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Carbon Assimilation in *Posidonia oceanica*: Biotic Determinants

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Carbon assimilation in the Mediterranean seagrass *Posidonia oceanica* was measured by means of the ^{14}C technique. Whole shoots were harvested seasonally at 5 and 22 m depth at Lacco Ameno (Gulf of Naples) and incubated at constant saturating light in the laboratory. Carbon incorporation of different leaf sections as well as epiphytic assimilation were evaluated. Mean assimilation values of 1.42 ± 0.62 μgC mg^{-1} DW h^{-1} (N = 60) and 1.43 ± 0.70 μgC mg^{-1} DW h^{-1} (N = 48) were found in plants of *P. oceanica* collected at 5 and 22 m depth, respectively. Maximum carbon assimilation values, up to 2.98 μgC mg^{-1} DW h^{-1}, were recorded in February. The highest rates, as well as the lowest variability in carbon assimilation across seasons and depths, were generally recorded in mid-sections of leaves of rank II through IV, which pointed to a fundamental homogeneity in assimilative response of the bulk of the photosynthetic tissue. Epiphytic carbon assimilation was estimated to range between 33 and 52% of total *P. oceanica* shoot production, except for February when the epiphytic coverage was minor, in particular at 22 m. Tissue age, as expressed by leaf rank and tissue position along the leaf blade, was the major biotic factor affecting carbon assimilation capacity. On the other hand, depth seemed to have a minor influence on carbon production potential of *P. oceanica* leaves in comparison to the other factors. It is hypothesized that in seagrasses tissue age determines the capacity of carbon assimilation, while *in situ* light regimes regulates the plant adaptations to different depths.

Introduction

Production ecology of seagrasses has long been investigated, especially in relation to the factors that can affect growth patterns (see Hillman *et al.* 1989 for a review). In the Mediterranean species *Posidonia oceanica* (L.) Delile, production and growth are known to vary along depth gradients and to follow seasonal patterns (Buia *et al.* 1992, Alcoverro *et al.* 1995, Zupo *et al.* 1997). *Posidonia oceanica* meadows extend from near the surface down to 40 m depth, being exposed to a broad range of physical gradients, e. g. light. The adaptation of the plant to these different environmental conditions should rely on the ability to respond to external constraints as well as on inner regulating mechanisms (Ott 1979, Pirc 1989). The balance between the intrinsic and extrinsic factors is crucial for the success of colonization and for the stability of meadows. The slow growth, the particular reproductive strategy of the plant and the low genetic variability of populations result in a high fragility of the system and at present *P. oceanica* is a potentially endangered species (Buia and Mazzella 1991, Marbà *et al.* 1996, Procaccini *et al.* 1996).

Various methods have been employed to measure production in *P. oceanica* in relation to production yields and seasonal growth patterns. These include marking methods (Buia *et al.* 1992), measurements of oxygen evolution (Pirc 1986, Lorenti *et al.* 1995), ^{14}C assimilation (Libes and Boudouresque 1987) and reconstructive methods (i. e. lepidochronology, Pergent-Martini *et al.* 1994).

The aim of the present work was to evaluate the intrinsic carbon assimilation potential relatively independent of the different spatial and temporal plant locations. As light availability is widely considered to be the main factor governing plant production (Zimmermann *et al.* 1994), an experimental approach was devised to discriminate its role from other factors. To this end, carbon incorporation of plants sampled at different *in situ* light levels was measured at constant, saturating irradiance in the laboratory. In addition, the aim was to highlight the role of tissue age in relation to leaf growth patterns at different depths. The contribution of epiphytes in the carbon assimilation budget of the shoot was also approached. For this study, the ^{14}C incorporation technique was selected as the most suitable method.

Materials and Methods

The experiments were performed on *Posidonia oceanica* plants from Lacco Ameno (Island of Ischia, Gulf of Naples, Italy), a site characterized by a continuous meadow extending from 1 to 33 meters depth where studies have been conducted for several years (e. g. Wittman 1984, Pirc 1986, Mazzella *et al.* 1989, Buia *et al.* 1992). Environmental and biological parameters of the sampling site have been reported in Buia *et al.* (1992). In particular, *in situ* temperatures,

as measured in 1988–1990, have an annual average of 20.2° at 5 m and of 18.6° at 22 m. In summer, due to thermal stratification, a difference of 6.6° was recorded in July, while this difference was less than 0.1° in February. Differences in irradiance were even more remarkable between the two depths considered. Measurements of photosynthetically active radiation (PAR) at the top of the canopy showed a reduction of incident irradiance of about 80% between the two depths, the annual average of *in situ* irradiance at noon being 480 $\mu E\ m^{-2}\ s^{-1}$ and 105 $\mu E\ m^{-2}\ s^{-1}$ at 5 and 22 m depth, respectively.

Whole shoots of *P. oceanica*, still attached to the rhizome, were sampled by SCUBA diving at 5 and 22 m depths in November 1993 and in February, May and August 1994.

For the incubation experiments, one whole shoot was carefully separated from the others, rinsed with filtered seawater and inserted in the incubation device (Fig. 1). The incubation bottle, specifically devised, was a two-chamber cylinder made of plexiglas with the upper chamber, designed to contain the shoot,

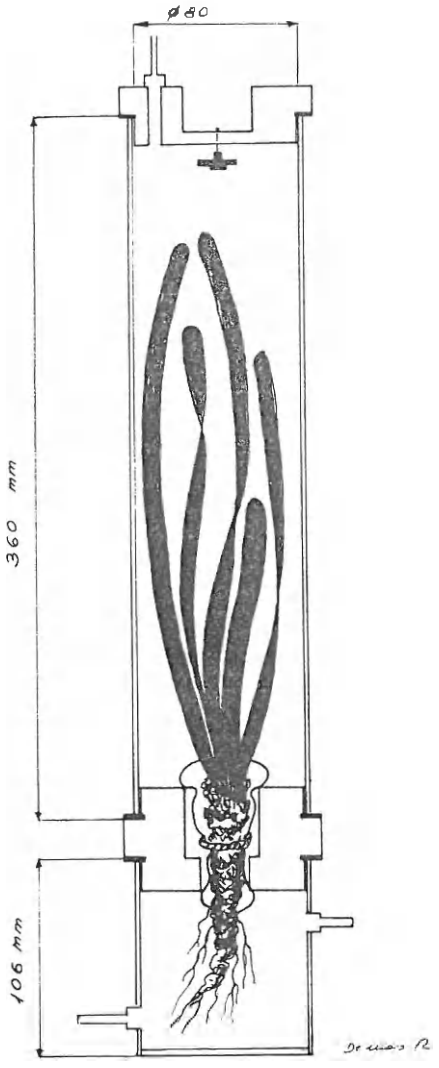

Fig. 1. Incubation vessel used for determination of *Posidonia oceanica* carbon incorporation.

having a volume of 1.72 L. The two chambers were connected through a hole and a latex seal around the basis of the plant prevented any passage of liquid between the two chambers. The two chambers of the cylinder were filled with filtered seawater and 40 µCi of $Na_2\ ^{14}CO_3$ were injected into the upper chamber through an opening in the lid. The lower chamber, holding the rhizome, contained no radioactive carbon. A magnetic bar applied below the lid of the upper chamber provided gentle stirring throughout the incubation which was carried out for three hours at the temperature recorded *in situ*. Two white fluorescent lamps, placed at either side of the cylinder, gave an irradiance of 250 $\mu E\ m^{-2}\ s^{-1}$, measured inside the cylinder by means of a Biospherical submersible quantum probe (QSI-140). This value is above the saturation light level reported for *Posidonia* (Pirc 1986, Lorenti *et al.* 1995).

In order to distinguish between *Posidonia* and epiphyte production, some additional leaves were carefully freed from their epiphytic coverage and incubated in the same chamber as the whole shoot. Furthermore, several leaf sections of 15 cm length were incubated in 200 mL tubes at the same experimental conditions as those described for the cylinder. In order to assess dark carbon assimilation, some incubation experiments using the 200 mL tubes were also performed in the dark.

After incubation, the shoot was rinsed several times in filtered seawater and each leaf was measured and numbered, 'leaf 1' being the youngest green leaf, and epiphytic coverage evaluated. Each leaf was divided into three sections of equal length, a proximal, a median and an apical section. For leaves less than 18 cm long the whole blade was used. Some older leaves had a brown (dead) tip which was considered separately from the green apical part. For digestion of *Posidonia* tissue, a method modified after Lewis *et al.* (1982) was developed. Three 2 cm pieces from each section were cut off with a razor blade, put into a scintillation vial with 10 mL of concentrated HNO_3 for 48 hours. The sheath of adult leaves, dead sheaths, as well as slices of the rhizome were cut into pieces and acid digested. One mL of the acid extract was diluted with 9 mL of TRIS buffer. One mL of the resulting solution was mixed with 9 mL of Aquasol scintillation cocktail, left overnight and thereafter read with a Packard Liquid Scintillator. The $Na_2\ ^{14}CO_3$ solution was standardized at each experiment. For each kind of tissue (leaves, sheath and rhizome), several specimens were prepared as described above, without adding the radioactive carbon and the scintillator reading subtracted as a blank. In order to distinguish the carbon assimilation of *Posidonia* from that of the epiphytic community, the three scintillator readings for each leaf section were pooled and 'scraped' leaf values were subtracted from the untreated leaf values, taking care to consider leaves of similar rank and epiphyte coverage. As a control,

some leaves apparently without any epiphytes were scraped and incubated.

The evaluation of dry weight per unit area was performed on leaves of different age and different sections within the leaves. No obvious pattern of variation could be detected, thus an average value of 4.4 mg DW cm^{-2} (SD = 0.697, n = 40) has been used.

Multifactor analysis of variance (M-ANOVA) was performed in order to assess the effect of different factors (depth, month, leaf rank and 'tissue level', i. e. distance of tissue in cm from leaf basis) on carbon assimilation. A MANOVA test was also performed on data collected at each month in order to determine seasonal differences in the effect of the considered factors on the assimilation rates. Linear regression analyses were conducted to determine the effect of 'tissue level' on carbon incorporation for both different leaf ranks and seasons. A multiple range test was performed in order to investigate the difference in carbon incorporation pattern along the blade by leaves of different rank. All analyses were performed with the aid of the STATGRAPHICS PLUS statistical package (Manugistics Inc. 1994).

Results

Among the analyzed shoots, the number of leaves ranged between 4 (August at 5 m) and 7 (February at 22 m). At 5 m, leaf length varied between 5.5 cm for the youngest leaf to 62 cm for the III leaf both being recorded in August, while at 22 m it was between 5 cm for the youngest leaf in November to 86 cm for the III leaf in August.

When the whole pool of data was considered, *Posidonia* free from epiphytes showed no significant difference in production potential at the two stations considered: 1.42 ± 0.62 μgC mg^{-1} DW h^{-1} at 5 m (N = 60) and 1.43 ± 0.70 μgC mg^{-1} DW h^{-1} (N = 48) at 22 m (t = 0.366, d. f. = 104, p = 0.71).

Dark carbon assimilation by leaves was always detected and showed similar values for both stations, 0.25 ± 0.03 and 0.27 ± 0.02 μgC mg^{-1} DW h^{-1} for 5 and 22 m, respectively. On the contrary, scintillator readings for sheaths and slices of the rhizome, after 'blank' values had been subtracted, were too low to be significant.

Considering leaf sections, carbon assimilation in plants from both depths was highest in the mid sections of leaves ranking from II to IV, where values up to 2.98 μgC mg^{-1} DW h^{-1} were recorded (Figs 2, 3). The apical part of bare *Posidonia* leaves showed generally lower assimilation and very low values were recorded for brown tips, max. 0.13 μgC mg^{-1} DW h^{-1}.

Assimilation measurements performed in the 200 mL tubes were not dissimilar from the data obtained for the cylinder incubation, when leaf rank and leaf section were taken into account.

On a seasonal basis, the highest carbon assimilation rates for both stations were recorded in February (2.07 ± 0.45 μgC mg^{-1} DW h^{-1} at 5 m and 2.22 ± 0.96 μgC mg^{-1} DW h^{-1} at 22 m both in leaf mid sections), when a wider range of values were found as compared to those recorded in other months, based on a greater variability in assimilation among different leaf sections (Figs 2, 3).

Differences in production between the two stations as well as between seasons were found when carbon assimilation on a leaf surface basis (i. e. by integrating assimilation by the whole area of individual leaf portions) was considered, due to the substantial differences both for the length and the number of leaves in a shoot. The highest contribution by individual leaves, as well as the highest differences between depths, were recorded in August when maximal leaf length was observed at 22 m (Figs 4A, 4B).

Considering the whole shoot, at 5 m the highest value of organic carbon production was observed in February when leaf surface was not at its maximum (Fig. 5A), while at 22 m, the maximum carbon assimilation per shoot was recorded in August when the highest value of leaf surface was also recorded (Fig. 5B).

Epiphytic carbon assimilation, calculated on the basis of *Posidonia* leaf surface is here reported for the whole shoot. Epiphyte carbon assimilation rates on plants from 5 m depth ranged from 59.8 μgC $shoot^{-1}$ h^{-1} in November to 133.4 μgC $shoot^{-1}$ h^{-1} in August, while at 22 m it ranged from 7.95 μgC $shoot^{-1}$ h^{-1} in February to 223 μgC $shoot^{-1}$ h^{-1} in August (Fig. 5A, 5B). For the leaves that were scraped before incubation although no visible epiphytes were observed (control), the scintillator readings were similar to those of untreated leaves of similar rank with no visible epiphytes.

The older the leaves the more consistent was the epiphytic coverage, in particular along the leaf margins and in the distal section. The youngest (I) leaf had no visible epiphytes at all or at most 5% coverage in the distal part. In the apical section of older leaves, the percentage of leaf surface covered by epiphytes was up to 60–80% (Table I). Most of the epiphytic algae were encrusting soft and calcareous algae, such as *Myrionema*, *Hydrolithon*, and *Pneophyllum*, but some erect algae (*Castagnea*, *Giraudya*, *Laurencia*) were also observed, mainly in summer. Heterotrophic epiphytes (e. g. Hydrozoa, Bryozoa, Polychaeta) were also present, mainly in February at 5 m. Epiphyte assimilation varied according to the position along the leaf blade; in particular, epiphytes of green apical parts showed higher carbon assimilation values as compared to those growing an brown tips of the same leaf. Epiphyte production was estimated to represent 33–52% of total shoot production except for February when the epiphytic coverage was minor in

particular at 22 m. Maximum relative contribution was recorded at 22 m in November (Fig. 6).

A multifactor ANOVA analysis conducted on the whole set of data revealed the major importance of the season in affecting assimilative performance by leaves, followed by 'tissue level', (i.e. the distance of the blade section from the leaf basis, in cm) and leaf rank (Table II). Results of the MANOVA performed on data collected at each month are reported in Table III. Only in November depth had some effect. Tissue age effect, as described by differences in assimilation by tissue level and leaf rank, was significant in February; in particular, tissue position along the blade was highly significant. None of the factors significantly affected the carbon assimilation in May and August.

A comparison of carbon incorporation rates in leaves of different ranks (pooled across seasons), performed by means of a multiple range test, showed how the generally oldest leaf (no. VI) differed from

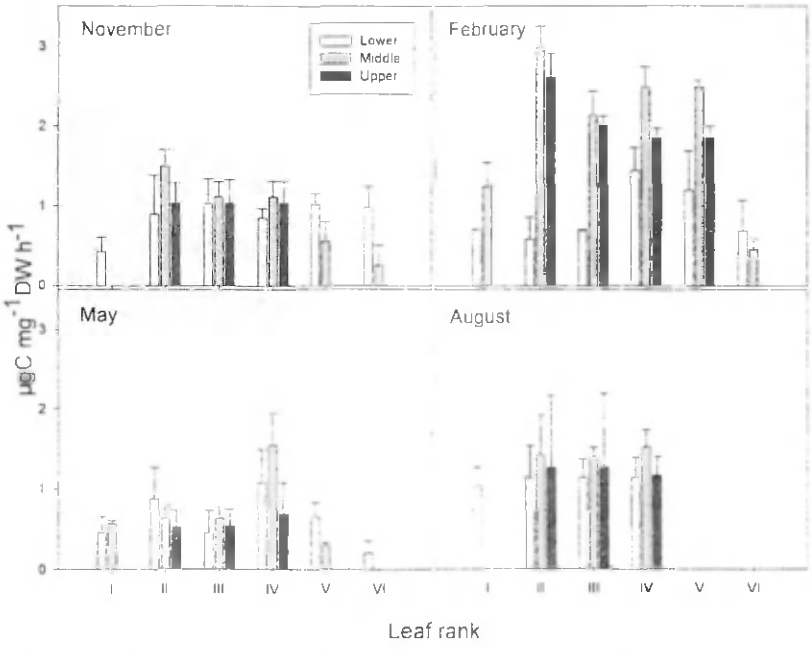

Fig. 2. Rates of carbon incorporation of *P. oceanica* shoots from 5 m depth, divided by leaf rank and blade portion (mean ± standard errors).

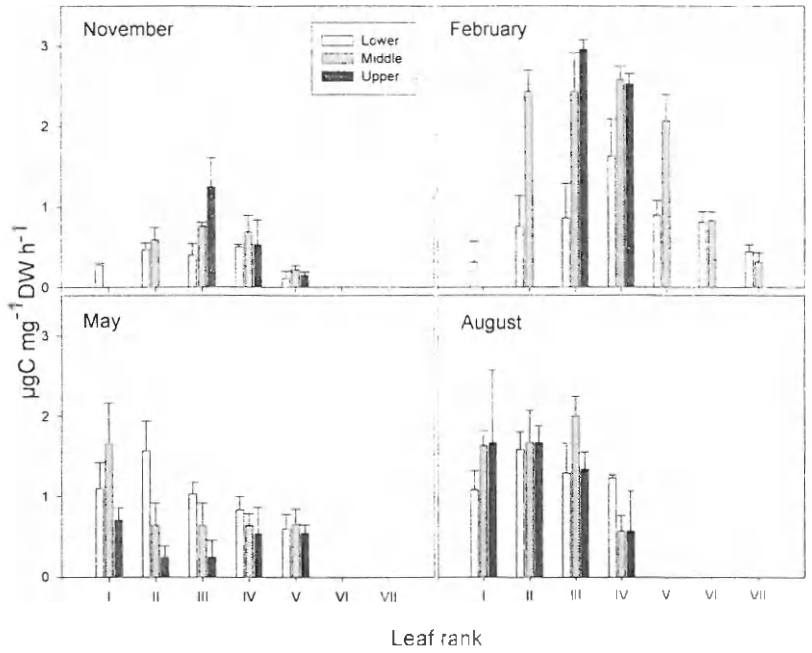

Fig. 3. Rates of carbon incorporation of *P. oceanica* shoots from 22 m depth, divided by leaf rank and blade portion (means ± standard errors).

leaves II–IV, but not from the first and fifth leaf (Table IV).

In leaves of different ranks, carbon assimilation was correlated with distance from leaf basis in leaf I and leaf V, but the sign was reversed (Table V).

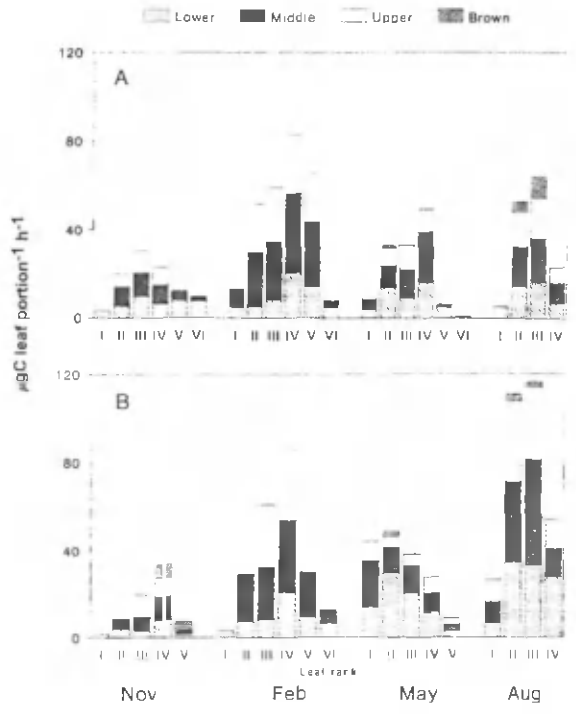

Fig. 4. Rates of carbon incorporation by different leaf portions of *P. oceanica* shoots from 5 m (a) and 22 m (b) depth.

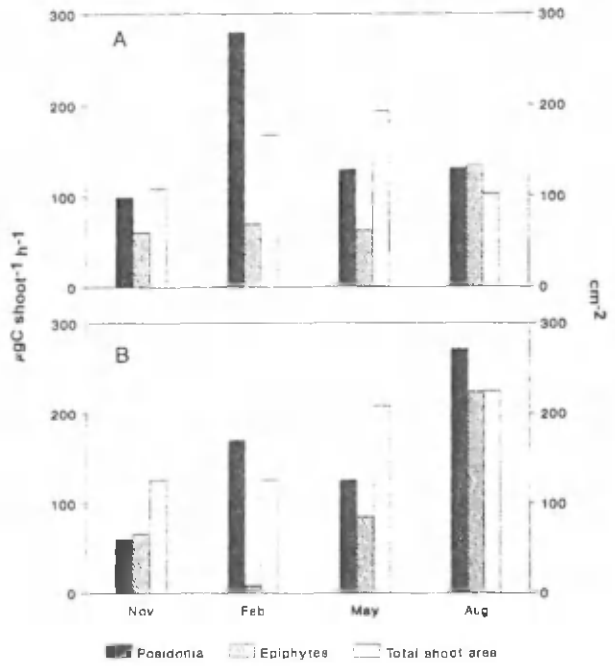

Fig. 5. Rates of total carbon assimilation by leaf tissue and epiphytes in the analyzed *P. oceanica* shoots. On the second Y axis the total shoot area is plotted.

Discussion and Conclusion

The present study showed a low variability in carbon assimilation of *Posidonia oceanica* leaves at constant saturating irradiance. By controlling irradiance, it was possible to assess to which extent other factors affected carbon assimilation. Within the low variability recorded, however, factors which have a major role in the capacity of carbon assimilation by *P. oceanica* were identified. In particular, leaf age and leaf rank seem to be driving factors, from which the importance of the month in relation to the seasonality found in the leaf growth (Buia *et al.* 1992) derives.

The highest as well as the less variable rates of carbon incorporation were found for leaf tissue from the leaves of intermediate ranks (II–IV) both on a within-shoot and a seasonal basis. On the other hand, lower values and higher variability in carbon assimilation rates occurred both in senescent and newly formed tissue as compared to those observed for leaves II–IV. The diversity between these latter leaves and the others was confirmed by the statistical comparison of assimilation rates in leaf VI, generally the oldest of the shoot in this study, with those of each of the other leaves. Assimilation levels of leaves I, V and VI do not differ significantly, although the meaning of such similarity is clearly two-edged, in the sense that the young tissue of leaf I has not yet reached the physiological maturity whereas senescent leaves have already passed such stage. Furthermore, gradients of carbon assimilation rates along the leaf, which were directly related to tissue age, were evident in leaves I and V. These gradients followed an opposite trend in the youngest versus the oldest leaves, increasing towards the tip for the youngest and decreasing with increasing distance from the sheath in the oldest leaves. The lack of a significant trend in carbon assimilation along the blade of leaf VI might be explained by this leaf being almost completely senescent. On the contrary, the same lack of axial trend in leaves II–IV supports the view of a homogeneity in production by the most active photosynthetic tissues.

In short, the bulk of shoot carbon assimilation was performed by physiologically mature tissues, which were represented by the intermediate leaves (from II to IV), and in particular by their mid-portions where photosynthetic performance was relatively high and stable. This is in accordance with what has been previously found by using the Zieman leaf marking method, whereby only some leaves (II and III, in this case) could be representative of the whole shoot production (Zupo *et al.* 1997). Similarly, Libes and Boudouresque (1987) reported the highest carbon assimilation to occur in leaves II to IV. The low variability of the carbon assimilation measurements reported (Libes and Boudouresque 1987 and this study) seems to validate well the ^{14}C approach for measuring productivity in *P. oceanica*, at least for short (2–3 hours)

Table I. Percentage of epiphyte covering on leaves of *P. oceanica* of different ranks.

	Leaf portion	5 m						22 m						
		I	II	III	IV	V	VI	I	II	III	IV	V	VI	VII
November	Middle	–	–	–	40	50	50	–	–	–	50	50		
	Upper	–	15	30	40	50	50	–	5	20	60	60		
February	Middle	–	–	–	50	50	60	–	–	–	–	1	–	20
	Upper	–	25	30	50	60	70	–	–	5	5	10	15	20
May	Middle	–	10	10	20	30	60	–	–	20	20	70		
	Upper	5	35	40	40	30	60	–	5	30	40	70		
August	Middle	–	25	30	50			–	–	–	50	70		
	Upper	–	75	80	50			5	40	40	70	70		

– denotes covering estimates below 5%.

incubations. Furthermore, studies on oxygen evolution, converted in terms of carbon assimilation, performed on whole *P. oceanica* plants (Pirc 1986) or on leaf sections (Lorenti *et al.* 1995), reported values in the same range as those recorded in the present study.

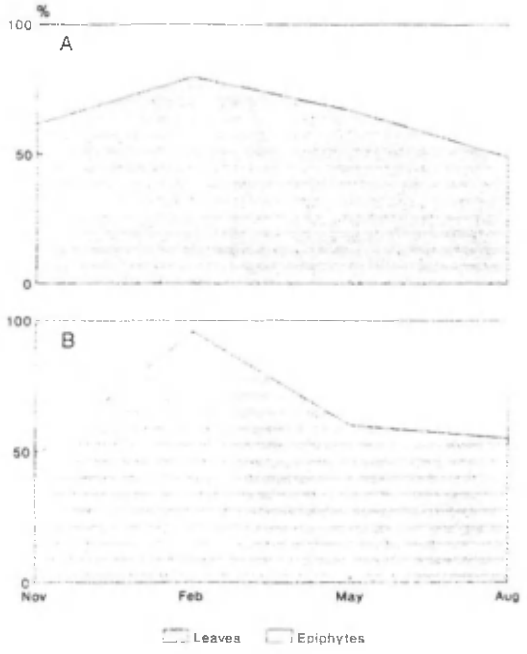

Fig. 6. Relative contribution of leaf tissue and epiphytes to total *P. oceanica* shoot production in plants from 5 m (a) and 22 m (b) depth.

Table II. Results of MANOVA comparing the effects of different factors on carbon assimilation by leaf tissue of *P. oceanica* (pooled data).

Source	D.f.	F	p	sign.
Depth	1	0.42	0.53	NS
Tissue	22	1.91	0.02	*
Month	3	16.75	0.00	***
Leaf rank	5	2.99	0.02	*

NS = non significant; * $p < 0.05$; *** $p < 0.001$

The results found in *P. oceanica* are consistent with patterns detected in *Zostera marina* L., where light and tissue ages were found to be the major determinants in photosynthesis vs. irradiance relationships (Mazzella and Alberte 1986, Zimmermann *et al.* 1995). Different growth patterns and different persistence of leaves in the shoot (i.e. higher specific growth in *Z. marina* vs. lower leaf renewal rates in *P. oceanica*) can account for some differences found between the two species (leaf apices in *Z. marina* accounting for the highest rates).

Transfer of photosynthates from the leaves to the sheaths and the rhizome has been shown to occur in *Posidonia oceanica* (Libes and Boudouresque 1987); however, the short duration of the incubations in this study (3 hours), did not permit a measurable accumulation of marked carbon in non-photosynthetic tissues.

An issue which warrants further investigation is the occurrence of dark carbon assimilation by *Posidonia* leaves. Previous authors have reported such phenomenon to occur in *P. oceanica*, equal to up to 2.5% of the light carbon assimilation (Libes 1984), as well as in other marine macrophytes (Cabello-Pasini and Alberte 1997). In the present study, the dark carbon assimilation amounted to an average of 15% of the values recorded in the light incubations. This figure is quite high and needs confirmation through further experimental work.

The contribution of the epiphytic community was substantial, ranging between 33 and 52% of total shoot production. Epiphyte biomass, evaluated in previous studies (Buia *et al.* 1992, Mazzella and Ott 1984) can represent at most 20–40% of *Posidonia* leaf biomass. However, photosynthetic efficiency of the epiphytic community has been shown to be higher than that of the *Posidonia* plant itself (Libes 1984, Mazzella and Ott 1984). The higher efficiency of the epiphytic community can be seen in the different morphology and growth strategies of macroalgae vs vascular plants, according to the model of Littler and Littler (1980). Macroalgae invest more in

Table III. Results of MANOVA comparing the effects of different factors on carbon assimilation by leaf tissue of *P. oceanica* in the four months.

Source	November			February			May			August		
	D.f.	F	p	D.f.	F	p	D.f.	F	p	D.f.	F	p
Depth	1	8.13	*	1	0.03	NS	1	0.21	NS	1	0.04	NS
Tissue level	10	0.60	NS	9	5.28	***	11	1.01	NS	12	0.68	NS
Leaf rank	5	1.27	NS	5	2.99	*	5	1.06	NS	3	0.61	NS

NS = non significant; * $p < 0.05$; *** $p < 0.001$

Table IV. Results of multiple range analysis for the means of carbon assimilation rates in leaves of *P. oceanica* of different ranks.

Leaf no.	Difference	Interval
VI-I	0.316	0.60
VI-II	0.644*	0.56
VI-III	0.593*	0.55
VI-IV	0.596*	0.55
VI-V	0.284	0.59

* denotes a statistically significant difference

Table V. Correlation coefficients (r) for the effect of 'tissue level' on carbon assimilation by *P. oceanica* leaf tissue.

Leaf rank	r	p	
I	0.69	0.01	**
II	−0.11	0.63	NS
III	−0.02	0.94	NS
IV	−0.25	0.23	NS
V	−0.56	0.05	*
VI	−0.34	0.45	NS

NS = non significant; * $p < 0.05$; ** $p < 0.01$

production than in other processes, as vascular plants also do (e. g. storage in the rhizomes). Moreover, seagrasses, but not the algae, have been reported to be CO_2 limited at present day's marine CO_2 concentrations (Beer 1989, Durako 1993, Zimmermann *et al.* 1995, Beer and Koch 1996). On the other hand, a higher variability in epiphyte production can be in relation to seasonal fluctuations which are more pronounced than in plant leaves and are more influenced by environmental factors. This explains the variability in the contribution of epiphytes found both within and between species (Borowitzka 1989). The interactions between *P. oceanica*, as well as other vascular plants, and their epiphytes are still to be clarified, although some functional links have been reported to occur (e. g. Penhale 1977, Fresi and Saggiomo 1981, Libes and Boudouresque 1987).

In summary, our results point to a fundamental homogeneity in carbon assimilation of *P. oceanica* even within a variability linked to different factors, mainly to tissue age. In particular, in May and August no significant effect on plant assimilation potential was exerted either by depth of growth site or by season. However, differences in carbon uptake did occur and they were related to tissue age as described by leaf rank and different leaf portions. This was most evident in February when at both stations a major age differentiation among the leaves occur, coupled to a greater proportion in terms of biomass of young tissue (Buia *et al.* 1992). In November, depth seems to differentiate between the two stations, and again, this is related to the leaf developmental status. In fact, a marked difference between the two depths has been reported in November, as far as pattern of leaf elongation and leaf shedding and renewal are concerned. On the other hand, the similar carbon assimilation rates recorded in spring and summer reflect the homogeneity of leaf development experienced at the two stations (Buia *et al.* 1992).

Light is supposed to be the major factor affecting production levels in marine plants and with the approach used for this study, i. e. incubating at constant saturating irradiance levels, the seasonality and difference between stations are mainly attributable to plant biological features. Our results indicate that tissue age is the best indicator of carbon assimilation capacity, excepting environmental parameters, first of all irradiance and/or temperature and nutrient availability (Hillman *et al.* 1989, Zupo *et al.* 1997). Changes in biomass and growth rates of *P. oceanica* in relation to depth (Buia *et al.* 1992) are caused primarily by the variation in irradiance parameters and by adaptations of the plant to them (Mazzella and Alberte 1986, Hillman *et al.* 1989).

In conclusion, the effect of tissue age on seagrass carbon assimilation is a major intrinsic factor, which can be assumed to be a valid parameter to be taken into consideration for these clonal plants. Differences between species can be in relation to the specific growth rates of a single seagrass species. It can be synthetized that tissue age, in relation to species-specific growth patterns, determines the capacity of carbon assimilation, while light regulates the plant adaptations to different depths.

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