

Photosynthetic and respiratory responses of the mangrove-associated red algae, *Bostrychia radicans* and *Caloglossa leprieurii*

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Net photosynthetic and respiratory rates of two estuarine algae, *Bostrychia radicans* Mont. and *Caloglossa leprieurii* (Mont.) J. Ag. collected from the Mgeni Estuary mangrove swamp, were studied. Both species are intertidal and common on *Avicennia marina* (Forssk.) Vierh. pneumatophores. Maximum photosynthetic rates of *B. radicans* were evident between 25% and 58% desiccation. Respiratory rates were constant up to 58% desiccation and decreased thereafter. *C. leprieurii* showed highest photosynthetic rates under submerged conditions, whilst respiratory rates were highest under saturated conditions. Both species showed increases in photosynthetic and respiratory rates with increase in temperature. Photosynthetic rates peaked at 32°C to 37°C, whilst respiratory rates peaked at 37°C. With increases in light intensity, maximum photosynthetic rates of *C. leprieurii* and *B. radicans* occurred at 140 to 225 $\mu\text{E m}^{-2} \text{s}^{-1}$ and 225 to 550 $\mu\text{E m}^{-2} \text{s}^{-1}$ respectively. Both species were tolerant of a range of salinities. The ecological implications of these results are discussed.

Netto fotosintese- en respirasietempo's van twee riviermondalge, *Bostrychia radicans* Mont., en *Caloglossa leprieurii* (Mont.) J. Ag., versamel in die Mgeni Riviermond-manglietmoeras, is bestudeer. Beide spesies kom algemeen op *Avicennia marina* (Forssk.) Vierh. pneumatofore in die intergetygebied voor. Maksimum fotosintese tempo's van *B. radicans* het tussen 25% en 58%-uitdroging voorgekom. Respirasietempo's was konstant tot 58%-uitdroging en het daarna afgeneem. *C. leprieurii* het die hoogste fotosintese tempo's onder ondergedompelde toestande getoon terwyl respirasietempo's die hoogste was onder versadigde toestande. Beide spesies het 'n verhoging in fotosintese en respirasietempo's by 37°C getoon. Met verhogings in lig-intensiteit het maksimum fotosintese tempo's van *C. leprieurii* en *B. radicans* voorgekom by 140 tot 225 $\mu\text{E m}^{-2} \text{s}^{-1}$ en 225 tot 550 $\mu\text{E m}^{-2} \text{s}^{-1}$ respektiewelik. Beide spesies is verdraagsaam teenoor 'n reeks soutgehaltes. Die ekologiese implikasies van hierdie resultate word bespreek.

Keywords: Environmental responses, mangrove-associated algae, photosynthesis, respiration

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Introduction

Algal epiphytes are widespread in mangrove swamps (Macnae 1968). In southern Africa, *Bostrychia radicans* Mont. and *Caloglossa leprieurii* (Mont.) J. Ag. occur commonly on *Avicennia marina* (Forssk.) Vierh. pneumatophores (Lambert *et al.* 1987).

A study of seasonal variations in biomass of epiphytic algae in the St Lucia Estuary has indicated that they are a significant component of the ecosystem (Steinke unpublished data). Algae, epiphytic on mangroves, are subjected to fluctuating environmental conditions on a daily basis. The effects of such environmental variations on photosynthetic and respiratory rates of mangrove algae has received little attention (Dawes *et al.* 1978; Davis & Dawes 1981). Work on marine intertidal and subtidal populations of other algae has been conducted almost exclusively under submerged conditions and the effects of environmental factors under exposed conditions has received little attention (Newell & Pye 1968; Mathieson & Dawes 1974; Fralick & Mathieson 1975; Dawes *et al.* 1976; King & Schramm 1976; Durako & Dawes 1980).

A study investigating the effect of environmental conditions on these algae was conducted in order to (a) gain an understanding of seasonal variations in productivity, (b) evaluate their productivity under different estuarine conditions and (c) gain greater insight into distribution patterns of algae in the Mgeni Estuary.

This study examined the effect of periods of desiccation, temperature and light intensity under exposed and submerged conditions as well as salinity on net photosynthetic and respiratory rates of mangrove-associated populations of *B. radicans* and *C. leprieurii*.

Materials and Methods

Pneumatophores with *B. radicans* and *C. leprieurii* as epiphytes were collected from an intertidal locality in the Mgeni Estuary mangrove swamp between August and October 1986. Pneumatophores were transported to the laboratory in channel water at ambient temperatures within 30 min of collection. Algae were carefully scraped off the pneumatophores to ensure minimal damage and washed in several changes of autoclaved seawater. The final wash contained 30 mg l⁻¹ chloramphenicol and was carried out for 2 h to reduce the bacterial flora.

Algae were held in aerated aquaria in a growth cabinet at 22°C and 25‰ salinity for no more than 5 days. After this period, material was discarded in order to avoid unreliable results. A light/dark cycle of 12 h:12 h was utilized and the light intensity was 100 $\mu\text{E m}^{-2} \text{s}^{-1}$.

Plants used for salinity studies were acclimatized to salinities ranging from 0‰ to 45‰ for 2 days in order to conform with other workers in this field (Fralick & Mathieson 1975; Davis & Dawes 1981). At the Mgeni Estuary mangrove swamp, channel salinities ranging from 0‰ to 35‰ have been recorded. Lower salinities were obtained by diluting seawater with distilled water and higher salinities by adding hypersaline water. Salinity was measured by a handheld refractometer.

Desiccation studies compared photosynthetic and respiratory rates of submerged and saturated algae with algae subjected to different degrees of desiccation. Submerged algae were covered by 6 ml water whilst saturated algae were dipped in seawater and then exposed. To achieve different degrees of desiccation, saturated algae, which had been placed in a growth cabinet at 22°C, were removed at

intervals for up to 6 h. Percentage desiccation was expressed as

$$\frac{\text{initial wet mass} - \text{final wet mass}}{\text{initial wet mass} - \text{dry mass}} \times \frac{100}{1} \quad (\text{Hodgson 1981}).$$

Water saturation is represented by 0% desiccation and entire water loss, i.e. the dry weight, by 100% desiccation. Recovery was tested after extreme desiccation by re-immersing algae in water and recording rates of photosynthesis and respiration.

The rates of net photosynthesis and respiration were determined in a single valve differential Gilson Respirometer using standard volumetric procedures. This technique has been used by a number of researchers working on mangrove-associated algae (Dawes *et al.* 1978; Hoffman & Dawes 1980; Davis & Dawes 1981).

The respirometer was equipped with 14 30W reflector lamps and gave a light intensity of $225 \mu\text{E m}^{-2} \text{s}^{-1}$. For light intensity experiments, the light intensity was increased using 60W lamps and lower light intensities were achieved by tying shade cloth around the reaction vessels.

Light intensity was measured at the base of the reaction vessels in $\mu\text{E m}^{-2} \text{s}^{-1}$, using a Li-cor Quantum-meter Model L.I. — 1854 and a 192S sensor. Light intensities ranged from $40 \mu\text{E m}^{-2} \text{s}^{-1}$ to $900 \mu\text{E m}^{-2} \text{s}^{-1}$. At the Mgeni Estuary mangrove swamp, light intensities ranging from $21 \mu\text{E m}^{-2} \text{s}^{-1}$ to $1\,000 \mu\text{E m}^{-2} \text{s}^{-1}$ have been recorded in air and from $15 \mu\text{E m}^{-2} \text{s}^{-1}$ to $600 \mu\text{E m}^{-2} \text{s}^{-1}$ in the channel. For temperature experiments, a range from 12°C to 37°C was used. Temperatures at the Mgeni Estuary mangrove swamp of between 17°C and 27°C have been recorded in the channel. The minimum and maximum air temperatures recorded at Louis Botha airport are $13,7^\circ\text{C}$ and $28,7^\circ\text{C}$ respectively.

Preliminary work showed no endogenous diurnal rhythms present in the production or uptake of O_2 in the laboratory under experimental conditions and thus

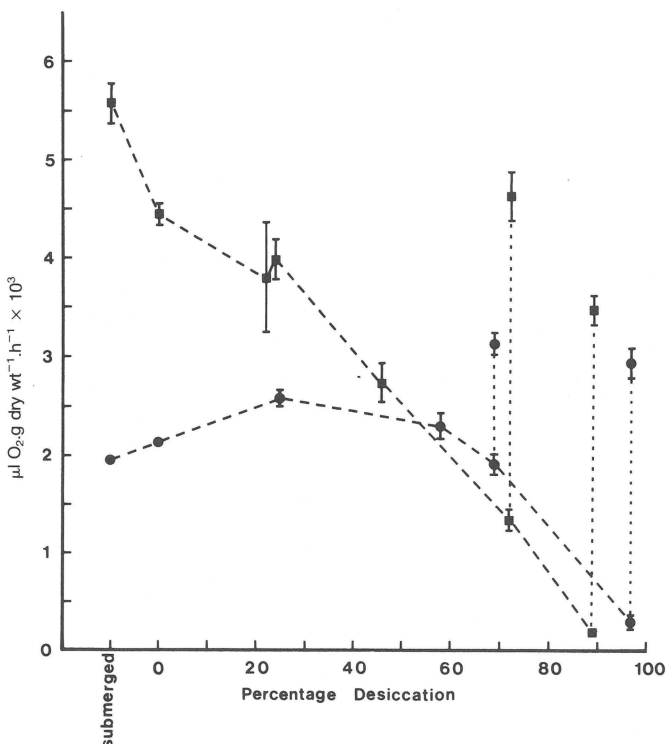


Figure 1 Net photosynthetic rates of *B. radicans* (●) and *C. leprieurii* (■) at various degrees of desiccation and after subsequent re-immersion. The vertical dotted lines represent values after re-immersion. The vertical bars represent one standard error.

experiments were conducted throughout the day. The amount of fresh material (0,1 g) and the duration of each experiment (1 h) was also determined from preliminary work. Readings were taken every 15 min. A linear photosynthetic response was observed from 20 min to 3 h and a linear respiratory response from 20 min to 5 h. Material was equilibrated for 30 min prior to determinations.

A 1% CO_2 atmosphere was maintained in the vessels using the Pardee method (Umbreit *et al.* 1964) using a CO_2 buffer and fluted filter paper placed in the central wall. For experiments conducted under submerged conditions, the vessels contained 6 ml of autoclaved seawater with a salinity of 25‰. This was a common salinity recorded in the field. For experiments under exposed conditions, the algae were carefully blotted dry to remove surface moisture. Water was placed in the side arm to ensure a humid atmosphere, to prevent algae from drying out during the experiment. Vessels for respiration determinations were covered with aluminium foil and heavy duty black plastic bags. Four replicate vessels were used for each experiment. All experiments (except temperature experiments) were conducted at 22°C , the mean annual water temperature for the experimental site. The mean annual air temperature recorded at Louis Botha airport was $20,5^\circ\text{C}$.

A control vessel was also set up containing only seawater and CO_2 buffer, but these showed no uptake or production of O_2 . The results were analysed statistically by analysis of variance.

Results

The influence of desiccation

Net photosynthetic rates of *B. radicans* were significantly higher between 25% and 58% desiccation ($P < 0,05$) (Figure 1). Rates decreased thereafter, reaching very low levels at 97% desiccation. After being desiccated to 69% and 97%, on subsequent rehydration, *B. radicans* exhibited rates exceeding former maximum rates. This result represents a mean of 4 readings taken every 15 min for an hour after resubmergence and a half-hour equilibration period. A closer examination of these readings revealed that rates were high for the first 15 min of the hour, decreasing steadily thereafter. Rates for the last 15 min were similar to rates recorded previously under submerged conditions.

The highest photosynthetic rates ($P < 0,05$) of *C. leprieurii* occurred under submerged conditions and the rate decreased steadily thereafter with increasing percentage desiccation to the lowest level at 89% desiccation. After desiccation of 72% and 89% and subsequent rehydration, only partial recovery of the previous maximum rate occurred.

Rates of respiration of *B. radicans* showed a gradual but not significant increase up to 58% desiccation (Figure 2). Rates decreased thereafter and ceased at 97% desiccation. Recovery after rehydration at 69% and 97% was good and rates similar to previous maximum rates were obtained.

Maximum rates of respiration of *C. leprieurii* occurred under saturated conditions (0% desiccation) ($P < 0,05$) and decreased steadily thereafter. Recovery after rehydration at 72% and 89% desiccation occurred, but with only partial recovery of the previous maximum rate.

The influence of temperature

Net photosynthetic rates of both species increased with increasing temperature (Figure 3). Maximum photosynthetic rates of *B. radicans* occurred at 37°C under submerged conditions ($P < 0,05$) and at 32°C to 37°C under exposed conditions ($P < 0,01$). Photosynthetic rates of *B.*

radicans were significantly higher under exposed conditions at all temperatures ($P < 0,05$), which is similar to results obtained in the desiccation experiments.

Maximum photosynthetic rates of *C. leprieurii* occurred at 32°C under submerged conditions ($P < 0,01$) and at 32°C to 37°C under exposed conditions ($P < 0,01$).

Respiratory rates of *B. radicans* and *C. leprieurii* in response to temperature are shown in Figure 4. *B. radicans* exhibited no significant increase in respiration between

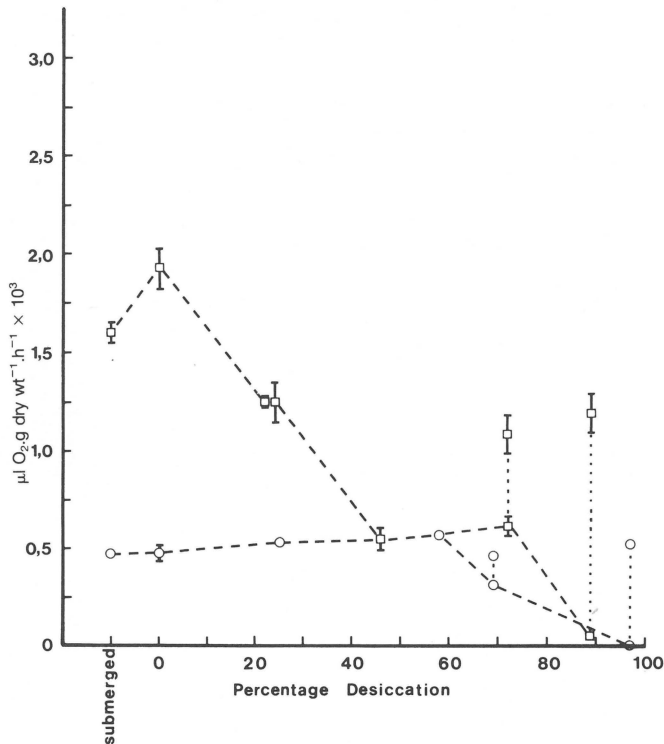


Figure 2 Respiratory rates of *B. radicans* (○) and *C. leprieurii* (□) at various degrees of desiccation and after subsequent re-submergence. The vertical dotted lines represent values after re-submergence. The vertical bars represent one standard error.

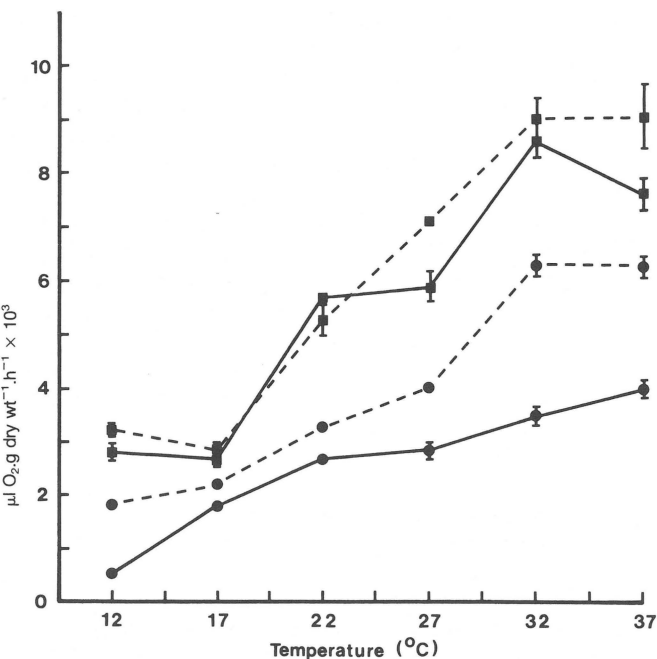


Figure 3 Net photosynthetic rates of *B. radicans* (●) and *C. leprieurii* (■) at various temperatures under submerged (—) and exposed (---) conditions. The vertical bars represent one standard error.

17°C and 37°C under submerged conditions and between 22°C and 37°C under exposed conditions. Rates of respiration of *B. radicans* were significantly higher under exposed conditions than submerged conditions from 22°C and 37°C ($P < 0,01$).

Maximum rates of respiration of *C. leprieurii* occurred at 37°C under submerged conditions ($P < 0,05$) and between 32°C and 37°C under exposed conditions ($P < 0,05$). No significant differences occurred between rates of respiration under exposed and submerged conditions over the range of experimental temperatures.

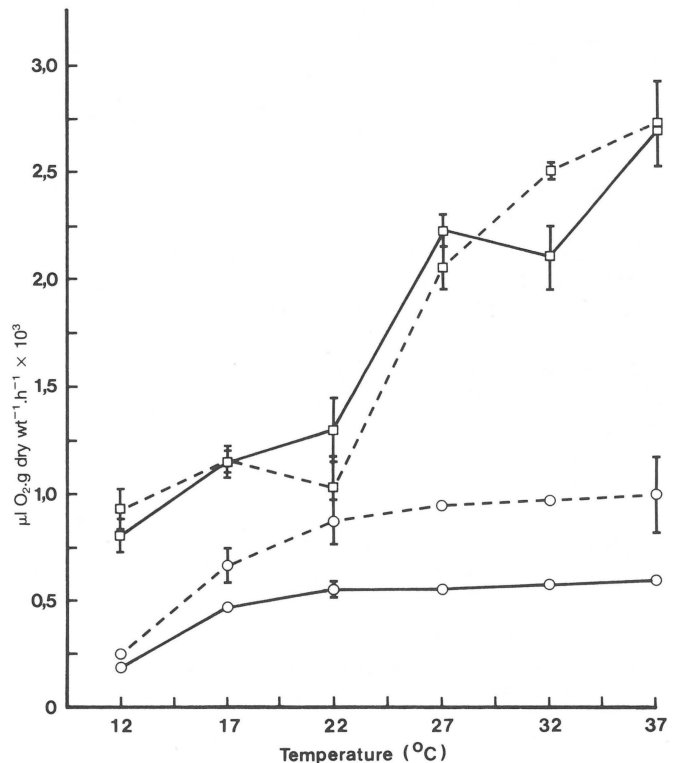


Figure 4 Respiratory rates of *B. radicans* (○) and *C. leprieurii* (□) at various temperatures under submerged (—) and exposed (---) conditions. The vertical bars represent one standard error.

The influence of light intensity

Net photosynthetic rates of *B. radicans* under exposed conditions maximized at light intensities of between 225 $\mu\text{E m}^{-2} \text{s}^{-1}$ and 550 $\mu\text{E m}^{-2} \text{s}^{-1}$ ($P < 0,01$) (Figure 5). Under submerged conditions, photosynthetic rates increased up to a maximum of 550 $\mu\text{E m}^{-2} \text{s}^{-1}$ ($P < 0,01$). Rates of photosynthesis of *B. radicans* under exposed conditions were significantly higher than under submerged conditions below 310 $\mu\text{E m}^{-2} \text{s}^{-1}$ ($P < 0,05$). Thereafter, photosynthetic rates were significantly higher under submerged conditions.

Photosynthetic rates of *C. leprieurii* under exposed conditions increased sharply up to 140 $\mu\text{E m}^{-2} \text{s}^{-1}$ and 225 $\mu\text{E m}^{-2} \text{s}^{-1}$ ($P < 0,01$) and rates decreased thereafter. Under submerged conditions, the rates of photosynthesis increased up to a maximum at 225 $\mu\text{E m}^{-2} \text{s}^{-1}$ ($P < 0,01$) and declined thereafter. No significant differences occurred between exposed and submerged conditions.

The influence of salinity

No significant differences occurred in photosynthetic rates of *B. radicans* over the experimental range of salinities (Figure 6). The maximum rate of respiration occurred at 25‰ ($P < 0,05$) and a marginal decline was apparent at

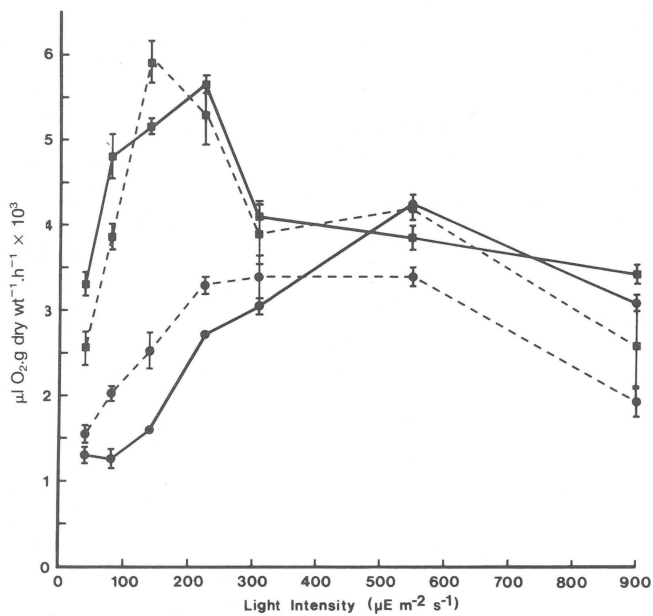


Figure 5 Net photosynthetic rates of *B. radicans* (●) and *C. leprieurii* (■) at various light intensities under submerged (—) and exposed (---) conditions. The vertical bars represent one standard error.

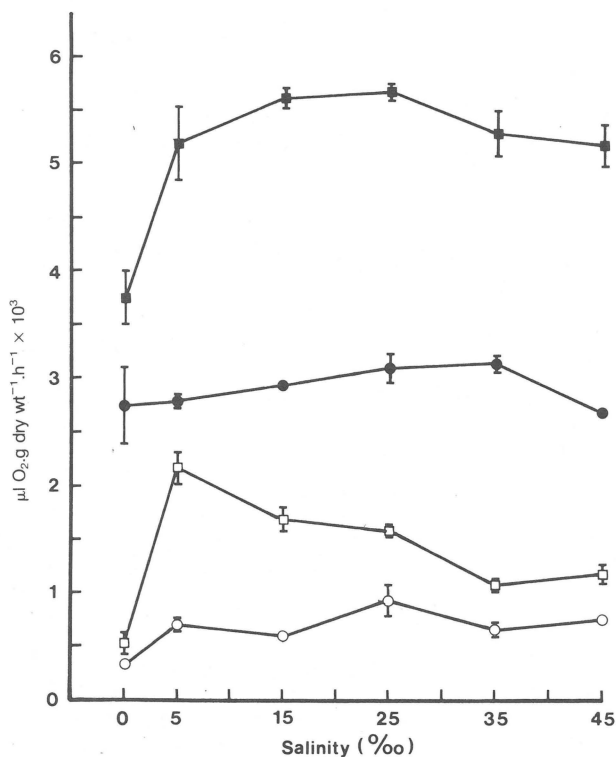


Figure 6 Net photosynthetic and respiratory rates of *B. radicans* (●) and *C. leprieurii* (■) at various salinities. Photosynthetic rates are represented by closed symbols and respiratory rates by open symbols. The vertical bars represent one standard error.

salinities greater than or less than this value.

The photosynthetic rates of *C. leprieurii* did not vary significantly with salinities ranging from 5 to 45‰. The rate was significantly lower at 0‰ ($P < 0,01$). The maximum rate of respiration occurred at 5‰ ($P < 0,01$) and at 0‰, rates were significantly lower than at any other salinity ($P < 0,01$).

Discussion

The influence of desiccation

B. radicans can withstand desiccation of up to 58% without photosynthetic and respiratory rates being adversely affected. *C. leprieurii* appears to be more sensitive to desiccation, with maximum photosynthetic rates occurring under submerged conditions. This coincides with their differences in natural habitats. In the Mgeni Estuary mangrove swamp, *C. leprieurii* occurs more commonly on the lower region of the pneumatophore, exhibiting a lower intertidal range of distribution (A. Strong pers. comm.). Desiccation in the field is therefore not as great as for *B. radicans*, which occurs above this in the middle to upper intertidal regions. Comparable results have been reported for mangrove-associated *B. binderi* Harvey by Dawes *et al.* (1978) and for more marine intertidal algae by Brinkhuis *et al.* (1976). Johnson *et al.* (1974) showed the photosynthetic rates of temperate middle and upper intertidal algae, even after an appreciable amount of drying in air, to be 1,6 to 6,6 times higher than when submerged. Lower intertidal algae had reduced photosynthetic capacities whilst exposed. Slight increases in respiration with increase in desiccation of *B. radicans* are in agreement with Mathieson & Burns (1971) and Dawes *et al.* (1978).

Ogata & Matsui (1968) suggested that a good indication of the tolerance of a plant to desiccation is its ability to recover metabolically after re-immersion. After high levels of desiccation, both photosynthetic and respiratory rates of *B. radicans* recovered fully, whilst *C. leprieurii* only recovered some of its initial activity. This appears to indicate that *B. radicans* is more tolerant of desiccation than *C. leprieurii*.

The influence of temperature

Both species exhibited broad temperature tolerances, with the highest photosynthetic and respiratory rates occurring between 32°C and 37°C. Similar tolerances have been shown for mangrove-associated *B. binderi* by Dawes *et al.* (1978), although it is suggested that high rates of photosynthesis at higher temperatures may be short term. Experiments were conducted for only 1 h. The effect of longer exposure to higher temperatures should be investigated. Results published for other estuarine algae indicated lower temperature optima (Mathieson & Burns 1971; Fralick & Mathieson 1975; Dawes *et al.* 1976; Davis & Dawes 1981). The rapid increase in respiration of *C. leprieurii* above 22°C may indicate thermal damage at high temperatures and greater rates of photosynthesis at high temperatures may well be short-lived. The rates of photosynthesis appear to be dropping by 37°C.

No significant increase in respiration occurred in *B. radicans* between 17°C and 37°C under submerged conditions and 22°C and 37°C under exposed conditions, showing possibly a greater tolerance of higher temperatures than *C. leprieurii*. In the field, *B. radicans* appears better adapted to higher temperatures and it is therefore able to occur higher on the pneumatophore, where it is exposed to high air temperatures for longer periods of time.

The influence of light intensity

The optimal light requirements for photosynthesis are higher in *B. radicans* than *C. leprieurii*. This could explain the generally higher position occupied on the pneumatophore by *B. radicans*, which is therefore exposed to higher light intensities for longer periods of time than *C. leprieurii*. Results show an adaptation to lower light intensities and a tolerance of higher light intensities over short experimental periods of 1 h. *B. radicans* appears to withstand higher light intensities to a greater extent under

submerged conditions and rates of photosynthesis are higher under these conditions, whereas up to $310 \mu\text{E m}^{-2} \text{s}^{-1}$, rates were higher under exposed conditions. Optimum light intensities for *B. radicans* under submerged conditions are higher than reported for other intertidal mangrove-associated algae (Dawes *et al.* 1978; Davis & Dawes 1981). Rates recorded for *C. leprieurii* under submerged conditions are comparable to results of these researchers. Very little work has been conducted on the effect of light intensity on photosynthesis under exposed conditions. Hodgson (1981) recorded a saturation light intensity of $100\text{--}120 \mu\text{E m}^{-2} \text{s}^{-1}$ for an intertidal population of *Gastroclonium coulteri* (Harvey) Kylin. This result is similar to our recording for *C. leprieurii* but lower than that of *B. radicans*.

In our experiment it is significant to note that shade cloth was used to vary the light intensity. This does not affect the light quality at lower light intensities. Many researchers used a rheostat to obtain lower light intensities (Mathieson & Burns 1971; Dawes *et al.* 1978) and this results in a predominance of red light not present in the field (Dawes *et al.* 1976). Moon & Dawes (1976) have shown that the red alga *Eucheunia isiforme* (C. Agardh) J. Agardh var. *denudatum* Cheney exhibited significant differences in photosynthetic responses under red light and under broad spectral white light.

The influence of salinity

Results show that *B. radicans* and *C. leprieurii* are euryhaline. Similar findings have been reported by various researchers on other estuarine algae (Dawes *et al.* 1978; Yarish *et al.* 1979; Davis & Dawes 1981). No significant differences were found in rates of photosynthesis for salinities ranging from 5 to 45‰. This is in contrast to the findings of Yarish *et al.* (1979) who recorded a maximum rate of photosynthesis of between 15 and 25‰ for *C. leprieurii* and 25‰ for *B. radicans*. Low rates of photosynthesis at 0‰ have been recorded by other researchers (Yarish *et al.* 1979; Davis & Dawes 1981). However, it has been demonstrated that the type of water used in the dilution of seawater to obtain lower salinities can markedly affect the results, as photosynthesis is dependent on the number of bicarbonate ions in the water (Ogata & Matsui 1968; Zavodnik 1975; Dawes & McIntosh 1981). These researchers have shown that dilution with distilled water suppresses O_2 production at all salinities, whereas dilution with spring water increases O_2 production. Low rates of respiration recorded at 0‰ are in contrast to those reported in the literature (Dawes *et al.* 1978; Davis & Dawes 1981). This suggests that short-term exposure to salinities of 0‰ are not always as limiting as has been suggested by various researchers. In a preliminary survey of the upper region of the Mgeni Estuary, which is freshwater, *C. leprieurii* and *B. radicans* have not been found. This suggests that long-term exposures to fresh water may be limiting.

Conclusion

B. radicans and *C. leprieurii* were shown to be tolerant of wide ranges of temperature, light intensity and salinity to which they are exposed on a daily basis. These algae are also tolerant of exposure to fresh water for up to two days. It is significant that both species have the capacity to maintain positive and in the case of *B. radicans*, high light intensities and temperatures can also be related to vertical zonation of these algae.

It is clear that more work is necessary before the effects of environmental conditions on rates of photosynthesis and respiration are fully understood. The effect of long-term exposures to extreme environmental conditions needs to be investigated. Seasonal variation in responses to environmental factors should be considered. Chlorophyll a

determinations would enable a possible comparison of photosynthetic rates of different species of algae.

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