

Epiphyte Accrual on *Posidonia oceanica* (L.) Delile Leaves: Implications for Light Absorption

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We examined the pattern of epiphyte accrual along the life-span of *Posidonia oceanica* leaves, both for the total epiphyte community and the main epiphyte groups (i. e. red encrusting algae and brown erect algae). Moreover, we document the importance of this epiphyte accrual pattern for evaluating *P. oceanica*-epiphyte interactions by assessing the dependence of the quantity and quality of light absorbed by epiphytes on their accrual pattern. Epiphyte biomass increased with leaf age following a sigmoidal curve ($r^2 = 0.90$, $P < 0.001$), both for the epiphyte community and for the two main groups. Total epiphyte biomass increased with leaf age at a rate of about 0.03 day^{-1} to reach a constant maximum value of $2.60 \text{ mg DW cm}^{-2}$ on leaves older than 200 days. Brown erect algae grew about an order of magnitude faster (0.120 day^{-1}) than red encrusting ones (0.017 day^{-1}). However, the former group of algae reached their maximum biomass (1 mg DW cm^{-2}) on 150 days-old leaves, whereas red encrusting algae continued to grow along the whole leaf life-span to reach a maximum biomass of $1.70 \text{ mg DW cm}^{-2}$. The non-linear increase in epiphyte biomass with leaf age involved a non-linear increase in epiphyte light absorption with leaf age, which reached a maximum constant value of 30% of incident light on 250 days-old leaves. Moreover, because red encrusting algae contribute a higher fraction to total epiphyte biomass on older leaves, we observed a shift in absorbed light quality with increasing leaf-age. Our results indicate the importance of accounting for the pattern of epiphyte accrual with leaf age when assessing seagrass-epiphytes interactions, especially for long-lived seagrass species where epiphytes may differ much in growth and biomass between young and old leaves.

Introduction

The seagrass species *Posidonia oceanica* (L.) Delile is widely distributed along the Mediterranean Coast (Den Hartog 1970) and has an important ecological role. Meadows of *P. oceanica* fuel a large food web and provide shelter for a high number of species (Templado 1984, Gambi *et al.* 1989). This is a long-lived species, whose leaves may attain a maximum age of 300 days (Duarte 1991). As a result of their long life span, old *P. oceanica* leaves normally support high epiphyte loads (Casola *et al.* 1987, Romero 1988). High epiphyte loads may exert substantial effects on the growth of seagrass leaves, such as shading (Hootsmans and Vermaat 1985, Silberstein *et al.* 1986), or gas and nutrient exchange with host leaves (McRoy and Goering 1974, Sand-Jensen 1977). For *P. oceanica*, the importance of these effects should depend on the pattern of epiphyte accrual along the leaf-life span, because epiphyte loads increase greatly from young to old leaves (Casola *et al.* 1987). Yet, the pattern of epiphyte accrual along the life-span of *P. oceanica* leaves remains to be described with precision.

One of the major problems to establish accurately the pattern of epiphyte accrual on leaves results from the classical method to estimate the age of *P. oceanica* leaves (i. e. the leaf marking technique). This technique confers both low resolution and accuracy to leaf age estimates, because it only allows as many age estimates as mean number of leaves per shoot and derives a mean age estimate for each leaf order (Ott 1980). This problem was solved by the application of the method of Erickson and Michellini (1957) and subsequent derivation of continuous values of leaf age (Cebrián *et al.* 1994). This technique has proved very useful to ascertain the time course of leaf-age dependent properties, such as leaf consumption by herbivores (Cebrián *et al.* 1996 a, b).

In this paper we characterise the epiphyte community on *P. oceanica* leaves in spring, and we use the method proposed by Cebrián *et al.* (1994) to derive the patterns of epiphyte accrual along the life-span of *P. oceanica* leaves. We do it both for the total epiphyte community and for the most abundant groups at the sampling time, i. e., the red encrusting algae and the brown erect algae. Furthermore we an-

analyse the dependence of light absorption by epiphytes on their accrual pattern, as an example of the importance of accounting for the pattern of epiphyte accrual on *P. oceanica* leaves when addressing the interactions between this seagrass and its epiphytes.

Methods

Fifty shoots of *Posidonia oceanica* were collected at the depth of maximum density in Cala Jonquet (42°18.26' N, 3°18.11' E, Spanish Mediterranean Coast) in April 1993. The length and order of all leaves in each shoot were recorded. Epiphytes were recovered with a scalpel from consecutive 5 cm leaf sections from base to apex and sorted under a dissecting microscope into the four dominant groups (red encrusting algae, brown erect algae, bryozoa and hydrozoa; Ballesteros *et al.* 1984). After drying the samples overnight at 80 °C, we derived the mean epiphyte biomass (mg DW cm⁻²) for the consecutive 5 cm leaf sections both for the total epiphyte community and main groups.

Leaf age was estimated by the method proposed by Cebrián *et al.* (1994). This technique uses a geometrical approach to derive the age of the youngest leaf in a shoot as a fraction of one plastochrone interval (Erickson and Michellini 1957). The age of any older leaf in the shoot can be calculated by adding its order minus one to the age of the youngest leaf. Age values in plastochrone interval units can be converted into days from knowledge of the chronological equivalence of the plastochrone interval (Cebrián *et al.* 1994). The age estimates obtained by this procedure refer only to the leaf apex.

We examined the patterns in epiphyte accrual with increasing leaf age (epiphytes on the apical 5 cm leaf sections) and accrual along the leaf blade, both for the total epiphyte community and for the main groups (red encrusting and brown erect algae). Because the precision of the age estimates corresponds to the mean chronological equivalence of one plastochrone interval (Cebrián *et al.* 1994), the relationship between epiphyte biomass and leaf age was derived after averaging the measurements of epiphyte biomass over 30-day leaf age intervals. A von Bertalanffy equation (Peters 1982) was fitted by least-squares regression analyses to the relationship between epiphyte biomass and leaf age:

$$B_t = \frac{B_{\max} B_0 e^{gt}}{B_{\max} - B_0 + (B_0 e^{gt})}$$

where B_t , B_{\max} , B_0 (all in mg DW cm⁻²) are the epiphyte biomass at leaf age t (days), maximal and initial biomass, respectively, and g (day⁻¹) is the epiphyte net maximal growth rate.

To provide an example of the importance of considering the pattern of epiphyte accrual along the lifespan of *Posidonia oceanica* leaves when addressing the interactions between the seagrass and its epi-

phytes, we analysed the leaf-age dependence of light absorption by epiphytes. We measured light absorption and not light extinction (Sand-Jensen and Sondergaard 1981), because light absorption is inherent to the optical properties of epiphytes, whereas light extinction is highly dependent on the radiation field used (Preisendorfer 1961). Epiphyte biomass and light absorption were measured on the apical 5 cm sections of 47 leaves encompassing the entire range of leaf age. Moreover we explored light absorption at biomasses higher than those found on the sampled leaves to best resolve specific absorption coefficients (i. e. slope of the initial linear increment in light absorption with epiphyte biomass). Light absorption was measured on glass fibre filter (Whatman GF/F) at 1 nm intervals along the PAR range (between 400–700 nm) in a Shimadzu UV-2100 dual-beam scanning spectrophotometer. A wet glass fibre filter was used as a blank (Mitchell and Kiefer 1988). We used the measurements at 675 nm to represent the absorption by photo-epiphytes and that at 400 nm to represent the absorption by the total epiphyte community (Agustí and Cruzado 1992). These measurements were corrected by subtracting the absorption at 750 nm, thereby excluding residual scattering and non-pigment red light absorption (Duysens 1956). Light absorption was expressed as absorptance (i. e. the fractional light absorbed by pigments), which was derived from absorbance (i. e. optical density, which reflects the logarithmic light absorption) using the equation (Clayton 1973):

$$\text{Fraction absorbed} = 1 - 10^{-\text{absorbance}}$$

Each measurement was triplicated to account for epiphyte patchiness on the leaf tips considered. The specific absorption coefficients of red encrusting and brown erect algae were also examined.

We only estimated light absorption by epiphytic pigments, and did not make any effort to account for the absorption by inorganic compounds. Furthermore, scraping may disrupt the physical structure of epiphytes, thereby altering their absorption properties. However, we did not intend to estimate total shading by epiphytes on *Posidonia oceanica* leaves, but to document the relevance of the epiphyte accrual pattern on *P. oceanica* leaves to address *P. oceanica*-epiphyte interactions.

Results and Discussion

Total epiphyte biomass ranged from < 0.1 mg DW cm⁻² to 4.6 mg DW cm⁻², with a mean value of 0.97 (± 0.16) mg DW cm⁻². These values are very similar to those reported elsewhere during the same season (Mazella and Ott 1984, Ballesteros 1987, Romero 1988). On the average, red encrusting algae and brown erect algae accounted for 76% and 21% of the total epiphyte biomass, respectively. Bryozoa and hydrozoa were much less abundant, representing

about 2.9% and 0.1% of the total biomass, respectively. These relative abundances are consistent with previous findings (Ballesteros 1987).

Epiphyte biomass increased from the leaf base towards the apex, and on the average epiphytes reached higher biomasses on the blades of older leaves (Fig. 1). The relative abundance of each epiphyte group differed notably along the leaf blade. Red encrusting algae tended to increase linearly from base to apex, whereas brown erect algae tended to increase exponentially (Fig. 1). Bryozoa reached maximal biomasses at intermediate blade sections, in accordance with previous findings (Casola *et al.* 1987). The need for a relatively rigid leaf substratum could explain bryozoa selection of intermediate leaf portions over apical ones (Casola *et al.* 1987).

Epiphyte biomass increased with leaf age following a sigmoidal curve ($r^2 = 0.90$, $P < 0.001$), both for total biomass and for red encrusting and brown erect algae (Fig. 2). This is in agreement with previous observations for other seagrass species (Borum 1987, Vermaat and Hootsmans 1991). The initial exponential increase in total epiphyte biomass with increasing leaf age ($g = 0.03 \text{ day}^{-1}$, Fig. 2) indicates that epi-

phyte growth far exceeds losses by grazing or dislodgement (Bothwell 1983). Total biomass reached a maximum value of about $2.60 \text{ mg DW cm}^{-2}$ on leaves older than 200 days, pointing to a balance between epiphyte growth and loss processes (Borum 1987).

The maximal growth rate of brown erect algae ($g = 0.120 \text{ day}^{-1}$) was about on order of magnitude faster than that of red encrusting algae ($g = 0.017 \text{ day}^{-1}$) (Fig. 2). Brown erect algae reached a maximal biomass of about 1 mg DW cm^{-2} at half the leaf life-span (i. e. about 150 days), whereas red encrusting algae continued to increase over the entire leaf life-span to reach a maximal biomass of about $1.70 \text{ mg DW cm}^{-2}$. These differences resulted in a progressive dominance of encrusting red algae over brown erect algae with increasing leaf age.

Light absorption by epiphytes increased non-linearly with epiphyte biomass (Fig. 3), as described by the equations:

$$\begin{aligned} \text{Absorptance (675 nm)} \\ &= 10.15 + 13.07 \text{ Epiphyte biomass} \\ &\quad - 0.57 \text{ Epiphyte biomass}^2 \\ (n = 60; R^2 = 0.85; F = 162.33; P < 0.0001) \end{aligned}$$

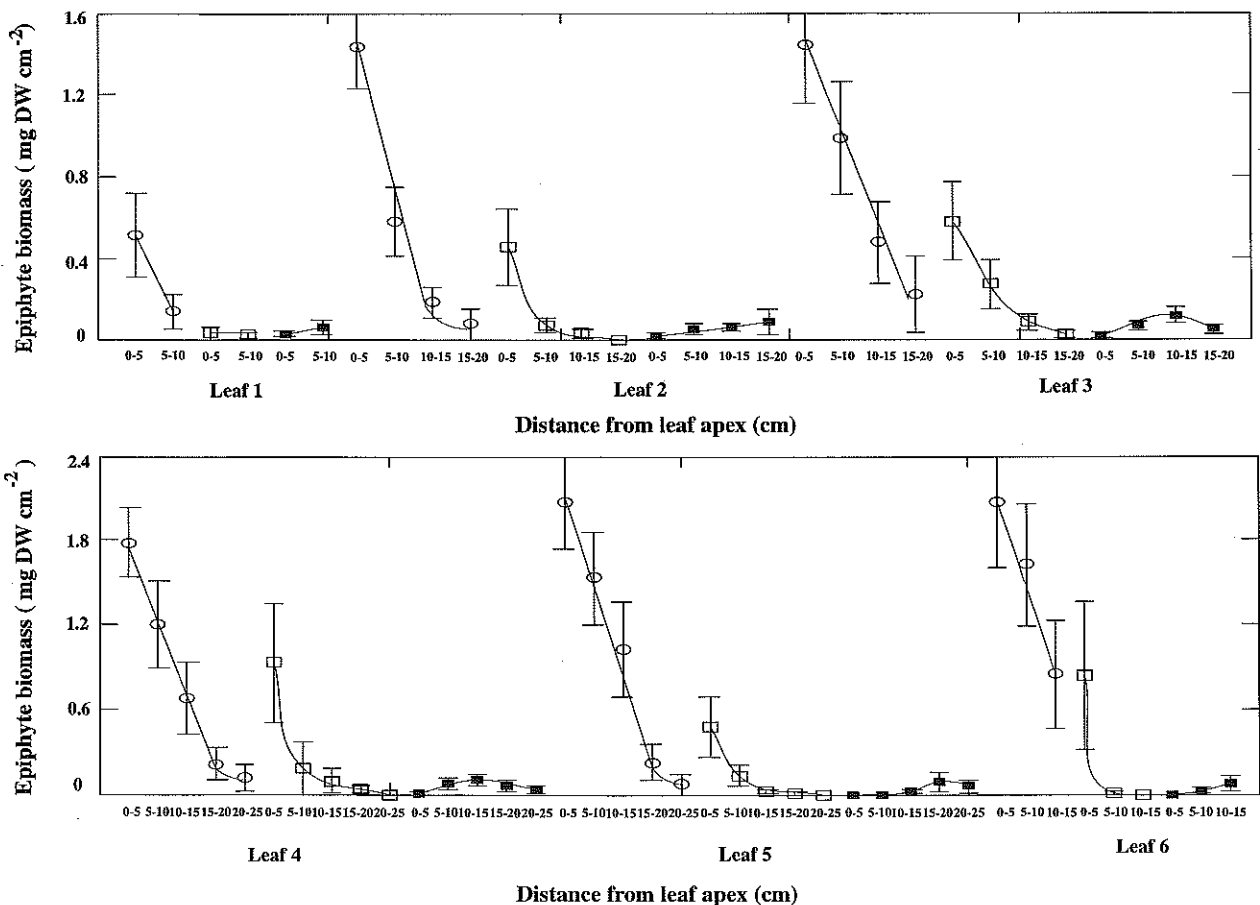


Fig. 1. Distribution of epiphyte biomass along the blades of each *P. oceanica* leaf order. Leaf 1 corresponds to the youngest leaf, whereas leaf 6 corresponds to the oldest one. Points and bars represent the mean and standard error for consecutive 5 cm long leaf sections from apex to base. Symbols correspond to red encrusting algae (○), brown erect algae (□) and bryozoa (■). Lines depict the observed trends.

$$\begin{aligned} \text{Absorbance (400 nm)} \\ &= 22.40 + 13.38 \text{ Epiphyte biomass} \\ &\quad - 0.62 \text{ Epiphyte biomass}^2 \\ (n = 59; R^2 = 0.83; F = 144.31; P < 0.0001) \end{aligned}$$

These equations are indicative of a similar increase in light absorption at 675 and 400 nm with increasing biomass (H_0 : equality between specific absorption coefficients, $P > 0.05$), although for any epiphyte biomass absorption in the blue region was significantly higher ($P < 0.01$) than that in the red region. After an initial rapid increment, light absorption by epiphytes reached a maximum value of about 60–70% of incident light at biomasses higher than 5 mg DW cm⁻² (Fig. 3). This pattern is consistent with the general parabolic law that governs light capture by photosynthetic organisms (Agustí *et al.* 1994).

The increment in light absorption with epiphyte biomass is conducive to the tendency for light absorption by epiphytes to increase on older leaf ages

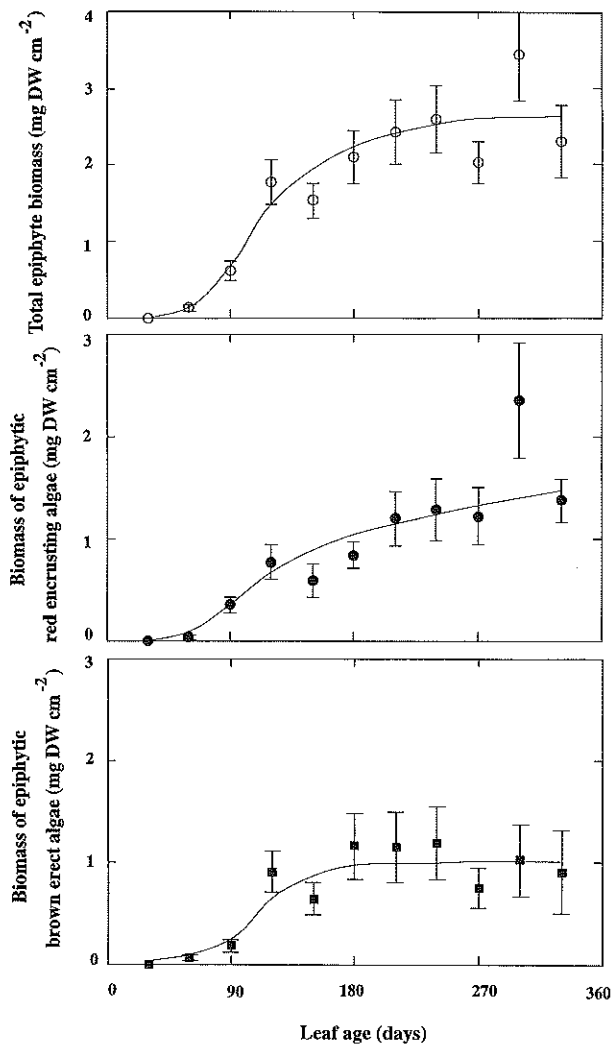


Fig. 2. The relationship between epiphyte biomass and age of *P. oceanica* leaves, both for the total community and main groups of epiphytes. Lines depict the sigmoidal equations fitted to the relationship (see text). Bars represent standard error.

(Fig. 4). Maximum absorption (40% and 28.60% at 400 and 675 nm, respectively) was reached on 200–250 days leaves, coinciding with maximal epiphyte biomass (Fig. 2). The apparent drop in light absorption on the oldest leaves (i. e. 300 days) probably results from the low number of 300-days old leaves within the 47 leaves sampled, and must be regarded as a sampling flaw.

The dependence of light absorption by epiphytes on epiphyte biomass and leaf age has also been

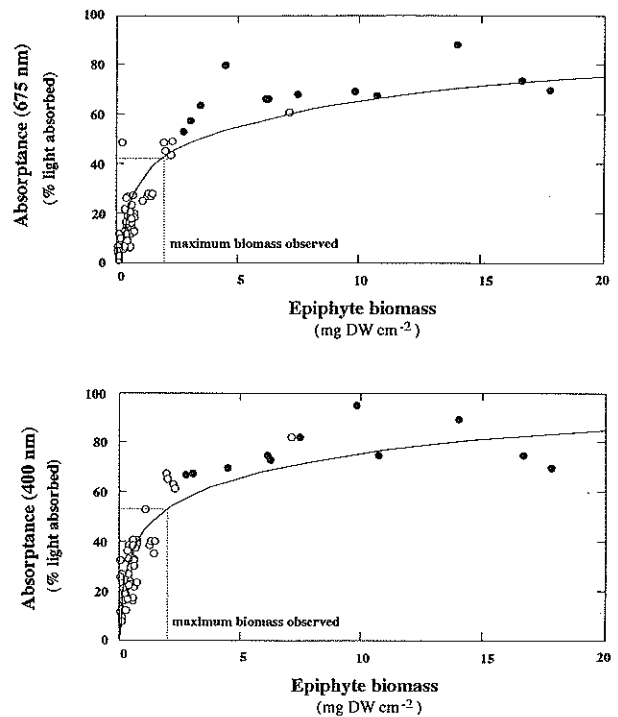


Fig. 3. The relationship between light absorption by epiphytes and epiphyte biomass both at red (675 nm) and blue light (400 nm). Continuous lines represent the fitted polynomial curves. Dotted lines indicate the absorption for the mean maximal epiphyte biomass observed. Open circles correspond to samples obtained from individual leaves, whereas filled circles correspond to composite samples obtained by pooling epiphytes obtained from several leaves (see text).

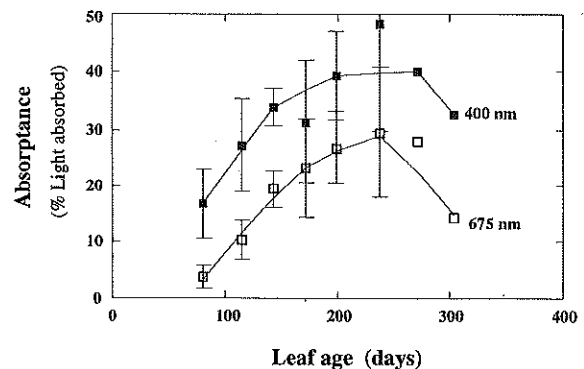


Fig. 4. The relationship between light absorption by epiphytes and leaf age both at red (675 nm) and blue light (400 nm). Lines represent the observed trend.

shown for many other seagrass species (see reviews by van Montfrans *et al.* 1984 and by Jernakoff *et al.* 1996). For instance, Sand-Jensen (1977) and Mazella and Alberte (1986) show that light absorption and photosynthesis by epiphytes on *Zostera marina* L. leaves, while being unimportant on younger leaves, increase to noticeable values on older leaves. Similarly, the accumulation of epiphyte biomass along the life-span of *Heterozostera tasmanica* (Marten *ex* Aschers.) den Hartog leaves results into a parallel increase of light absorption by epiphytes, which can amount to 50% of the incident radiation (Bulthuis and Woelkerling 1983). These results indicate that the reduction of leaf photosynthesis by epiphyte light absorption must also be a leaf-age dependent process. Accordingly, epiphytes may reduce by 30% the photosynthesis of old *Zostera marina* leaves, but have a negligible effect on the photosynthesis of younger leaves (Sand-Jensen 1977). In addition, the tendency towards higher light absorption by epiphytes with increasing leaf age (Fig. 4), combined with reports of light-productivity relationships of *Posidonia oceanica* leaves (Libes 1986), suggest that epiphytes may reduce by 25% the productivity of old *P. oceanica* leaves under non-saturating light intensities, whereas this reduction seems unimportant on younger leaves.

Specific absorption coefficients were 3–4 fold higher for red algae (6.86 ± 0.96 and 11.06 ± 2.18 % light absorbed $\text{cm}^2 \text{mg DW}^{-1}$ at 675 and 400 nm, respectively) than for brown algae (2.11 ± 0.24 and 3.33 ± 0.51 % light absorbed $\text{cm}^2 \text{mg DW}^{-1}$ at 675 and 400 nm respectively) (Fig. 5). Hence, the increasing contribution of red encrusting algae to total epiphyte biomass with older leaf ages (Fig. 2) suggests red encrusting algae should also contribute more to total light absorption by epiphytes on older leaves. Furthermore, because red and brown algae adsorb different wave-lengths (Enrriquez *et al.* 1994), increasing relative abundances of red algae should also entail a shift in the quality of light absorption.

Conclusion

We have characterised the patterns of increment in epiphyte biomass along the blades and with the age of *Posidonia oceanica* leaves, both for the total epiphyte community and for the main epiphytic groups. We have enhanced the accuracy and precision of past relationships between epiphyte biomass and *P. oceanica* leaves age by using the method proposed by Cebrian *et al.* (1994). Epiphyte biomass, both for the total community and main groups, follows a sigmoidal increment along the leaf life-span. The epiphytic growth

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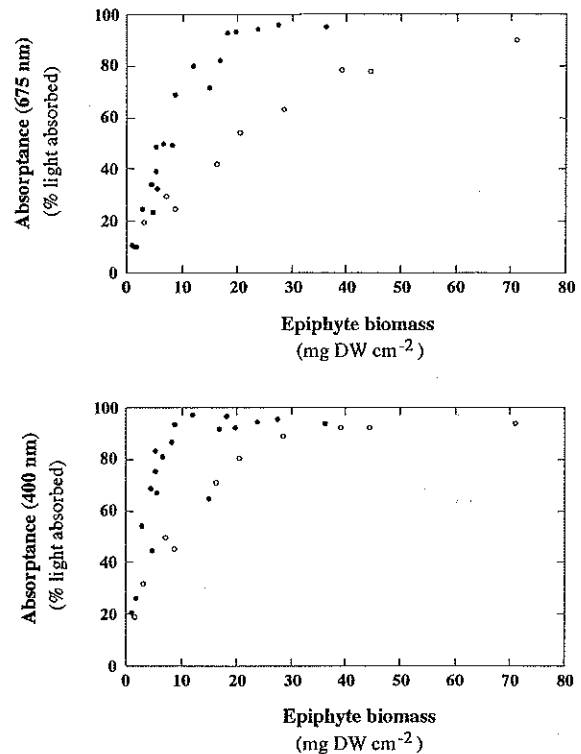


Fig. 5. The relationship between light absorption and biomass for red encrusting (filled circles) and brown erect algae (open circles), both at red (675 nm) and blue light (400 nm).

rates, and magnitude and timing of maximum epiphyte biomass characteristic of this sigmoidal pattern have important consequences for the interactions between *P. oceanica* and its epiphytes. As an example, we show how light absorption by epiphytes is determined by this sigmoidal pattern. Hence, we advocate that it is important to consider the pattern of epiphyte accrual with leaf age for assessing the interaction between seagrasses and epiphytes. This is particularly relevant for long-lived seagrass species where epiphyte growth and biomass may show contrasting differences between young and old leaves. The method proposed by Cebrian *et al.* (1994) provides an accurate way of scaling epiphyte biomass to seagrass leaf age.

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