

Primary production and vegetative cycle in *Posidonia oceanica* when in competition with the green algae *Caulerpa taxifolia* and *Caulerpa racemosa*

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Vegetative annual cycle and primary production were described in the sea grass *Posidonia oceanica* in competition with two Ulvophyceae, *Caulerpa taxifolia* (Cap Martin, France) and *Caulerpa racemosa* (Antignano, Italy). Sampling was performed at three stations exhibiting increasing levels of interaction with *Caulerpa*. Significant differences were observed as a function of the *Caulerpa* species, season and level of interaction. For each interaction, the different parameters have some seasonal variations. Any effects of the two *Caulerpa* species has been detected on the seasonal variability of our parameters. For all seasons, with increasing levels of interaction, the *P. oceanica* adult and intermediate leaf lengths, leaf index and mean age of the leaves always decrease whereas percentage of leaves having lost their apices, epiphyte biomass per unit surface area, mean number of leaves produced per shoot and per year always increase. Conversely, mean number of leaves per shoot or below-ground tissue production do not seem to be affected by *Caulerpa*. Finally, primary production of *P. oceanica*, by an increased turnover of the foliar tissues, was greater in the case of high interaction.

INTRODUCTION

The marine phanerogam *Posidonia oceanica* (L.) Delile is one of the key species to inhabit littoral Mediterranean ecosystems because of its high primary production, base of the food web, hatcheries and nurseries, sedimentary stability, protection against erosion, etc. (Bell & Harmelin-Vivien, 1982; Velimirov, 1984; Jeudy De Grissac & Boudouresque, 1985; Pergent et al., 1994; Francour, 1997). Due to its wide distribution throughout the Mediterranean basin, *P. oceanica* is also a species that is extensively used as a bio-indicator of stress (anthropogenic pressures, interspecific competition).

The genus *Caulerpa*, which belongs to the Class Ulvophyceae, is made up of approximately 100 species, most of which are found in temperate and warm waters. *Caulerpa taxifolia* (Vahl) C. Agardh and *Caulerpa racemosa* (Forskål) J. Agardh are currently spreading through the Mediterranean. *Caulerpa racemosa* is generally considered to be a Lessepsian immigrant, as are *C. scalpelliformis* (R. Brown ex Turner) C. Agardh and *C. mexicana* (Sonder ex Kützting) J. Agardh (Boudouresque et al., 1996; Piazzini et al., 1997). Conversely, the presence of the species *C. taxifolia* within the Mediterranean is due to the accidental release of this alga from a public aquarium in the 1980s (Meinesz & Hesse, 1991; Jousson et al., 1998; Wiedenmann et al., 2001).

Caulerpa taxifolia and *C. racemosa* can exert two types of pressure on *P. oceanica*. The first is an exploitation competition and involves either the interception of light by the alga thalli or the utilization of nutrients. The second is an interference competition (allelopathy: production of bioactive substances) (Villèle & Verlaque, 1995). It would also

appear that the growth of these species leads to overgrazing of the neighbouring *P. oceanica* sea grass beds, in particular by macro-herbivores (Villèle, 1992; Villèle & Verlaque, 1995). This last phenomenon is probably the result of both an ichthyotoxicity (Bartfai & Vicente, 1996) and a repulsive effect caused by the secondary metabolites released by *C. taxifolia* and *C. racemosa* (Norris & Fenical, 1982; Brayle, 1994). These toxic substances are only regularly released because of thallus damages following natural events (like sea storms). Indeed, Dini et al. (1996) did not find the toxic substances in the seawater medium of the aquaria where intact thalli of *C. taxifolia* were growing, but in mediums which contain some damaged thalli, evidence of toxicity on crustaceans and molluscs were found.

The aim of the present study was to reveal and quantify the impact of *C. taxifolia* and *C. racemosa* on the growth of *P. oceanica* sea grass beds through a study of the vegetative cycle and primary production of this phanerogam in sites presenting a gradient of interaction with the invasive algae.

MATERIALS AND METHODS

Samples of *Posidonia oceanica* were taken from the site Cap Martin (Alpes Maritime, France), at a depth of 10.0 m, in order to study the effects of interaction with *Caulerpa taxifolia*. Samples were similarly taken from the site of Antignano (Tuscany, Italy), at a depth of 2.0 m, to study interaction with *C. racemosa* (Figure 1). Sampling was performed every two months, from May 1999 to May 2000. For each of the two sites, three levels of interaction were examined (Table 1).

The sampling stations at each site were within the same meadow and exhibited similar biological/physical and

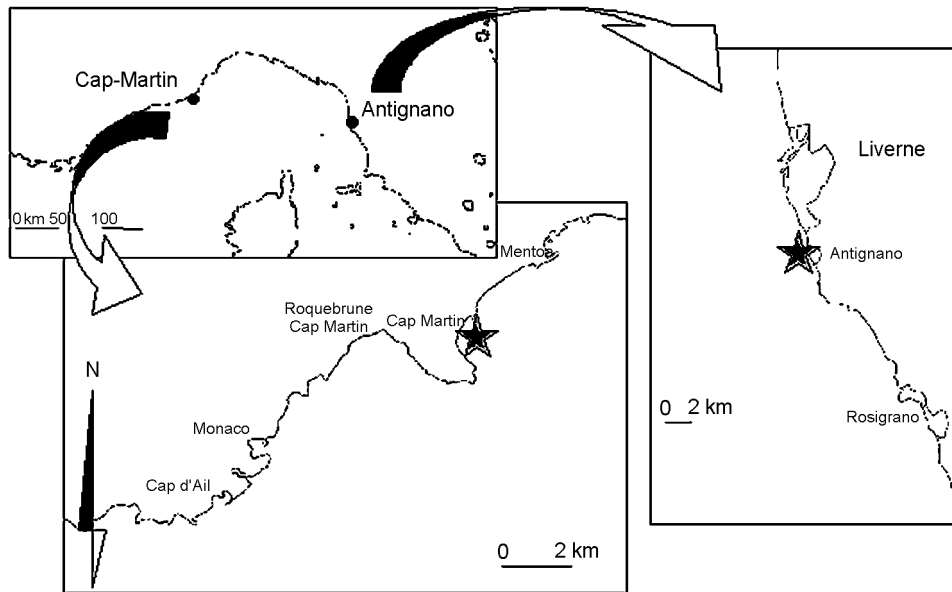


Figure 1. Location of the sampling sites: Roquebrune-Cap Martin (France) for *Caulerpa taxifolia* and Antignano (Livorno, Italy) for *Caulerpa racemosa*.

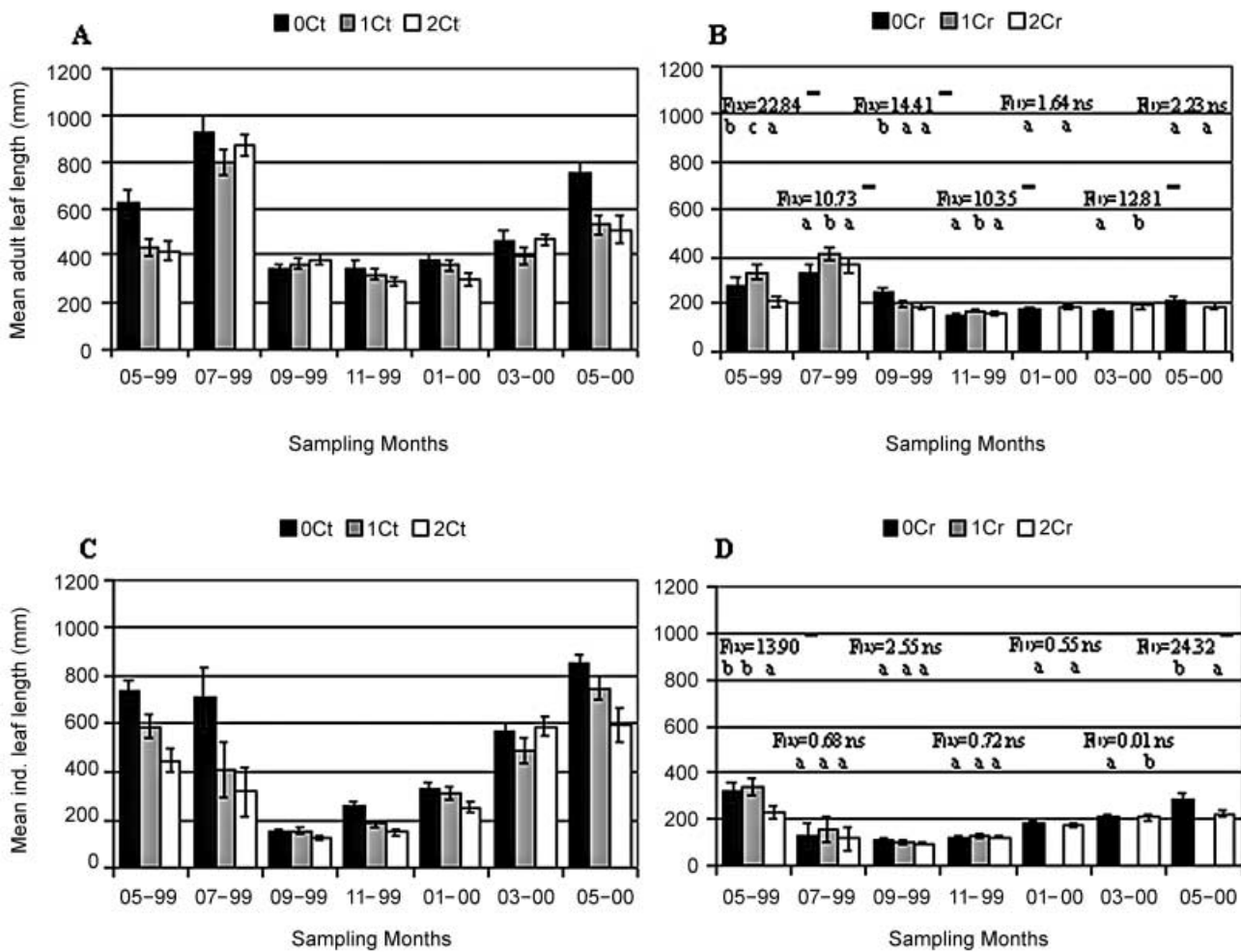


Figure 2. Mean adult leaf lengths (resp. intermediate) of *Posidonia oceanica* in competition with *Caulerpa taxifolia* (A, resp. C) and *C. racemosa* (B, resp. D). Note. Also shown are the ANOVA tests results: degrees of freedom, F values, significance level (ns, non significant; *, $P < 0.05$; **, $P < 0.001$). Tukey test is presented when ANOVA is significant: values that do not differ at the 0.05 level are noted with the same letter.

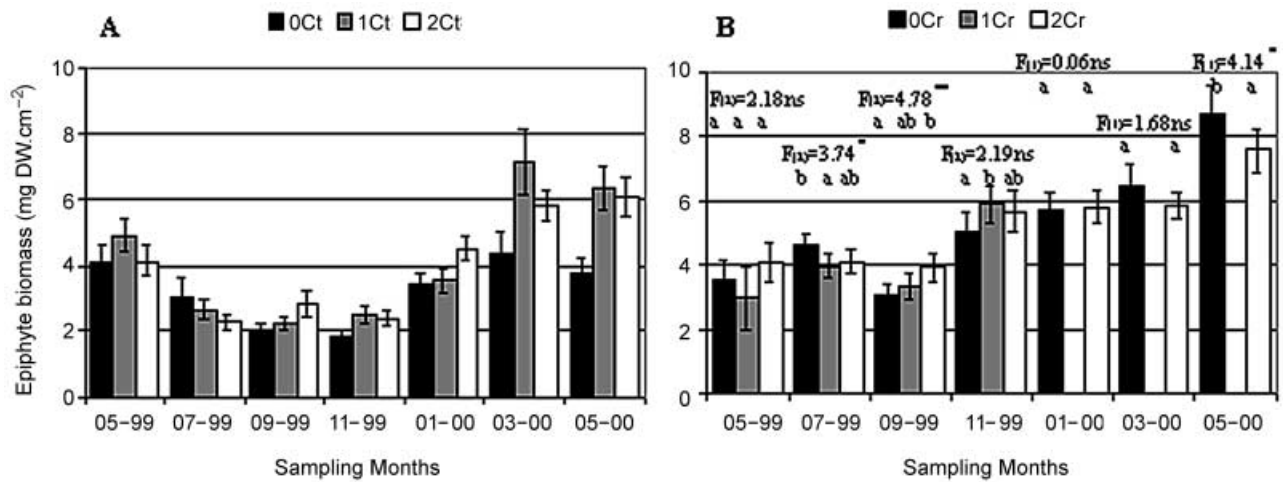


Figure 3. Epiphyte biomass per unit surface of the first adult leaves (the oldest one) in *Posidonia oceanica* in competition with *Caulerpa taxifolia* (A) and *C. racemosa* (B). Note. Also shown are the ANOVA tests results: degrees of freedom, *F* values, significance level (ns, non significant; *, $P < 0.05$; **, $P < 0.001$). Tukey test is presented when ANOVA is significant: values that do not differ at the 0.05 level are noted with the same letter.

chemical characteristics (shoot density, sediment, depth, temperature, salinity, hydrodynamics, etc.). The only difference between stations involved the presence and/or density of *C. taxifolia* or *C. racemosa*.

Two stations without *P. oceanica* (monospecific meadow of *C. taxifolia* or *C. racemosa*) were also sampled in order to describe the vegetative cycle of the algal species in the absence of interaction with *P. oceanica*, noted as 'Po'.

At each of the stations, the sea grass bed density was estimated using a 20-cm side quadrat (three replicates), and 30 orthotropic shoots of *P. oceanica* were sampled, as were 40 thalli of *Caulerpa*, when these species were present.

A phenological analysis was carried out on the *P. oceanica* shoots sampled according to the protocol described by Giraud (1979) and Pergent et al. (1995). The following variables were examined: the number of adult and intermediate leaves, the leaf biometry, the coefficient A (percentage of leaves having lost their apices) and the leaf index (leaf surface area per shoot). The adult leaves are those which have a sheath of at least 2 mm length. If the sheath is lower than two millimetres, but with a total length of the leaf exceeding five centimetres, it is an intermediate leaf, if not (less than 5-cm length), it is a youthful leaf. Lepidochronological analysis was also carried out

using the method outlined by Pergent (1990) in order to estimate annual primary production of the leaves and rhizomes of *P. oceanica* (Pergent & Pergent-Martini, 1991; Esteban et al., 1990).

The biomass (dry weight) of the leaves and the sheaths of the oldest adult leaves (that have thus ceased to grow) were measured, as was the epiphyte biomass, this last measurement being expressed per unit leaf area so that this parameter could be compared between the various stations.

Two-way analyses of variance (ANOVAs), (for interaction with *C. taxifolia*) and one-way ANOVAs (for interaction with *C. racemosa*; due to the lack of stations during winter 2000) combined with Tukey multiple comparison tests were used to make comparisons of the phenological parameters of *P. oceanica*, according to the two studied factors: 'station' (three levels of interaction intensity) and 'season' (seven sampling periods). Beforehand, normality and homoscedasticity were verified by Kolmogorov–Smirnov and Bartlett tests, respectively. Two-way ANOVAs were also used to observe variations in phenological parameters of *C. taxifolia* or *C. racemosa*.

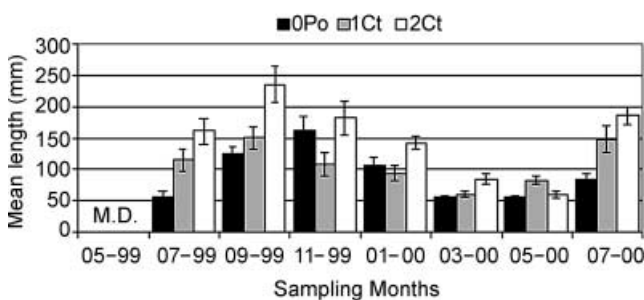


Figure 4. Mean thalli length of *Caulerpa taxifolia* at different levels of interaction with *Posidonia oceanica* (M.D., missing data).

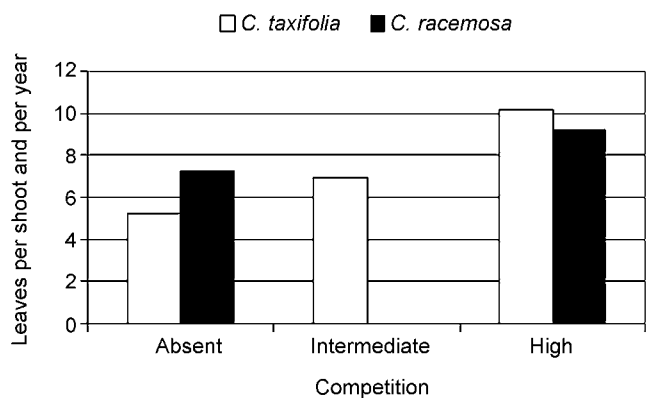


Figure 5. Mean number of leaves of *Posidonia oceanica* produced per shoot and per year as a function of the type and level of interaction.

Table 1. Description of the different levels of interaction examined and attributed notations.

| Competition | Description | Notation | |
|--------------------------|----------------------------------------------------------------------------|---------------------------|--------------------------|
| | | <i>Caulerpa taxifolia</i> | <i>Caulerpa racemosa</i> |
| Absent Competition | Absence of <i>Caulerpa</i> species. | 0Ct | 0Cr |
| Intermediate Competition | Simple contact of <i>Caulerpa</i> species with <i>Posidonia oceanica</i> . | 1Ct | 1Cr |
| High Competition | Algal stolons intertwined within the rhizomes and mat. | 2Ct | 2Cr |

Table 2. Results of two-way ANOVA for phenological parameters of *Posidonia oceanica* in interaction with *Caulerpa taxifolia*. Tukey test is presented: values that do not differ at the 0.05 level are noted with the same letter.

| Parameter | Source of variability | F | df | P | Tukey post hoc tests |
|-------------------------------|-----------------------|--------|----|--------|----------------------------------------------------------------------------------------------------------------------------|
| Mean adult leaf length | Season | 292.20 | 6 | <0.001 | May ^d Jul ^f Sept ^b Nov ^a Jan ^{ab} Mar ^c May ^e |
| | Station | 40.07 | 2 | <0.001 | 0Ct ^a 1Ct ^b 2Ct ^b |
| Mean intermediate leaf length | Season | 271.79 | 6 | <0.001 | May ^e Jul ^c Sept ^a Nov ^a Jan ^b Mar ^d May ^f |
| | Station | 54.81 | 2 | <0.001 | 0Ct ^a 1Ct ^b 2Ct ^c |
| Number of leaves per shoot | Season | 39.71 | 6 | <0.001 | May ^b Jul ^a Sept ^{cd} Nov ^e Jan ^{cd} Mar ^c May ^{ab} |
| | Station | 2.54 | 2 | 0.085 | 0Ct ^a 1Ct ^a 2Ct ^a |
| Coefficient A | Season | 36.68 | 6 | <0.001 | May ^b Jul ^b Sept ^b Nov ^a Jan ^b Mar ^c May ^b |
| | Station | 13.63 | 2 | <0.001 | 0Ct ^a 1Ct ^b 2Ct ^b |
| Epiphyte biomass | Season | 96.30 | 6 | <0.001 | May ^c Jul ^a Sept ^a Nov ^a Jan ^b Mar ^d May ^d |
| | Station | 27.98 | 2 | <0.001 | 0Ct ^a 1Ct ^b 2Ct ^b |
| Leaf Index | Season | 271.04 | 6 | <0.001 | May ^{cd} Jul ^{de} Sept ^a Nov ^a Jan ^b Mar ^c May ^e |
| | Station | 76.95 | 2 | <0.001 | 0Ct ^b 1Ct ^a 2Ct ^a |

Table 3. Results of one-way ANOVA for the seasonal variation of the phenological parameters of *Posidonia oceanica* in interaction with *Caulerpa racemosa* at each station. Tukey test is presented: values that do not differ at the 0.05 level are noted with the same letter.

| Parameter | Station | F | df | P | Tukey post hoc tests |
|-------------------------------|---------|-------|----|--------|----------------------------------------------------------------------------------------------------------------------------|
| Mean adult leaf length | 0Cr | 54.20 | 6 | <0.001 | May ^c Jul ^d Oct ^c Nov ^a Jan ^{ab} Mar ^a May ^b |
| | 1Cr | — | — | — | — |
| | 2Cr | 81.59 | 6 | <0.001 | May ^c Jul ^d Oct ^c Nov ^a Jan ^{ab} Mar ^c May ^c |
| Mean intermediate leaf length | 0Cr | 67.87 | 6 | <0.001 | May ^c Jul ^{ab} Oct ^a Nov ^a Jan ^{bc} Mar ^c May ^d |
| | 1Cr | — | — | — | — |
| | 2Cr | 36.92 | 6 | <0.001 | May ^c Jul ^a Oct ^a Nov ^a Jan ^b Mar ^c May ^c |
| Number of leaves per shoot | 0Cr | 41.96 | 6 | <0.001 | May ^{bc} Jul ^a Oct ^d Nov ^d Jan ^{bc} Mar ^c May ^b |
| | 1Cr | — | — | — | — |
| | 2Cr | 45.18 | 6 | <0.001 | May ^a Jul ^a Oct ^b Nov ^d Jan ^c Mar ^c May ^b |
| Coefficient A | 0Cr | 84.47 | 6 | <0.001 | May ^c Jul ^c Oct ^a Nov ^b Jan ^c Mar ^c May ^c |
| | 1Cr | — | — | — | — |
| | 2Cr | 83.37 | 6 | <0.001 | May ^c Jul ^b Oct ^a Nov ^b Jan ^c Mar ^c May ^c |
| Epiphyte biomass | 0Cr | 39.61 | 6 | <0.001 | May ^{ab} Jul ^{bc} Oct ^a Nov ^c Jan ^{cd} Mar ^d May ^d |
| | 1Cr | — | — | — | — |
| | 2Cr | 24.18 | 6 | <0.001 | May ^a Jul ^a Oct ^a Nov ^b Jan ^b Mar ^b May ^c |
| Leaf Index | 0Cr | 34.21 | 6 | <0.001 | May ^c Jul ^b Oct ^{ab} Nov ^a Jan ^b Mar ^{ab} May ^c |
| | 1Cr | — | — | — | — |
| | 2Cr | 14.82 | 6 | <0.001 | May ^{cd} Jul ^d Oct ^a Nov ^{ab} Jan ^{bc} Mar ^d May ^{cd} |

Table 4. Results of two-way ANOVAs for the seasonal variation of the phenological parameters of *Caulerpa taxifolia* in interaction with *Posidonia oceanica* at each station. Tukey test is presented: values that do not differ at the 0.05 level are noted with the same letter.

| Parameter | Source of variability | F | df | P | Tukey post hoc tests |
|--------------------|-----------------------|-------|----|--------|-------------------------------------------------------------------------------------------------------------------------|
| Mean thalli length | Season | 67.46 | 6 | <0.001 | Jul ^b Sept ^d Nov ^c Jan ^b Mar ^a May ^a Jul ^c |
| | Station | 89.86 | 2 | <0.001 | 0Ct ^a 1Ct ^b 2Ct ^c |

Table 5. Results of one-way ANOVAs for the variation of the lepidochronological parameters of *Posidonia oceanica* in interaction with *Caulerpa taxifolia* and *C. racemosa* at each station. Tukey test is presented: values that do not differ at the 0.05 level are noted with the same letter.

| Parameter | <i>Caulerpa</i> species | F | df | P | Tukey post hoc tests |
|----------------------------|-------------------------|-------|----|--------|----------------------------------------------------|
| Mean leaf longevity | <i>C. taxifolia</i> | 14.41 | 2 | <0.001 | 0Ct ^b 1Ct ^b 2Ct ^a |
| | <i>C. racemosa</i> | 4.38 | 1 | 0.055 | 0Ct ^a 2Ct ^a |
| Leaf primary production | <i>C. taxifolia</i> | 44.17 | 2 | <0.001 | 0Ct ^a 1Ct ^a 2Ct ^b |
| | <i>C. racemosa</i> | 14.40 | 1 | <0.001 | 0Ct ^a 2Ct ^b |
| Sheath primary production | <i>C. taxifolia</i> | 72.09 | 2 | <0.001 | 0Ct ^a 1Ct ^b 2Ct ^c |
| | <i>C. racemosa</i> | 32.62 | 1 | <0.001 | 0Ct ^a 2Ct ^b |
| Rhizome primary production | <i>C. taxifolia</i> | 0.26 | 2 | 0.773 | 0Ct ^a 1Ct ^a 2Ct ^a |
| | <i>C. racemosa</i> | 0.64 | 1 | 0.425 | 0Ct ^a 2Ct ^a |

For lepidochronological analysis, data were processed by one-way ANOVAs in order to enable the level of competition comparison for each parameter. The software Statgraphics plus (v. 2.1) for Windows was used.

RESULTS

Significant seasonal variations were observed for all of the phenological parameters examined regardless of the level of interaction (see ANOVAs results Tables 2 & 3). Thus, the adult and intermediate leaf lengths of *Posidonia oceanica* were greater in summer than in winter (Figure 2A–D). As is generally found, the number of leaves per shoot exhibited maximum values in autumn (6.5 ± 0.3 and 7.0 ± 0.3 leaves shoot⁻¹ at stations 0Ct and 0Cr, respectively) and minimum values in summer (3.6 ± 0.3 and 4.3 ± 0.2 leaves.shoot⁻¹, respectively). Conversely, coefficient A remained relatively constant throughout the year (annual mean of 49.5 ± 17.2 and 85.6 ± 17.5 at stations 0Ct and 0Cr, respectively), with the exception of the winter values which were significantly lower (10.3 ± 5.0 and 33.5 ± 4.0 , respectively). Finally, the epiphyte biomass per unit surface area reached a

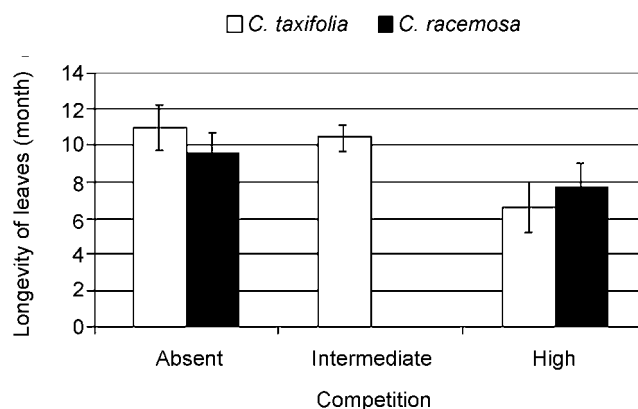
maximum in spring and a minimum in autumn (Figure 3A,B). The adult and intermediate leaf lengths and the leaf index differed significantly as a function of the level of interaction, for both *Caulerpa taxifolia* and *C. racemosa* (see ANOVAs results Tables 2 & 3 and Figure 2A–D). In addition, the mean leaf length and leaf index decreased with increasing level of interaction. For example, adult *P. oceanica* leaf lengths measured at Station 0Ct in May 2000 were in the order of 752.3 ± 43.1 mm (absence of *C. taxifolia*), whereas this parameter was 509.7 ± 55.3 mm at Station 2Ct (maximum level of interaction).

Conversely, both the coefficient A in the adult leaves and epiphyte biomass per unit surface area increased with increasing levels of interaction (see ANOVAs results Tables 2 & 3 and Figure 3A,B). This is particularly true for the interaction with *C. taxifolia*. Indeed, in November 1999, the coefficient A ranged from 10.3 ± 5.0 for the station without interaction (Station 0Ct) to 34.1 ± 10.6 for the station presenting the highest level of interaction (Station 2Ct). The mean number of leaves per shoot, however, remained relatively constant, regardless of the level of interaction. The leaf index (leaf surface area per shoot) therefore decreased with increasing levels of interaction: in case of *C. taxifolia*, the annual mean at Station 0Ct was 8215.7 ± 2607.7 mm² shoot⁻¹ and at Station 2Ct, the annual mean of leaf index was 6546.2 ± 2005.3 mm² shoot⁻¹, which represents a decrease of 20% (see ANOVAs results Table 2).

Table 6. Evolution of the various phenological and lepidochronological variables in *Posidonia oceanica* when subject to increasing levels of interaction.

| | Interaction | |
|---------------------------------------------|---------------------|--------------------------|
| | <i>C. taxifolia</i> | <i>C. racemosa</i> |
| Leaf length (Ad., Int., Base) | Y decrease | Y decrease |
| Number of leaves per shoot | N — | N — |
| Coefficient A | Y increase | N — |
| Epiphyte biomass per unit leaf surface area | Y increase | N — |
| Leaf Index | Y decrease | Y decrease |
| Number of leaves produced annually | Y increase | Y increase |
| Mean leaf longevity | Y decrease | Decrease not significant |
| Leaf primary production | Y increase | Y increase |
| Sheath primary production | Y increase | Y increase |
| Rhizome primary production | N — | N — |

N, no effect; Y, significant impact.

**Figure 6.** Mean longevity of *Posidonia oceanica* leaves (estimated between June 1999 and May 2000) as a function of the type and level of interaction.

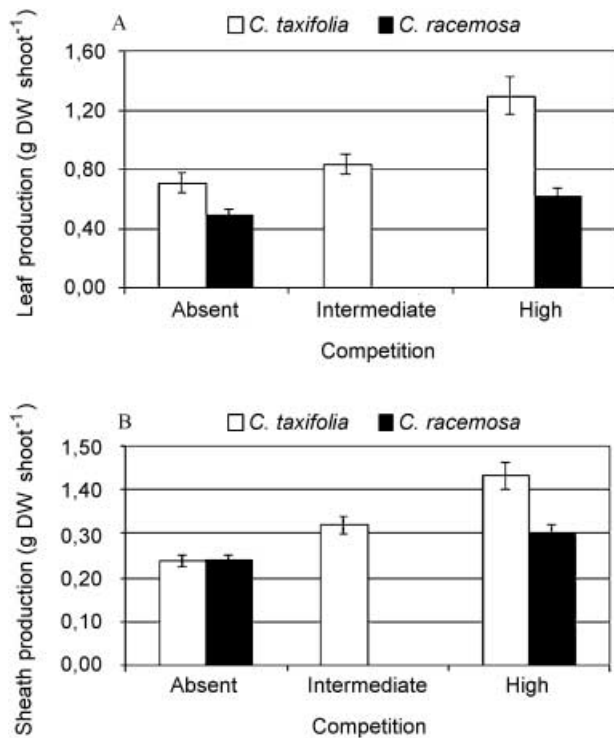


Figure 7. Annual leaf production of *Posidonia oceanica* (expressed in g DW shoot⁻¹) as a function of the type and level of interaction (A, leaf production; b, sheath production).

The length of the *C. taxifolia* thalli varied as a function of both season and level of interaction with the *P. oceanica* sea grass bed (see ANOVAs results Table 4 and Figure 4). Thus, the mean thalli length presented maximum values in autumn (September–November) and minimum values in spring (March–May), whereas the longest thalli were always observed at the station presenting the highest level of interaction (Station 2Ct). Thus, in July 2000, the *C. taxifolia* thalli in close contact with *P. oceanica* exhibited

mean lengths in the order of 185.5 ± 13.9 mm, vs 84.5 ± 8.1 mm when no such interaction with *P. oceanica* exists (Station 0Po); the station presenting intermediate levels of interaction (Station 1Ct) exhibited a mean value of 148.1 ± 20.3 mm.

The same pattern seems to exist for *C. racemosa*, for which thallus length also varied as a function of both season (maximum value in November—one-way ANOVAs; $F=21.22$ to 56.10 ; $P<0.001$) and level of interaction (largest thalli observed at Station 2Cr—one-way ANOVAs; $F=3.70$ to 9.67 ; $P<0.05$). For example, in October 1999, the mean thalli length varied from 19.1 ± 2.6 mm (Station 2Cr) to 14.9 ± 1.9 mm (Station 0Po); the station presenting intermediate levels of interaction (Station 1Cr) exhibited a mean value of 17.2 ± 1.8 mm.

Any significant differences were showed for the sea grass bed density as a function of level of interaction in Cap-Martin or Antignano sampling sites (one-way ANOVA, $F=2.2$, $df=2$, $P<0.05$). Thus, 435 ± 64 shoot m^{-2} were found for the absent interaction station with *C. taxifolia* (0Ct), and 565 ± 158 shoot m^{-2} , for the high interaction Station (2Ct).

The study of leaf growth using the lepidochronology method revealed that the mean number of leaves produced per shoot and per year increased with increasing levels of interaction, for competition with either *C. taxifolia* or *C. racemosa* (Figure 5). Conversely, the mean age of the leaves decreased with increasing levels of interaction with *C. taxifolia* but not significantly with *C. racemosa* (see ANOVAs results Table 5 and Figure 6). The increase in the number of leaves produced annually leads to a significant increase in leaf production with increasing levels of interaction with either *C. taxifolia* or *C. racemosa* (see ANOVAs results Table 5 and Figure 7A,B). Indeed, mean leaf production per shoot increased by 42% between stations 0Ct and 2Ct (Figure 8A) and by 19% between stations 0Cr and 2Cr (Figure 8B). Conversely, no such significant differences were detected for the below-ground tissues (see ANOVAs results Table 5 and Figure 8A,B).

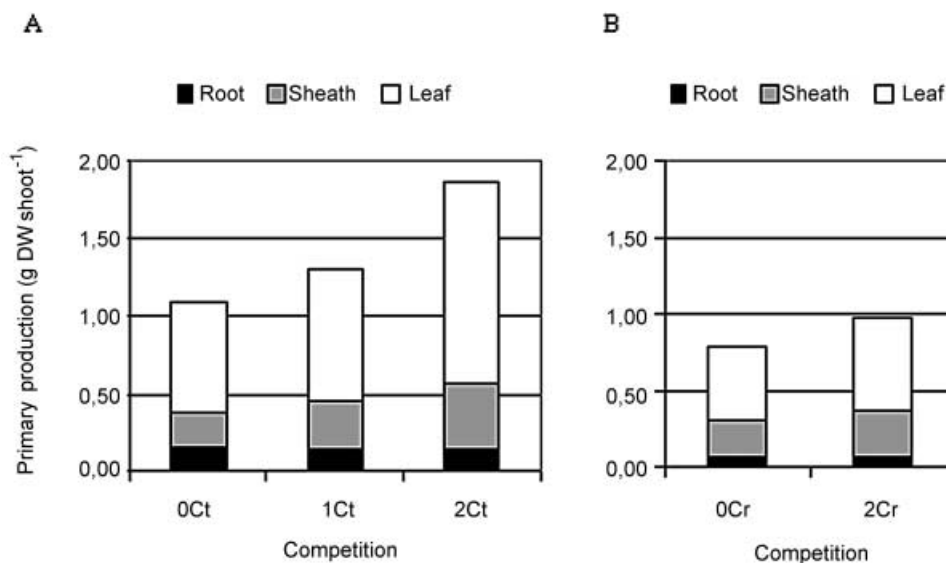


Figure 8. Mean total annual primary production (leaf, sheath and root) of *Posidonia oceanica* (expressed in g DW shoot⁻¹) when in competition with *Caulerpa taxifolia* (A) and *C. racemosa* (B).

DISCUSSION AND CONCLUSION

The seasonal variations observed for the various variables examined (number of leaves, leaf biometry, coefficient A) are consistent with the results found in the literature (Pergent & Pergent-Martini, 1988; Romero, 1989; Buia et al., 1992). Similarly, the epiphyte biomass follows the classical pattern of maximum spring values and minimum autumn values (Lepoint et al., 1999). The seasonal cycle of the phenological parameters in *Posidonia oceanica* therefore do not appear to be affected by the presence of the invasive algae.

In addition to the seasonal variability observed, it seems that the level of interaction between *P. oceanica* and the two *Caulerpa* species significantly modifies the vegetative development of the sea grass (Table 6).

Very few studies have explored the effects of interaction with *Caulerpa taxifolia* and *C. racemosa* on the phenology and primary production of *P. oceanica*, and the results of the present study confirm preliminary results found by Villèle & Verlaque (1994, 1995). Recently research on the interaction of sea grass (e.g. *P. oceanica* or *Cymodocea nodosa* (Ucria) Ascherson) on *Caulerpa* on different variables such as nutrients or density of the sea grass and *Caulerpa* have been published (Ceccherelli & Cinelli, 1997, 1998, 1999).

If the significant effects of competition on the vegetative development of *P. oceanica* have been confirmed, including a decrease in the mean length of the leaves as well as a decrease in their longevity, this study has also revealed that there occurs a significant increase in the number of leaves produced per year, leading to both a higher turnover and a higher leaf production.

A variation in the length of the thalli in *C. taxifolia* throughout the year 1999–2000, with maximum lengths in early autumn and a minimum in spring was detected in the present study. This evolution is quite similar to that observed in *P. oceanica*, but presents a lag period of approximately three months. Indeed, leaf lengths in *P. oceanica* exhibit maximum values in June–July and minimum values in winter (Wittman, 1984; Pergent & Pergent-Martini, 1988). This would tend to confirm the hypothesis of a competition for light between these two photoautotrophs; growth of the *C. taxifolia* thalli corresponds to the response of the plant in the acquisition of this resource. Studies involving another invasive species, namely *Sargassum muticum* (Yendo) Fensholt, have revealed that the indigenous algal community is altered as a result of, or in response to, an interspecific competition for both nutrients and light (Stæhr et al., 2000). This phenomenon seems to occur when several species covet the same ecological niche.

Variations in the seasonal growth of *C. taxifolia* would appear to be widespread for this species within the Mediterranean. Indeed, such variations have also been reported by Meinesz et al. (1993) and Belsher et al. (1994), who described minimum growth in winter and spring and maximum values in summer and autumn. It would seem that such seasonal variations also exist in the thalli lengths of *C. racemosa* (Piazzi et al., 1997). Moreover, the increase of mean thalli lengths of *C. taxifolia* found at the edge of *P. oceanica* meadows are in agreement with preliminary results found by Ceccherelli & Cinelli (1998).

The decrease in the longevity of the leaves of *P. oceanica* may be linked to the secondary metabolites regularly released by *Caulerpa*. This kind of interaction, the allelopathy, is an interference competition using toxic secondary metabolites. Indeed, it has been shown that *C. taxifolia* is able to cause leaf chlorosis and necrosis, conditions that can kill the leaves of *P. oceanica* (Villèle & Verlaque, 1995). Similarly, studies involving either methanolic extracts or purified caulerpenyne from *Caulerpa* have revealed a decrease or inhibition in the growth of different algae as well as Chlorophyta and Phaeophyta (Clavero et al., 1994; Ferrer et al., 1997; Lemée et al., 1997; Bitou et al., 1999). According to Lemée et al. (1997), this phenomenon may be at first time directly linked to the caulerpenyne activity, and thereafter, the degradation products, which are more stable, may also be involved. This reduced longevity may also be the result of the increased epiphyte biomass, which leads to an increased fragility of the leaves (Fresi, 1982) and increased competition with respect to resources (nutrients and light), these epiphytes being able to substantially reduce both the photosynthetic surface area (up to 50% in Dalla Via et al., 1998) and the incident light (30% in Cebrian et al., 1999). The decrease in leaf longevity and the increase in leaf turnover could thus represent a means of attenuating the degradation effects caused by caulerpenyne and/or the increase in epiphyte load. The increase in coefficient A could be bound with the increased epiphyte biomass. Indeed, the grazers have a food preference towards the epiphyte population because of a better assimilation of the latter compared to the leaves of *P. oceanica* themselves (Alcoverro et al., 1997).

The significant increase in leaf primary production in *P. oceanica* under increasing levels of interaction with either *C. taxifolia* or *C. racemosa* is essentially due to the significant increase in annual leaf production. This may be the result of accelerated meristematic activity. Indeed, the induction or inhibition of plant activity by the production of secondary metabolites (allelopathy) has been repeatedly demonstrated over the last 20 years, particularly in terrestrial systems. These phenomena generally involve the inhibition of either germination and/or the growth of pioneer species (Bernhard-Reversat, 1999; Hirai et al., 2000; Kathiresan, 2000; Ohno & Doolan, 2001). Thus, the increase of the turnover, linked to a lower longevity of the leaves of *P. oceanica* would confirm the observations carried out on the impact of the secondary metabolites of *C. taxifolia* on the animal and vegetal cells where a more important mortality has been observed (Guerriero et al., 1996; Lemée et al., 1997).

In terms of energy allocation, it is clear that *P. oceanica* experiences high energy costs to ensure leaf production. This increased primary production, which is brought on by interspecific competition with either *C. taxifolia* or *C. racemosa*, may, in the long term, lead to a shortage of nutrients necessary for plant growth. Indeed, although an increased allocation of photosynthetic products can, at least in the short term, lead to an energy surplus to the shoots of *P. oceanica* (Libes, 1983; Duarte et al., 1996), such a mechanism will be studied over the long term with nutrient measurement too, particularly under conditions

of rapid algal spread, to appreciate a possible change of the photosynthetic products transfer toward one of the two kind of shoots: with or without interaction with *Caulerpa*.

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