

COMPARATIVE OBSERVATIONS ON SOME
PHYSIOLOGICAL ASPECTS OF ROCKY-SHORE AND
SALT MARSH POPULATIONS OF *PELVETIA CANALICULATA* (PHAEOPHYTA)

COMPARAÇÃO DE ALGUNS ASPECTOS
FISIOLÓGICOS ENTRE POPULAÇÕES DE *PELVETIA CANALICULATA*
(PHAEOPHYTA) DE COSTÕES ROCHOSOS E PÂNTANOS SALGADOS

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SUMMARY - Laboratory and field experiments were performed in order to compare some aspects of the physiology of the brown algae *Pelvetia canaliculata* growing on rocky-shore, and its marsh representative ecada *libera*, in North Wales. Rates of water loss are similar for both plants under laboratory conditions though there is a significant difference between the dry/fresh weight relation. In nature, the salt marsh form loses water much slower than the rocky-shore plants because of different environmental conditions. Both forms are very sensitive to continuous submergence and decay within a variable interval of time that increases with light intensity. Photosynthesis and respiration proceed at similar rates when submerged, or out of water in various states of desiccation of the thalli. The relations of photosynthesis and respiration to water content of the thalli were linear and could be detected with the Warburg manometer when the plants were at 10 - 20% of the saturation water content. A comparison of the water loss in the field and of assimilation in the laboratory under different water contents show that the marsh form is able to photosynthesize for a much longer time than the rocky-shore plants. The light compensation point in emersed water-saturated thalli ranges around 700 lux for both forms at 12° C. The vertical distribution of *Pelvetia canaliculata* is discussed in view of the new data presented here.

RESUMO - Vários aspectos da fisiologia da alga parda *Pelvetia canaliculata* foram estudados, analisando-se comparativamente os resultados obtidos com plantas que crescem em costões rochosos e plantas que crescem entre as angiospermas dos pântanos salgados do País de Gales. Em condições de laboratório, com umidade relativa constante, as taxas de perda d'água são praticamente idênticas embora as plantas do pântano apresentem uma maior relação peso seco/peso fresco. Na natureza, entretanto, a velocidade de dessecação entre as duas formas difere muito devido à maior umidade do ambiente em que vivem as plantas do pântano. Ambas as formas são bastante sensíveis à imersão contínua em água do mar corrente e entram em decomposição em um período que aumenta com a intensidade luminosa. As taxas de fotossíntese e respiração não diferem significativamente, tanto em plantas imersas como emersas e com diferente teor de água no talo, nas duas formas. As variações da fotossíntese e da respiração com o teor de água do talo são lineares, sendo que estes processos caem a níveis não detectáveis, com a técnica de Warburg utilizada, quando se atingem valores da ordem de 10 - 20% do total de saturação de água. As comparações das curvas de perda d'água no campo e de assimilação com diferente quantidade de água no talo mostram que as plantas de costões rochosos dispõem de um período muito mais curto para a fotossíntese. O ponto de compensação luminoso para ambas as formas é similar e encontra-se ao redor de 700 lux a 12° C. Com base nos dados apresentados e nos da literatura discute-se a distribuição vertical de *Pelvetia canaliculata*.

INTRODUCTION

One of the characteristic features of many salt marshes of the Northern Hemisphere is the presence, between the angiosperm association, of peculiar forms of the normal

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rocky-shore fucoids (Chapman 1960). These plants usually show a morphology quite different from the rocky-shore plants that, as is generally accepted, gave rise to them. The marsh forms have been interpreted differently by several authors as ecads, forms, varieties and even species (Baker 1912, Baker and Bohling 1916, Skrine 1928, Carter 1933a, 1933b).

Though the reproductive behaviour and the morphology of salt marsh and rocky-shore plants of *Pelvetia canaliculata* (L.) Dcne. and Thur. have been compared (Baker 1912, Chapman 1960) there is almost no literature concerning the possible physiological differences between these forms. Russel-Wells (1932) determined the fat content of both forms; Isaac (1933) studied the rate of water loss of rocky-shore plants and Haas and Hill (1933) determined the nitrogen and carbohydrate metabolism.

In this paper comparisons will be made between the water relations, the effect of continuous submergence, photosynthesis and respiration of rocky-shore and salt marsh plants.

PLANT MATERIALS

The plants referred to as the salt marsh form correspond to the description of *P. canaliculata* ecad *libera* sensu Baker (1912). They were collected on the salt marsh at Four Mile Bridge, Anglesey, Wales. Only those plants with the characteristics of ecad *libera* and growing amongst angiosperm vegetation (*Limonium*, *Armeria*, *Salicornia*) were selected. The rocky-shore form was collected in Anglesey, in the Menai Straits, adjacent to the Marine Science Laboratories.

WATER RELATIONS

In previous studies (Isaac 1933), rocky-shore *Pelvetia* was shown to lose up to 68% of its water in 8.5 hours at 72% RH. Most of this being lost in the first 3 hours. Such plants growing on bare rocks are obviously less protected from desiccation compared with plants growing in the moist conditions among angiosperm vegetation. It was thus instructive to compare the rates of water loss of rocky-shore and salt marsh plants under constant conditions.

Methods - Laboratory measurements of rates of water loss were made by suspending the plants in flasks over various concentrations of sulphuric acid at constant temperature. The plants were weighed periodically inside the flask to avoid exposure to the air. Dry weights were obtained after drying the plants in an oven at 105° C to constant weight. The fresh weight was determined by weighing the plants after overnight immersion in running sea-water. Field experiments were performed by weighing the plants *in situ* using a torsion balance. The weighings were started just after the plants became uncovered by the ebbing tide. Between weighings the rocky-shore plants were returned to precisely the same place from where they were taken between other specimens, kept in the right position with the help of a wire hook. Salt marsh forms were also replaced after weighings to their habitat between the *Armerietum*. Weighings took less than 1 minute for each determination. As a control, plants from both habitats were freely suspended in the open air near the balance. The evaporating power of the air was monitored using Piché evaporimeters which were placed as close as possible to the rocky-shore and

salt marsh specimens under investigation. Parallel measurements of temperature, light and relative humidity were also made.

Results - (a) Water loss under laboratory conditions. The rates of water loss in atmospheres of varying RH are shown in figure 1. The water loss was much greater in the first hour of exposure in all three RH tested. After a length of time which varied with and was proportional to the RH, the plants reached a water content that was in equilibrium with each relative humidity, e.g., at 95% RH the equilibrium was attained at a water content equivalent to 35% of the saturated water value and after a period of 25 hours; at 22% RH the water content in equilibrium was equivalent to 5% of the total water and took about 6 hours to equilibrate. The amount of water retained by *Pelvetia* in equilibrium with atmospheres of varying RH are shown in figure 2. The relation dry/fresh weight is significantly higher for the marsh form (Table 1).

(b) Water loss under field conditions. Since the results from three experiments were practically identical (1 in march and 2 in may), only the results obtained on the 23rd may are presented here (Figures 3 and 4). During the experimental period temperatures in sunshine ranged from 13 - 16° C, RH was 66 - 67% near the torsion balance, while light was over 10,000 lux throughout. From figure 3 it can be seen that plants *in situ* lose water at very different rates. The rocky-shore plants lose much more water and at a faster rate than the marsh forms. Plants hung in the open air however, lost water at much the same rate as each other. These results suggest that the surrounding angiosperm vegetation protects *Pelvetia* from drying out on the marsh. Figure 4 shows the results of monitoring the evaporating power of the air which was greater beside the rocky shore plants than beside those of the marsh. The water loss results are obviously related to this. Parallel measurements of atmospheric RH with hygrometers show poor correlation with the water loss of the plants because the evaporating power of the air depends also on air movements detectable by the evaporimeter but not by the hygrometer.

TABLE 1 - Relations between dry and fresh weight in the two forms of *Pelvetia canaliculata* (dry weight as % of fresh weight)

	\bar{X}	n	σ^2	σ_d	t
Salt marsh	32.05	51	3.0662	0.4772	6.37*
Rocky shore	29.01	31	5.2006		

* significant at the 0.1% level.

EFFECT OF CONTINUOUS SUBMERGENCE

The absence of *Pelvetia* at levels below MHWNT is usually attributed to its special ability to survive air desiccation in the upper eulittoral, and its exclusion from the lower shore by competition (Isaac 1933), or to its inability to sustain prolonged submersion

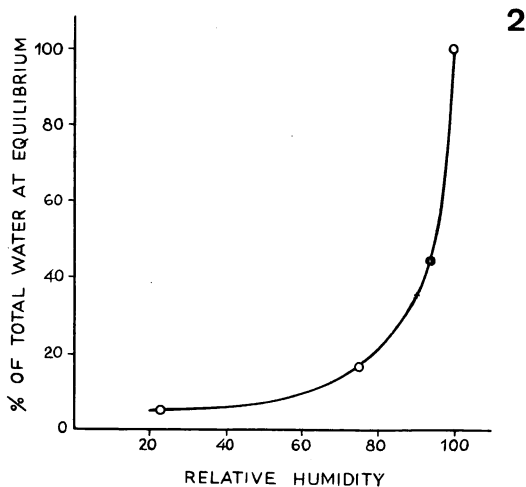
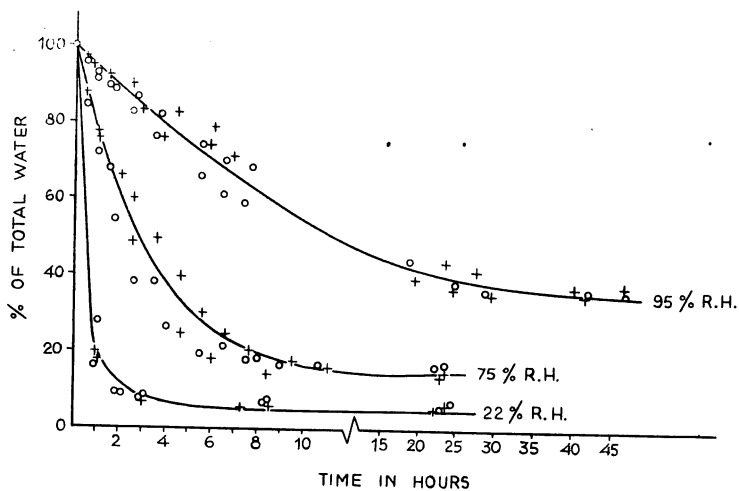


Fig. 1 - Perda de água de *Pelvetia canaliculata* em umidades relativas constantes, à 20° C (forma do pântano, o; forma do costão rochoso, +). Fig. 2 - Conteúdo de água do talo de *Pelvetia canaliculata* (forma de costão rochoso) em equilíbrio com diferentes valores de umidade relativa expressos em porcentagem do valor de saturação.

Fig. 1 - Water loss of *Pelvetia canaliculata* (salt marsh, o, and rocky shore, +, forms) under constant relative humidities at 20° C. Fig. 2 - Water contents in the thalli of *Pelvetia canaliculata* (rocky shore form) in equilibrium with different air humidities expressed as percentage of saturated water content.

(Baker 1912). Biebl (1962), quoting Fisher (1929), says that *Pelvetia* soon dies when completely immersed, probably by anoxia. However, Fischer stated that under continuous submersion *Pelvetia* died in less than 9 months.

Methods - To measure the resistance to submersion *Pelvetia* plants were kept continuously submerged in running seawater under various light intensities and a photoperiod of 12 hours.

Results - Figures 5 and 6 show the results of submitting the forms of *Pelvetia* to continuous or alternating periods of submersion. Both forms lost weight during the treatment, but the rocky-shore lost more and survived a shorter period than the salt marsh form. The weight loss, at least in the beginning of the experiment, can be attributed to utilization of food reserves. Decay was noted after 20 days. In the salt marsh plants this occurred at the basal portion, which decays in nature as a consequence of mud deposition. In the rocky plants the decay started at the apex, and the basal parts were more resistant. The effect of light is particularly interesting since it appears that a high light intensity allows a longer survival. This suggests that poor light intensity during winter or other unfavorable light conditions could be the limiting factor controlling the plants' distribution. Though the experiments were started with sterile plants, at the end of the experiments rocky-shore plants bore receptacles although the salt marsh plants remained sterile. The same was also observed in nature; it thus seems that the rocky-shore plants had already been induced to produce reproductive elements when they were collected. Both forms tolerated an alternation of submersion/emersion treatments using a 4 hours per day submersion period much better. This suggests that a recovery period of drought is necessary, following submersion.

PHOTOSYNTHESIS AND RESPIRATION

Most studies on photosynthesis and respiration were performed with immersed or water saturated thallus. Johnson et al. (1974) measured photosynthesis of 6 species of seaweed during progressive desiccation up to 50% of its maximum rate. Since *P. canaliculata* dries out in the field and can lose more than 80% of its total water in less than 3 hours we measured its photosynthetic rate at several stages during desiccation.

Methods - Rates of gas exchange were obtained using the Warburg manometer (Umbreit et al. 1964). Thalli were dried in air on a torsion balance until their water content reached the desired value. They were then placed in the center of a large Dickens-Semer-type flask (vol. c. 40 ml), without a suspending medium. The CO₂ tension in the atmosphere was maintained at 0.11 - 0.14% at 12°C using an external buffer system developed by Fletcher (1972), based on the method of Pardee (1949). 1.5 ml of this buffer plus a glass bead were placed in the side arm of the flask. The internal RH was 75%. Thalli were kept in running seawater overnight before use. Illumination during the experimental period was with 440 W Phillips daylight-type fluorescent tubes giving an intensity of 4,000 lux. Measurements with immersed plants used filtered sterile seawater.

Thalli were weighed before and after determination of rates of gas exchange. Frequently a change in weight of 1 - 3% occurred, so that the means of the two weights were used on the graphs. Saturation weight refers to thalli immersed overnight then blotted and weighed.

Results - The curves for respiration and photosynthesis as a function of thallus water

content are given in figures 7 and 8, respectively. Rates of respiration and photosynthesis are similar for both forms of *Pelvetia*, the response in both cases being linear. The rates are halved at 50% of saturated water content and reach zero at 10 - 20%. Frequently a small residual respiration rate was measurable at less than 10% saturated water content - perhaps due to bacteria or the fungus (*Mycosphaerella*) which is always associated with this plant. The scatter of the results could be due to age (cf. Kelly 1953) or variations in respiratory substrate (Rabinowitsch 1945).

The rates of photosynthesis of water saturated thalli at different light intensities are shown in figure 9. Photosynthesis continues linearly until at least 4,500 lux, so that it is possible that at even higher light intensities, assimilation would occur at a high rate even at low water content.

LIGHT COMPENSATION POINT

The determination of light compensation point of seaweeds has been much neglected in the literature despite its recognised importance in explaining algal distribution. Ehrke (1927, 1931) and Ogata and Matsui (1965) give measurements for some species. Experiments were planned in order to determine the light compensation point of both forms of *Pelvetia* out of water.

Methods - Light compensation points were measured using the cresol-red-buffer solution described by Lieth (1960). This solution quickly equilibrates with the CO₂ content of atmospheric air; loss of CO₂ is shown by a yellow colour. The light compensation point is indicated by a colour similar to that of normal air (control). Branches of *Pelvetia* were tied flat to a support attached to the stopper of a test-tube, in the base of which was placed 2 ml of cresol-red solution. Test tubes containing plants were arranged at varying distances from a light source (Phillips daylight fluorescent tube) at constant temperature (12°C ± 0.5). After 3 hours the colours in the test tubes were compared with test tubes containing no plants.

Results - Only a small difference was seen between the saxicolous and marsh plants which had values of 750 and 650 lux respectively. But since the spread overlapped it is safer to consider both forms as sun-plants. The results of previous workers (Ehrke 1929, 1931, and Ogata and Matsui 1965) are generally lower for the other seaweeds investigated, but were performed at higher temperature and the results not directly comparable. A temperature of 12°C was chosen for its similarity to field conditions.

DISCUSSION

The experiments on water relations lead to the conclusion that conditions on the marsh, where moisture is kept high for longer periods after exposure than on the rocky-shore, allow plants to metabolise at a high rate for longer time (fig. 10). This is very likely to be true because during daytime light intensity is always well above the compensation point. Even so the marsh plants are rather dwarfed when compared with those of the rocky-shores which could probably be related to silt deposition plus limiting amount or of nutrients since the former plants grow at a higher level and so stay longer out of the water. The ratio of dry weight to fresh weight of the two forms shows that marsh plants had a significantly lower "water capacity" than rocky-shore forms (Table I). If Zaneveld's (1937) conclusion that higher shore fucoids have higher water contents than

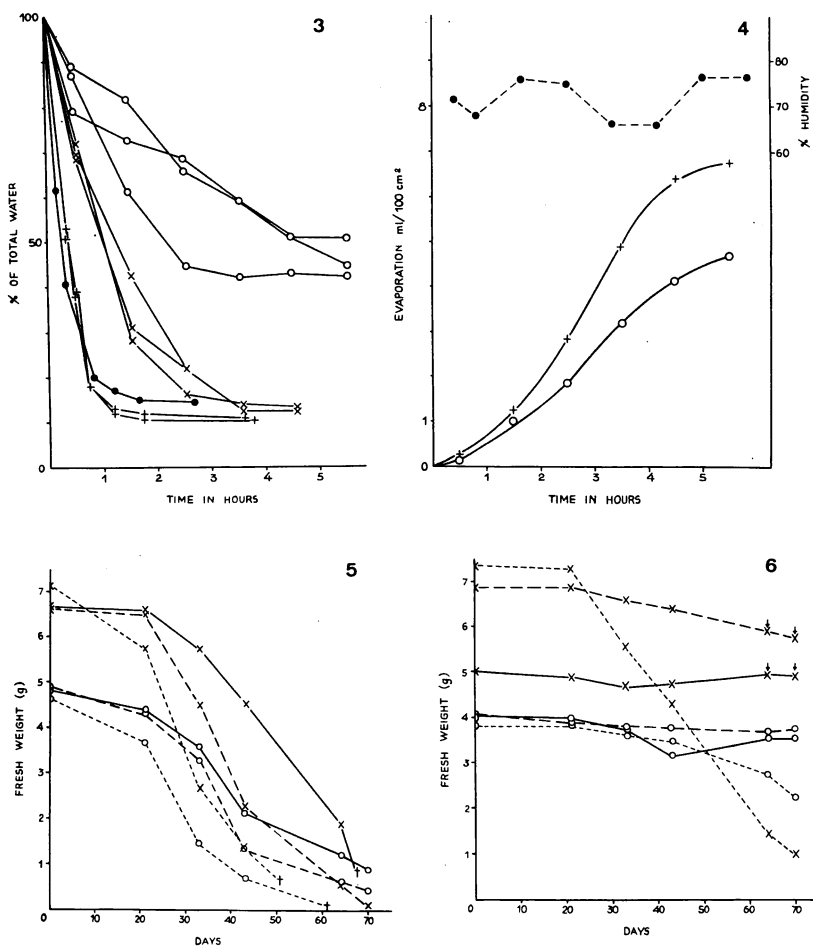


Fig. 3 - Perda de água de *Pelvetia canaliculata* em condições naturais - forma do pântano, "in situ" (o-o) e ao ar livre (●-●); forma do costão rochoso, "in situ" (x-x) e ao ar livre (+-+) under natural conditions. Fig. 4 - Umidade relativa, (●-●) e poder evaporante do ar no local de crescimento das plantas do pântano (o-o) e do costão rochoso (+-+). Medidas tomadas com higrômetro de cabelo e evaporímetro de Piché. Fig. 5 - Variação do peso de talos mantidos em imersão contínua em diferentes intensidades de luz. Forma do costão rochoso (o-o) 1.300 lux, (o--o) 600 lux, (o---o) 90 lux. Forma do pântano (x-x) 1.300 lux, (x--x) 600 lux, (x---x) 90 lux. Fig. 6 - Variação de peso de talos mantidos em regime de 20 horas de imersão/4 horas de emersão em diferentes intensidades luminosas. Veja fig. 5 para significado dos símbolos. As setas indicam o aparecimento de receptáculos.

Fig. 3 - Water loss of the salt marsh form of *Pelvetia canaliculata* "in situ" (o-o) and in the open air (●-●), and of the rocky shore form (x-x) "in situ" and in the open air (+-+) under natural conditions. Fig. 4 - Evaporative power of the air beside salt marsh (o-o) and rocky shore (+-+) forms of *Pelvetia canaliculata*, measured with a Piché evaporimeter. Relative humidity (●-●) measured with a whirling sling hygrometer. Fig. 5 - Weight variations of *Pelvetia canaliculata* under different light intensities and continuous submersion in the laboratory. Rocky shore form (o-o) 1,300 lux, (o--o) 600 lux, (o---o) 90 lux. Salt marsh form (x-x) 1,300 lux, (x--x) 600 lux, (x---x) 90 lux. Fig. 6 - Weight variations of *Pelvetia canaliculata* under different light intensities and a 20 hours submersion/ 4 hours emersion regime. Rocky shore form (o-o) 1,300 lux, (o--o) 600 lux, (o---o) 90 lux. Salt marsh form (x-x) 1,300 lux, (x--x) 600 lux, (x---x) 90 lux. The arrows indicate arising receptacles.

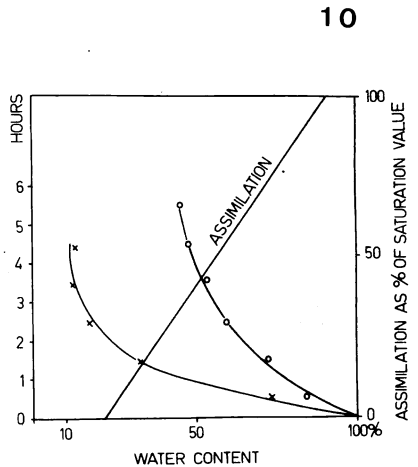
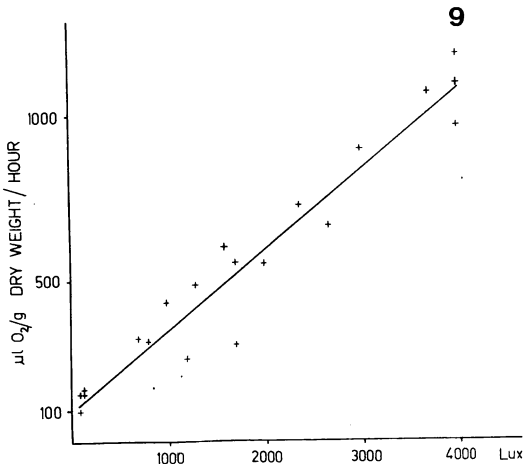
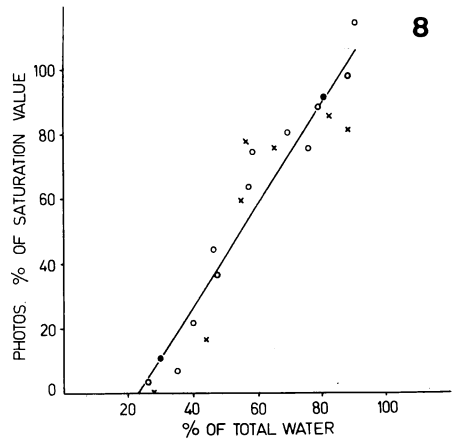
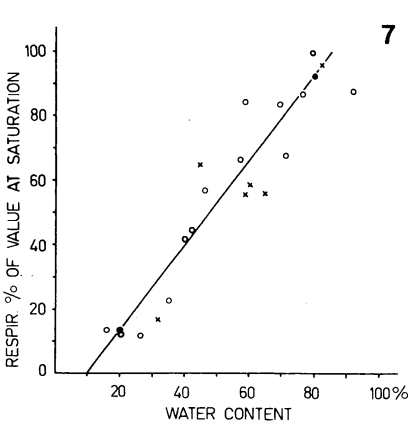


Fig. 7 – Respiração de talos de *Pelvetia canaliculata* com diferentes conteúdos de água, em termos de porcentagem do valor obtido com talos saturados de água. Dados obtidos a 12°C. o forma do pântano, (x) forma do costão rochoso. **Fig. 8** – Fotossíntese de talos com diferentes conteúdos de água em porcentagem do valor obtido com talos saturados. Símbolos e temperatura como na fig. 7. **Fig. 9** – Valores de fotossíntese de talos saturados de água em diferentes intensidades luminosas, à 12°C. **Fig. 10** – Comparação entre taxas de fotossíntese e conteúdo de água, na natureza, das formas do costão rochoso (o) e do pântano (x).

Fig. 7 – Respiration of rocky-shore (o) and salt marsh (x) plants of *Pelvetia canaliculata* expressed as % of water saturated thallus, under different water contents ($T^{\circ} 12^{\circ} C$). *Fig. 8* – Photosynthesis of rocky-shore (o) and salt marsh (x) plants of *Pelvetia canaliculata* expressed as % of water saturated thallus, under different water contents ($T^{\circ} 12^{\circ} C$). *Fig. 9* – Photosynthesis of rocky-shore plants of *Pelvetia canaliculata* under different light intensities at 12°C., for water saturated thalli. *Fig. 10* – Comparison between photosynthesis and water content (in the lab), and water loss (in the field) of rocky-shore (o) and salt marsh (x) plants of *Pelvetia canaliculata*.

those lower down is accepted, than it could be considered that the salt marsh *Pelvetia* occupies a physiologically "lower level" than the rocky-shore form. This conclusion is reasonable in the light of the results obtained in this paper, even though the salt marsh plants may be distributed at a comparatively higher level than the ones on rocky-shores.

The results of the continuous submergence experiment show that both forms are very sensitive to submergence and so indicates that the restriction of *Pelvetia* to the upper shore is due to its inability to support longer submersion periods rather than to competition. This supports the observation of Fischer (1929) for *Pelvetia canaliculata* and *Fucus spiralis*, of Den Hartog (1968) for several species, and of Rusanowski and Vadas (1973) for *Fucus edentatus* and *F. vesiculosus*. On the other hand, Edwards (1977) working with several species of green and red algae found that, independent of its level on the zonation all species grow best when completely submerged. Edwards did not accept the view of Den Hartog that contact with the air is important for some species and doubted the results of Rusanowski and Vadas, though recognizing that there is good evidence that continuous submergence is inimical to *P. canaliculata* and *F. spiralis*. The conclusion of Edwards that the upper shore species are those with a wide tolerance range of abiotic factors and are normally restricted to the upper shore levels because of a low competitive ability, seems valid only to the very particular conditions he utilised, i. e. pure culture in artificial media. We accept his approach as an important contribution for a better understanding of the causes of zonation, however one should allow that Edwards' cultures were kept for a too short period (4 - 8 day) and that the trend of the growing curves could be modified later on.

The conclusion of Edwards (1977) is also in disagreement with that of Johnson et al. (1974) who found that species growing higher upshore have photosynthetic rates up to 6.6 times greater in air than in water at the same illumination and temperature. Contrasting results were obtained by Bidewell and Craigie (1963) with *Fucus vesiculosus*. However these authors performed their measurements within a high CO₂ concentration. Kremer and Schmitz (1973) found an equal or smaller rate of photosynthesis during emersion, but found a good correlation between the level occupied by the species in the zonation and the ability to photosynthesize in the air. A requirement for alternating periods of wetting and drying was already observed for aquatic lichens (Ried 1960, Fletcl er, 1976).

In respect to this the conclusion from the available data is that some species live in the intertidal not only because they tolerate air exposure but also because this is beneficial to them. These species will not go downwards towards the infralittoral because they are less competitive under continuous submergence and vice-versa. This is not necessarily always the case for all species since some littoral belts may be controlled by a complex interaction between suboptimal conditions of abiotic parameters and biotic relationships. On the other hand, competition should exist at every level or defined zone; however as one goes up towards the supralittoral the conditions become gradually more restrictive and consequently the amount of competition decreases.

Comparing the results of respiration and photosynthesis at different water contents with the water loss at constant humidity, it appears that in environments where the RH is maintained over 75% during intertidal exposure, *Pelvetia* will be able to photosynthesize provided light is not limiting. Because of this it would be interesting to compare some phenological aspects, such as growth rate and reproduction, in places exposed to high and low humidities. Ardré (1969), for example, found that *Pelvetia* growing at different levels on the shore, or in north and south facing situations, had different de-

grees of receptacle development which is probably related to humidity. Fischer (1939) concluded that the factor controlling the upper limit of *Pelvetia* is not tide level but humidity (humidité résiduelle). This could indeed be important because these plants are emersed for a much longer period than they are immersed, and can photosynthesise efficiently at humidities of up to 75%.

In preliminary experiments rocky-shore *Pelvetia* could reach 70% of its optimum photosynthetic rate in 30 minutes after continuous desiccation of 20 hours and a loss of 90% of its total water. This suggests that desiccation recovery is not particularly important. By comparison other algae have been shown to be much more susceptible. Ogata and Matsui (1965) found that *Ulva* was seriously affected after only 69% dehydration, and *Gelidium* was reduced to zero photosynthesis after a water loss of 73%. *Porphyra* was more similar its response to *Pelvetia* since it could recover normal photosynthesis even after 90% water loss. Montfort (1937) reported that after 5 hours of desiccation *Fucus platycarpus*, *F. vesiculosus* and *F. serratus* had recovered to 97, 72 and 42% of their normal photosynthesis, respectively. The high recovery rate of *Pelvetia* is remarkably similar to results obtained for aquatic lichens (Ried 1960; Fletcher, 1972), and indeed the similarity in the ecology of rocky-shore *Pelvetia* with littoral lichens (Fletcher 1973) is particularly noteworthy. It is well known that *Pelvetia* has sometimes been considered to be a form of lichenised association with *Mycosphaerella* (Sutherland 1915), and it remains a possibility that the presence of the fungus exerts an influence on the ability of the alga to withstand desiccation.⁽³⁾

In conclusion, the comparison of the responses of both *Pelvetia* forms to the experiments described does not show a variation of behaviour that one would expect between two populations well-adapted to quite different environments.

Note added in proof - Further publications on the physiology of saxicolous *Pelvetia* are: Priou (1962, Bull. lab. marit. Dinard 48: 3-112) for water relation and Ried (1969, Ber. Dtsch. Bot. Ges. 82:127-141) for desiccation and high temperature resistance.

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