extent of nutrient limitation of the growth and photosynthesis of *C. bursa* was tested in summer, the time of greatest nutrient deficiency in Mediterranean plants (Ballesteros 1989, Pérez et al. 1991, 1994, Delgado et al. 1994, Alcoverro et al. 1995). The peculiar form of this algae, a hollow sphere, was used to examine its response to enrichment *in situ*, which was achieved by injecting nutrients into the internal lumen of the plants.

METHODS

Seasonal growth study. The study was conducted between February 1993 and May 1994 in Cala Jonquet, a protected, shallow cove in the NW Mediterranean (42° 18.26′ N, 3° 18.11′ E) where a dense *Codium bursa* stand grows on a rocky platform between 5 and 10 m depth. Growth of *C. bursa* was measured at 30 to 50 d intervals, using a plant marking technique by tagging at least 30 undisturbed *C. bursa* specimens ranging in size from 1 to 16 cm with a numbered float attached to the thick *C. bursa* by a plastic cable tied around their base or to a nail next to the smaller (< 4 cm) specimens. The loss of organisms or tags over the study was compensated by tagging new individuals to maintain a sample size greater than 30 individuals. On each visit, the diameter of tagged plants was measured *in situ* to the nearest 0.2 mm, using a calliper. Diameter measurements were converted into algal dry weight using a regression equation built with a large (~200) sample size (Geertz-Hansen et al. 1994). Specific growth rates (μ, d^{-1}) were calculated from the increase in algal size over each measurement period using the equation:

$$\mu = \frac{\left(\frac{W_t - W_0}{W_0}\right)}{t}$$

where t is the duration (d) of the measurement period, and W_t and W_0 are the final and initial dry weights of the specimens, respectively.

At each visit, 10 *Codium bursa* specimens, ranging in diameter between 1 and 20 cm, were collected for nutrient analysis. A 20 ml sample of the water filling the lumen of 2 mid-size (5 to 8 cm) and 2 large (15 to 20 cm) specimens, and duplicate samples of ambient water, were withdrawn with sterile syringes for analysis of dissolved inorganic nutrients, and stored frozen after adding 2 drops of a chloroform solution. The tissues of 4 small, 2 mid-size, and 4 large specimens were cleaned of epiphytes, the internal water drained off, and dried (24 h at 80°C) to be analysed for tissue C, N, and P concentrations.

***In situ* enrichment experiment.** The nutrient addition experiment was conducted between August and October 1993, following the detection of an increase in tissue C/P ratio and a decline in growth rate. The nutrient addition experiment was conducted *in situ* by adding nutrients directly to the water in the lumen of the plant, benefiting from the peculiar form of this species. Using SCUBA we injected 10 ml of a nutrient-rich medium containing 105 µmol of inorganic N (as nitrate), 4.3 µmol of inorganic P (as phosphate), as well as metals, and vitamins in proportions similar to f/2 medium (cf. Guillard & Ryther 1962), into the lumen of each of 40 specimens with relatively uniform sizes (7 to 14 cm diameter). A second needle inserted in the opposite side of the algae allowed evacuation of the excess water, thereby preventing any pressure stress, but involving some loss of added nutrients. We, therefore, evaluated the enrichment applied by sampling, using a syringe, the internal water of 5 additional organisms for nutrient analysis following injection of the nutrient solution. These samples indicated an initial nutrient concentration in the water of the internal lumen of fertilised specimens of 522.5 ± 93.3 µM of NO_3, 1.08 ± 0.04 µM of NH_4, and 13 ± 2.5 µM of PO_4, compared to 1.63 ± 0.50 µM of NO_3, 0.82 ± 0.43 µM of NH_4, and 0.03 ± 0.00 µM of PO_4 in that of control specimens. Nutrient addition, therefore, involved a 2 to 3 order-of-magnitude increase in nutrient concentrations, but did not alter the N/P ratio of the water in the internal lumen of the algae. A second nutrient addition was performed 10 d later to compensate for losses, since experiments with tritiated water indicate the residence time of the water in the internal lumen of *Codium bursa* to be short (about 1 to 2 d; O. Geertz-Hansen unpubl.).

Each of the individuals fertilised was subsequently tagged, as described above, to measure growth 50 d following the nutrient addition, ensuring sufficient time for a measurable growth response in this slow-growing plant. The growth of unenriched algae tagged as part of the seasonal growth study was used as control. In addition to the growth response (which must be moderate, provided the intrinsic slow growth of these organisms), we measured their photosynthetic rates as a shorter-term indicator of their response to nutrient additions. The photosynthetic rates were measured 10 and 50 d following nutrient enrichment of 5 fertilised and 5 control individuals. These organisms were trans-

ported to the laboratory in refrigerated seawater and used to determine photosynthesis versus irradiance (P-I) curves (0 to 500 µmol photons m^{-2} s^{-1}), and to measure chlorophyll *a* (chl *a*) and nutrient (C, N, and P) concentrations in their tissues.

The specimens collected for photosynthetic measurements were carefully cleaned of epiphytes and placed in wide-mouth, clear glass bottles. Photosynthetic activity was measured through changes in dissolved oxygen concentration, following the recommendations of Littler (1979), Littler & Arnold (1980) and Kemp et al. (1990), particularly in regard to incubation time, mixing, and sample size (fresh weight relative to bottle volume). The plant material was fitted into 140 ml Winkler bottles, filled with filtered (0.45 µm) seawater using a siphon to prevent bubbles and reduce variance in the oxygen concentration among replicates, and incubated at 20°C, in a MK X Incubator Shaker. Stirring was provided by continuous orbital shaking. Incubation time ranged between 45 min and 4 h, scaled to the rate of oxygen change to ensure accurate estimates of oxygen production in the light and consumption in the dark while avoiding bubble formation and oversaturation. The changes in dissolved oxygen upon incubation at irradiances increasing from darkness to 500 µmol photons m^{-2} s^{-1} were measured using an oxygen electrode and meter (Orbisphere, 2607 model, sensor 2112 with a built-in stirrer). We used 4 reference bottles (i.e. without plant tissue) incubated at the same light intensities and during the same time period. Illumination was provided by cool-white fluorescent tubes placed above the bottles, and the photon fluency rate was measured with a LI-COR datalogger fitted with a spherical LI-COR sensor.

The P-I curves obtained were used to calculate the photosynthetic efficiency [(mg O_2 g dry wt^{-1} h^{-1}) (µmol photons m^{-2} s^{-1})$^{-1}$] which represents the initial increment in oxygen evolution per unit light increase (cf. Kirk 1983), calculated, using linear regression, as the initial slope of the P-I curve (e.g. Lederman & Tett 1981); dark respiration rate (mg O_2 g dry wt^{-1} h^{-1}), calculated as the intercept on the ordinate of the regression equation used to calculate photosynthetic efficiency (Lederman & Tett 1981); the light compensation point (µmol photons m^{-2} s^{-1}), the irradiance at which photosynthesis and respiration are balanced, calculated as the intercept on the abscissa of the regression equation; and the maximum photosynthetic rate observed within the irradiance range assayed (mg O_2 g dry wt^{-1} h^{-1}).

Tissue carbon and nitrogen concentrations were determined for duplicate subsamples (4 mg dry wt each), using a Carlo-Erba CHN analyser, while phosphorus concentrations were determined colorimetrically in duplicate subsamples (8 mg dry wt each) following wet acid digestion (Koroleff 1983). Coefficients of variation of the duplicate analysis were 1% for C and N, and 6% for P. Nutrient concentrations (nitrate, nitrite, ammonia and phosphate) of the enclosed and ambient water were analysed colorimetrically on an autoanalyzer following Strickland & Parsons (1972).

Daily incident irradiance was obtained from a station 21 km south of the study site (St. Pere Pescador, Girona; collected by Mas Badía Experimental Research Station, Generalitat de Catalunya). Surface water temperature was measured at 0.5 m depth weekly at a site (L'Estartit, Girona; J. Pascual unpubl.) located 27.5 km south of the study site. We averaged water temperature by month and calculated the cumulative irradiance received during marking periods.

The relationship between seasonal growth rate and growth conditions (incoming irradiance, water temperature, and ambient nutrient concentrations) was examined using cross correlation analysis to allow for lagged growth responses. Differences in growth of fertilised versus control plants were tested using a 1-way ANOVA (Sokal & Rohlf 1981).

RESULTS AND DISCUSSION

Seasonal plant nutrient status and growth

The irradiance at the water surface ranged from 1721 E m^{-2} mo^{-1} in May 1993 to 292 E m^{-2} mo^{-1} in November 1993, with maximum irradiance at the surface being about 2000 µmol photons m^{-2} s^{-1}, which corresponds to 1200 and 730 µmol photons m^{-2} s^{-1} at 5 and 10 m depth, respectively. Surface water temperature showed a minimum of 12.3°C in February 1993, and a maximum of 22.3°C in August 1993 (Fig. 1). Minimum phosphate concentrations in ambient waters were observed in August 1993 (0.006 µM) and May 1994 (0.03 µM) while the highest concentration (0.85 µM) was observed at the beginning of the experiment (March 1993; Fig. 1). Dissolved inorganic nitrogen (DIN) showed a smooth temporal pattern with a maximum of 4.14 µM in November 1993 (Fig. 1), with nitrate and ammonium accounting, on average, for 42.01% and 53.71% of DIN, respectively.

Nutrient concentrations in the water enclosed within large *Codium bursa* individuals followed a pattern parallel to that of ambient nutrient concentrations ($r = 0.76$ and $r = 0.73$, $p < 0.005$, for PO_4 and NO_3, respectively; Fig. 1). Yet, DIN concentrations in the internal water largely exceeded (by about 10-fold) ambient concentrations, except from July to October, when they were similar (Fig. 1). In contrast, phosphate concentrations in the internal water were substantially lower than ambient concentrations,

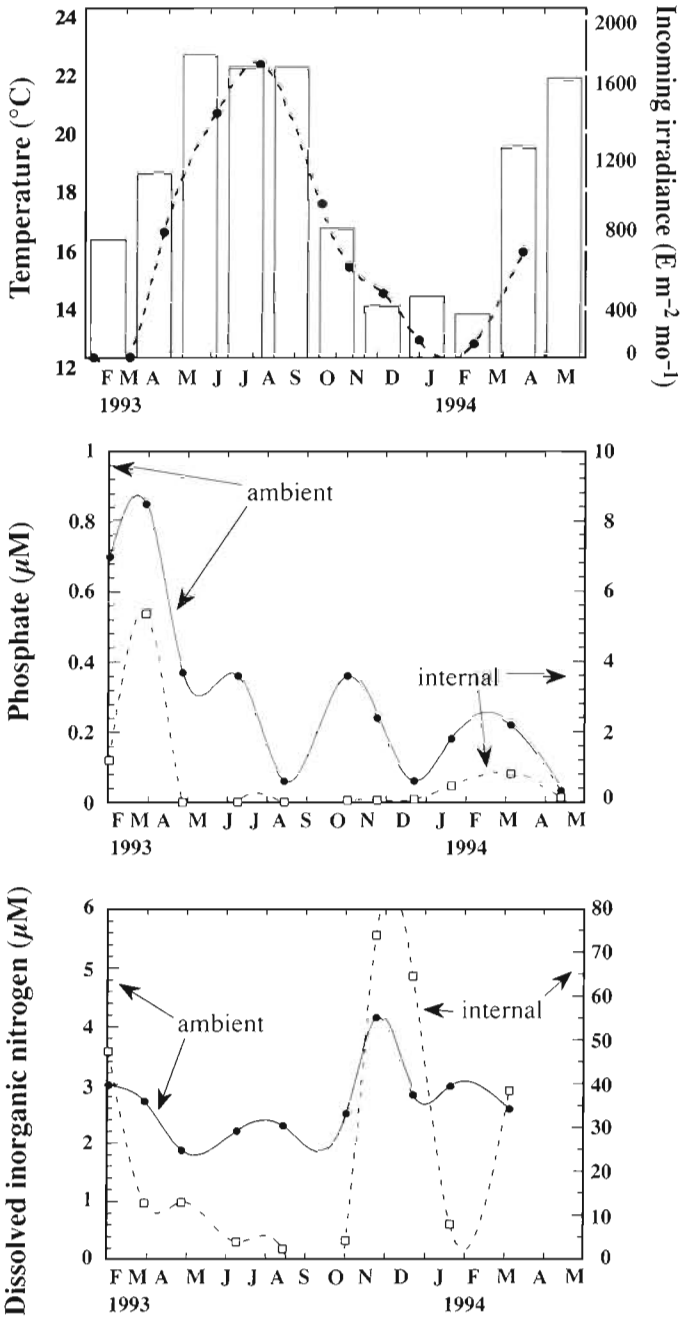

Fig. 1. Temporal variation of incoming irradiance (upper panel, bars), water temperature (upper panel, broken line), and phosphate (middle panel) and dissolved inorganic nitrogen (lower panel) concentrations in ambient and internal (i.e. within the lumen of 15 to 20 cm *Codium bursa* specimens) water during the study period

except in winter when internal concentrations exceeded ambient ones (Fig. 1). These results indicate that the water in the internal lumen may represent an important reservoir for N, but not for P, and points to a greater demand for P, relative to N, by the macroalga.

Tissue nutrient concentrations were very low (0.0318 ± 0.0065 and 0.76 ± 0.17% dry wt for P and N, respectively), as reported before (Geertz-Hansen et al. 1994), and showed a clear seasonal pattern, with C/P and C/N atomic ratios increasing in summer, both in large and small specimens (Fig. 2). Seasonal changes in tissue concentrations were correlated with those in ambient and internal waters, both for tissue C/P ($r = -0.72$ and -0.57 for ambient and internal water, respectively) and C/N atomic ratios ($r = -0.73$ and -0.64 for ambient and internal water, respectively). The tissue C/P ratios observed in summer were very high (C/P = 1712), while C/N ratios were only moderately high (C/N = 31.8), indicative of a greater phosphorus, compared to nitrogen, deficiency in summer.

Codium bursa grew very slowly (mean ± SE 2.257 ± 0.452 × 10^{-3} d^{-1}), indicative of rather long doubling times (1.24 ± 0.152 yr), but still shorter than those reported for some crustose red algae (Paine et al. 1979). The maximum specific growth rate was observed in May-June 1993, and a sec-

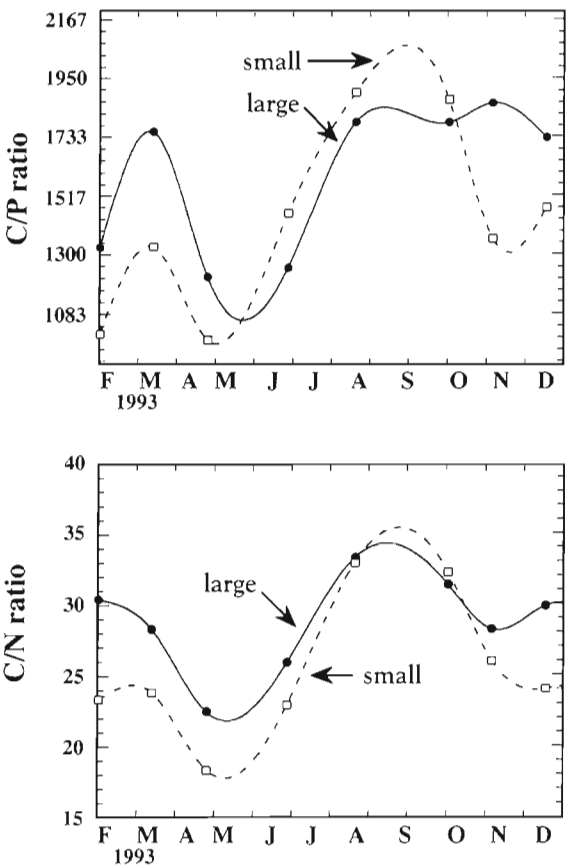

Fig. 2. *Codium bursa*. Seasonal variation in tissue C/P and C/N atomic ratio for large (15 to 20 cm diameter) and small (< 5 cm) specimens

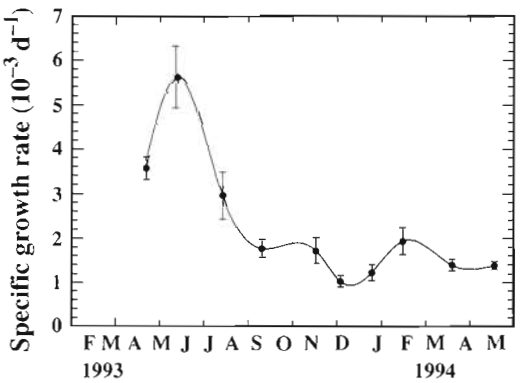

Fig. 3. *Codium bursa*. Average (± SE) specific growth rate during the study period

ondary maximum was observed in January 1994 (Fig. 3). Hence, growth rate did not appear to follow any clear seasonal pattern, and was independent of irradiance or temperature ($r = 0.12$, $p > 0.05$ and $r = 0.071$, $p > 0.05$, respectively). Instead, specific growth rates were closely correlated with ambient ($r = 0.64$, $p < 0.025$) and internal ($r = 0.83$, $p < 0.0005$) phosphate concentrations (Fig. 1). The correlation between growth rate and dissolved inorganic nitrogen was weaker and even negative ($r = -0.57$, $p < 0.05$) for ambient concentration, and non-significant ($r = -0.47$, $p > 0.05$) for internal concentration. In addition, the specific growth rate was closely correlated with the C/P ratio of the algal tissues ($r = -0.71$, $p < 0.025$), but not with C/N ratio ($r = -0.32$, $p > 0.05$). These results all point to a dominant role of phosphorus availability, rather than light or temperature, in controlling the specific growth rate of *C. bursa*. Accordingly, the absence of a clear seasonal pattern in *C. bursa* growth rate should derive from the great interannual variability in the seasonal pattern of phosphate concentrations in the NW Mediterranean littoral (J. Cebrián, C. M. Duarte & J. Pascual unpubl.).

Response to *in situ* nutrient enrichment

In situ nutrient additions to the water in the internal lumen of the algae resulted in a significant (ANOVA; $F = 5.2$, $p < 0.02$) growth enhancement, specific growth rates increasing by >100% in response to nutrient enrichment (Fig. 4). Tissue nutrient concentrations did not change significantly (*t*-test, $p > 0.4$ for both P and N) in response to nutrient additions. This is, however, expected, provided the long turnover rate of the organism, which implies that only a small fraction (about 12.3%) of the tissues had been produced over the 50 d experimental period. This growth response was paralleled by a similarly high (2-fold and 3-fold increase in August and October, respectively) increase in the photosynthetic efficiency of the organisms, and a significant decline in the respiration rate, as well as a reduction in chl *a* concentration, particularly in October (Fig. 4). The reduction in chl *a* concentration in response to nutrient enrichment is difficult to explain, but is consistent with previous observations for phytoplankton (e.g. Wehr 1989). At any rate, this reduction probably has no measurable influence on light acquisition by *Codium bursa*, whose chl *a* concentration is too high for efficient light absorption (cf. Geertz-Hansen et al. 1994). These results provide, along with the strong correlation between growth rate and ambient and internal phosphorus concentrations, clear evidence of a tight nutrient (likely phosphorus) control of *C. bursa* growth rates, and extend the range of nutrient-limited phototrophs in the Mediterranean

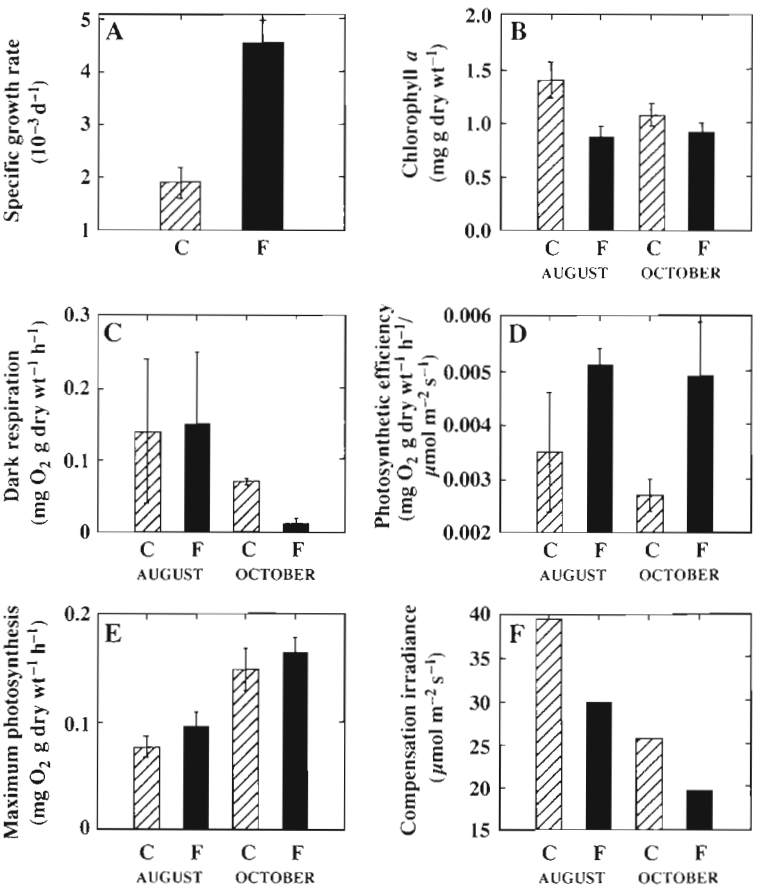

Fig. 4. *Codium bursa*. Response to *in situ* nutrient additions 10 (August) and 50 d (October) following nutrient enrichment. Bars represent average (± SE) for control (C) and fertilised (F) specimens

from phytoplankton (Estrada 1979, Krom et al. 1991), and seagrasses (Pérez et al. 1991, 1994), to the slowest-growing macroalgae.

There is abundant evidence of nutrient limitation of macroalgal growth rates (Mann et al. 1980, Valiela 1984, Ramus 1992), most of them derived from laboratory, or mesocosm experiments. The evidence of nutrient-limited *Codium bursa* growth provided here is particularly important, because of the inherently slow growth of this species and the fact that the experimental evidence was derived *in situ*, making use of the form of *C. bursa*. Consideration of this peculiar growth form predicts intrinsically low growth rates, derived from the very low photosynthetic rates associated to the spherical shape and thickness of its tissues (Geertz-Hansen et al. 1994), which could also suggest a light-dependence of growth rates. Yet, consideration of the low surface to volume ratio of *C. bursa* also predicts very low nutrient uptake rates (Hein et al. 1995). That *C. bursa* growth, and even photosynthetic rates, are controlled by nutrient supply demonstrates that the constraints the geometry of *C. bursa* imposes on its capacity to acquire nutrients overrule those imposed on the efficiency of light capture. Moreover, the control of *C. bursa* growth by nutrients was so severe as to uncouple it from the seasonal changes in light and temperature that determine the seasonal pattern of most Mediterranean macrophytes (Ballesteros 1991, Pérez & Romero 1992, Terrados & Ros 1992, Alcoverro et al. 1995).

The finding that an organism with exceedingly low intrinsic growth rates may have these reduced even further by nutrient limitation and still develop high biomasses (Geertz-Hansen et al. 1994) appears paradoxical. The only possible explanation for this paradox relies on the achievement of similarly reduced loss rates as the basis of the growth strategy of *Codium bursa*. Such reduced losses may be readily inferred from our results, which indicate that the life span of *C. bursa* exceeds 16 yr (i.e. the time to reach the largest size observed) in our study site. The results presented provide clear evidence that even inherently slow-growing organisms may be resource limited. Increasing resource availability at the ecosystem scale, however, would not be conducive to a better performance of *C. bursa*, for it will also favour growth of other, faster-growing plants (macroalgae, phytoplankton, epiphytic algae), also nutrient limited, which would shade, and eventually exclude *C. bursa*. Hence, resource-limited growth likely represents the most favourable growth condition for the development of *C. bursa* populations in the Mediterranean littoral.

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