

Photosynthesis of Intertidal Brown Algae During and After Periods of Emersion: A Renewed Search for Physiological Causes of Zonation

M. J. Dring and F. A. Brown

Department of Botany, The Queen's University, Belfast BT7 INN, Northern Ireland

ABSTRACT: CO₂-exchange of emersed plants and O₂-exchange of submersed plants were measured in 5 species of brown algae from different tidal heights on shores in Ireland and Helgoland (southern North Sea). The photosynthesis of emersed fucoids and *Laminaria digitata* increased as up to 25 % of tissue water was lost, but then declined with further desiccation. The relationship between decrease in photosynthesis and loss of tissue water was similar in 3 species of *Fucus*, and the photosynthetic apparatus of *F. spiralis* appeared to be no more resistant to desiccation than that of *F. serratus*. Recovery from severe desiccation took about 2 h in all species, regardless of their typical position on the shore, but the extent of recovery from a given degree of desiccation was greater in upper shore species. *Pelvetia canaliculata* and *F. spiralis* showed complete recovery from 80 to 90 % water loss, *F. vesiculosus* from about 70 %, *F. serratus* from 60 %, and *Laminaria digitata* from 55 % water loss. The photosynthetic rate of each species after full recovery decreased linearly as water loss increased beyond these values. It is in the extent of recovery of photosynthesis after desiccation that intertidal brown algae show the clearest correlation with their heights in the zonation pattern on European shores.

INTRODUCTION

Experimental phycologists have long sought a physiological explanation for the conspicuous zonation of algal species observed in the intertidal region of temperate rocky shores (e.g. Baker, 1909; Doty and Archer, 1950; Biebl, 1962; Chapman, 1966; Zaneveld, 1969). However, in a recent review of the ecology of macroscopic marine algae, Chapman (1974) reached the conclusion that: 'the search for causes of zonal discontinuities has been fruitless . . . because ecological zonation is largely dependent on the competitive relations of species . . . and physiological tolerance limits play no part in this explanation' (p. 69). This conclusion reflected the current shift in emphasis from laboratory-based investigations of physical factors to field-based investigations of biotic factors (involving the removal or exclusion of competitors or herbivores), and the success of the latter approach threatened, for a time, to eliminate the former - and to provide another example of competitive exclusion in the process. Recently, however, various workers have returned to the problem of physical factors in zonation, and have

provided clear evidence from the field that competition cannot provide as complete an explanation as Chapman's conclusion implies. For example, individual plants of *Pelvetia canaliculata*, *Fucus spiralis* and *Ascophyllum nodosum*, which were close to the upper limits of these species on the shore, were observed to be damaged and later killed following periods in the summer when neap tides coincided with hot, sunny weather (Schonbeck and Norton, 1978) and, in this way, the upper limits of these species in western Scotland were periodically 'pruned back'. Transplantation experiments in the field have also shown that intertidal algae grow more slowly and soon die in regions of the shore above the normal upper limit for the species, even when competition is prevented by clearing all other plants from the transplantation sites (Schonbeck and Norton, 1978, 1980). These observations re-affirm the conclusions of Connell (1961), based on studies of barnacle zonation, that the lower limits of intertidal species are usually determined by biotic factors (especially competition and predation), whereas the upper limits are more often determined by physical factors. It seems appropriate, therefore, to re-examine the pos-

sible mechanisms by which physical factors could exert differential effects on the distribution of algal species.

The work of Zaneveld (1937) suggested that algal species from the upper shore lose water more slowly than species from lower on the shore, and are, therefore, better able to survive long periods of emersion. However, this hypothesis has been re-examined by several workers (Kristensen, 1968; Schonbeck and Norton, 1979a; Dromgoole, 1980). All have concluded that the rate of water loss is not correlated with the height at which a species grows on the shore, but is mainly determined by the surface to volume ratio of the thallus. An explanation of the apparent inability of some species of intertidal algae to withstand severe desiccation must, therefore, be sought in the metabolic changes that occur in different species during or after periods of emersion.

The present investigation explores the effects of emersion on the photosynthesis of 5 species of brown algae, which characteristically occur in distinct zones on north-west European shores. The following 3 hypotheses have been examined in sequence, and the evidence presented suggests that the first 2 should be rejected, but the third retained:

- (1) Species from the upper shore are able to maintain active photosynthesis at lower tissue water contents than species from lower on the shore.
- (2) The rate of recovery of photosynthesis after a period of emersion is more rapid in species from the upper shore.
- (3) The recovery of photosynthesis after a period of emersion is more complete in species from the upper shore.

MATERIALS AND METHODS

Experimental Plants

Experiments involving infra-red gas analysis were conducted in Belfast in January–March 1980, and the experimental plants (*Pelvetia canaliculata* [L.] Dcne. et Thur., *Fucus spiralis* L., *F. vesiculosus* L., *F. serratus* L., *Laminaria digitata* [Huds.] Lamour.) were all collected from Strangford Lough, either from the east shore near Portaferry (Irish grid ref: J 592508) or from the west shore at Whiterock, Co. Down (J 527618). The plants were transported immediately to Belfast and were stored at 0 to 2 °C in the dark for a maximum of 5 d. The experiments based on oxygen measurements were conducted at the 'Meeresstation' of the 'Biologische Anstalt Helgoland' on Helgoland (southern North Sea) in October 1981; plants were collected from the north end of the island and were stored at 10 °C for up to 3 d.

Since *P. canaliculata* does not occur near Helgoland, this species could not be examined by both techniques. The morphology of the Helgoland forms of both *F. spiralis* and *F. vesiculosus* differs substantially from that of the Irish forms of these species (Kornmann and Sahling, 1977) but they occupy equivalent positions on the shore. The zone occupied by *F. vesiculosus* in Helgoland is, however, much narrower than the equivalent zone in Ireland, and it was not possible to distinguish 'upper shore' and 'lower shore' populations, as was done with the Irish material.

Gas Exchange of Emerged Plants

CO₂ exchange of emerged plants was measured with an infra-red gas analyser (IRGA; Analytical Development Co. Ltd., Series 225/2) in an open gas-flow system. The experimental chambers were 1 l Buchner flasks lying on their sides in a constant temperature room at 10 °C, and illuminated by a 400 W mercury vapour lamp giving a photon irradiance inside the flasks of 550 μmol m⁻² s⁻¹. Air was drawn from outside the building through a compressor and into a 25 l reservoir in the 10 °C room. A manifold permitted the air stream to be divided between four experimental chambers and a reference chamber, and 5 separate lines then passed through water traps and entered a gas handling unit (Analytical Development Co. Ltd., WA 161), which regulated the air flow to 1 l min⁻¹, and automatically switched from one experimental air-stream to another for measurement in the IRGA. The difference in CO₂ concentration between the air in each of the experimental chambers and that in the reference chamber was measured and recorded every 6 min.

The plant material for each experiment consisted of the apical 6 to 7 cm of a healthy frond, free of epiphytes, for each of the *Fucus* species, a small clump of thallus of equivalent fresh weight for *Pelvetia canaliculata*, and a 5 × 5 cm square cut from the blade within 50 cm of the stipe for *Laminaria digitata*. The fresh weight of each sample (usually between 0.5 and 1.0 g) was determined at the beginning of the experiment and, except for *P. canaliculata*, the surface area was also measured. In experiments in which drying was monitored at the same time as photosynthesis, the plants were taken out of the Buchner flasks at intervals, weighed and replaced. However, this procedure, in itself, caused the photosynthetic rate of *L. digitata* to change, so that this type of experiment was conducted only with the *Fucus* species. Throughout this investigation, the water content of the plant material is expressed as the percentage of tissue water remaining, i.e.:

$$\frac{(\text{fresh weight} - \text{intermediate weight})}{(\text{fresh weight} - \text{oven-dry weight})} \times 100$$

Plants with different water contents were obtained by drying fronds for various lengths of time within the experimental chambers themselves, and severe desiccation was effected by passing the air-stream through a saturated solution of MgCl_2 (giving a humidity of 34 %) before it entered the chambers. Drying treatments were never longer than about 16 h, and plants were exposed to temperatures higher than 15 °C only at the end of each experiment, when being oven-dried.

Gas Exchange of Submerged Plants

The metabolic activity of submerged plants was estimated from O_2 -measurements using a Clarke type polarographic electrode (Yellow Springs Instruments Inc., YSI 5331 oxygen probe) at 15 °C. The experimental chamber was circular, about 5 cm in diameter with a volume of about 30 ml, and was flushed at intervals (usually of 20 min or less) with filtered sea water, so that almost all measurements were made in water that was 80 to 95 % saturated with oxygen. The light source was a projector with a quartz-iodide lamp (24 V, 250 W) combined with Schott glass filters BG38 (2 mm thick) and GG4 (1 mm thick) to simulate the spectral distribution of underwater light at moderate depths in Type 5 coastal water (Lüning, 1980). All photosynthesis measurements were conducted at 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, which was found to saturate photosynthesis in all species.

The experiments with *Fucus spiralis* and *F. serratus* used discs of tissue (15 mm in diameter), which were cut from young fronds at about 5 cm behind the apex. Similar discs were used for *Laminaria digitata*, but these were cut at about 10 cm from the base of the blade of young plants (up to 0.5 m in length). For *F. vesiculosus*, 2 cm lengths of frond were cut at about 5 cm behind the apex of young plants. These frond segments were always 8 to 10 mm wide, so that their surface area was similar to that of the discs used for the other species. In all experiments with submerged plants, the photosynthesis of each disc or segment of frond was measured for about 60 min immediately after the disc was cut from a fresh frond. The disc was dried at 15 °C and 70 to 75 % humidity for up to 4 h, and photosynthesis was then re-measured as soon as possible after the disc was re-immersed in sea water. Measurements were continued for the next 2 to 10 h. Drying was sometimes accelerated by using a fan, but the temperature and humidity conditions were not changed. The discs and segments were weighed

before and after drying, and again after their recovery in water. Finally, they were dried to constant weight at 80 °C.

RESULTS

Photosynthesis During Emersion

The effects of desiccation on the photosynthetic rate of emersed thalli was investigated by monitoring the CO_2 exchange of a fresh thallus at frequent intervals as it dried out in the air stream. Four typical time-courses are shown in Fig. 1. In all species, photosynthesis

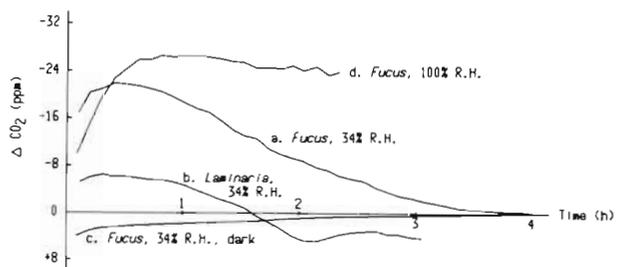


Fig. 1. Time-courses of CO_2 -exchange following emersion for plants of *Fucus serratus* (a, c, d) or *Laminaria digitata* (b) at 10 °C, as recorded by IRGA. Photon irradiance: 550 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (a, b, d) or darkness (c); relative humidity: 34 % (a, b, c) or 100 % (d)

increased during the first 30 to 40 min of the experiment, and reached a maximum value when 20 to 30 % of the initial water content had been lost. Photosynthesis then decreased as the thallus dried out further. In the fucoids (*Pelvetia canaliculata* and *Fucus* spp.), net photosynthesis usually declined gradually to a value close to zero (Fig. 1a), since the respiration rate in these species also decreased as the thalli dried (Fig. 1c). In *Laminaria digitata*, however, the respiration rate remained more or less constant during drying, so that net photosynthesis became negative after 1½ to 2 h in the light (Fig. 1b). In some experiments, the air in the experimental chambers was maintained at a high humidity (close to 100 %) by pouring some water into the air reservoir and placing soaked filter paper in the chambers. Under these conditions, the emersed plants did not lose more than about 20 % of their tissue water, and the photosynthetic rate did not decline substantially after the initial increase (Fig. 1d). In one experiment with *F. serratus*, photosynthesis was measured for 10 h in 100 % humidity, but no decline in the rate was observed.

The hypothesis that the photosynthetic apparatus of species from the upper shore might be more resistant to loss of water from the thallus (Hypothesis 1, p. 302) was tested by following the loss of weight in the same thalli

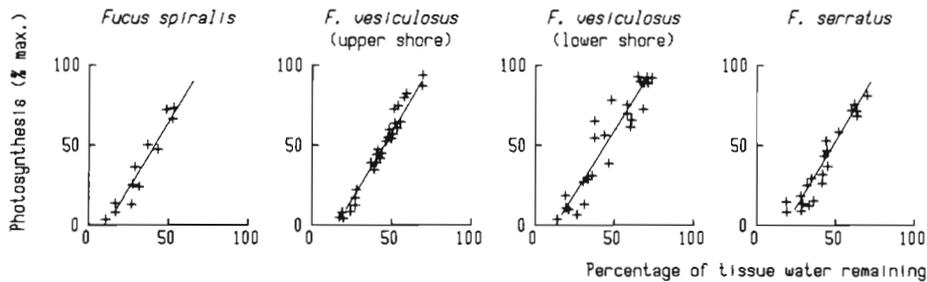


Fig. 2. Relationship between photosynthetic rate during emersion (measured by IRGA at 10°C and $550 \mu\text{mol m}^{-2} \text{s}^{-1}$) and the current water content of the thalli in plants from 4 populations of *Fucus* spp. growing at different heights on the shore at Portaferry, Co. Down. Linear regressions plotted for each of the 4 populations are not significantly different at $p = 0.05$

that were used for photosynthesis measurements. Several plants of *Fucus spiralis* and *F. serratus* and from 2 populations of *F. vesiculosus* (from the upper and the lower limits of the *F. vesiculosus/Ascophyllum* zone) were studied in this way, and the photosynthetic rate of all plants showed a positive correlation with water content between 10 and 70% (Fig. 2). Linear regressions were calculated for each set of data, but no significant differences could be detected between the four groups of results. Photosynthesis declines as rapidly with decreasing tissue water content in *Fucus spiralis* from the upper shore as it does in *F. vesiculosus* and *F. serratus* from lower on the shore. These results suggest, therefore, that Hypothesis 1 (p. 302) should be rejected.

Photosynthesis After Emersion:

Rate of Recovery

Rapid recovery of photosynthesis after a period of desiccation is a considerable ecological asset for plants growing on the upper shore, which may be covered by water for only 1 to 2 h in each tidal cycle. Hypothesis 2 was tested by measuring photosynthesis with the O_2 -electrode as soon as possible (usually 15 to 20 min) after a dried disc or segment of thallus had been re-immersed in sea water, and then following the recovery of photosynthesis over the next 2 to 10 h. In almost all experiments with every species, the first photosynthetic rate to be recorded was lower than the rate observed after full recovery (Fig. 3), but significant and sustained increases in rate usually occurred only during the first 2 h after re-immersion. The time required for the time-course of recovery to reach a plateau appeared to be very similar in *Fucus spiralis* (the uppermost fucoid in Helgoland) and in *Laminaria digitata*, which is restricted to the upper sublittoral zone. The intermediate species in the zonation, *F. vesiculosus* and *F. serratus*, are also similar. Recovery is often complete within an hour after less severe drying treatments (Fig. 3), but there is no evidence of substantial differences between species in the rate of recovery from any given level of desiccation. On the

basis of these results, therefore, Hypothesis 2 should also be rejected.

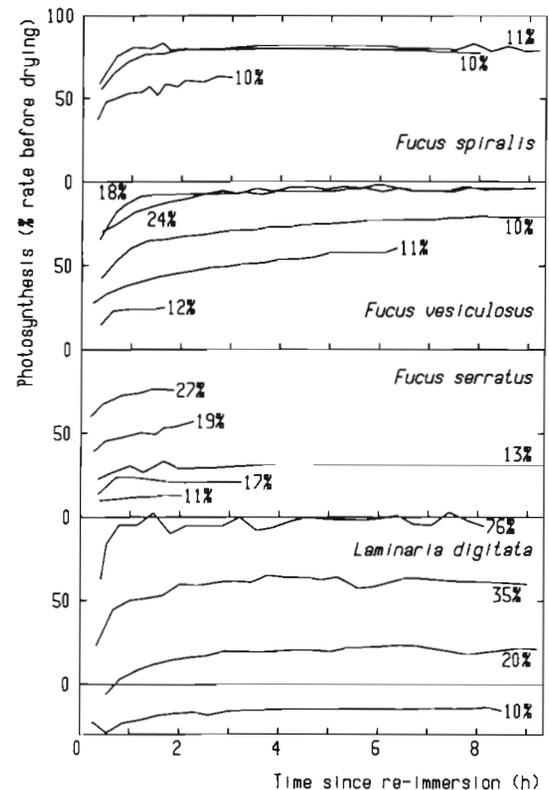


Fig. 3. Time-courses of net photosynthesis following re-immersion after various drying treatments for discs or segments cut from thalli of *Fucus spiralis*, *F. vesiculosus*, *F. serratus* or *Laminaria digitata*. Photosynthesis was measured by O_2 -electrode at 15°C and $500 \mu\text{mol m}^{-2} \text{s}^{-1}$, and is expressed as a percentage of the photosynthetic rate of the disc or thallus segment before drying. The percentage of tissue water remaining at the end of the drying treatment is shown for each time-course

Extent of Recovery

Since the photosynthesis of re-soaked thalli had usually reached a plateau within 2 h of re-immersion (Fig. 3), the rate after at least 2 h was used as an estimate of the photosynthetic rate after full recovery.

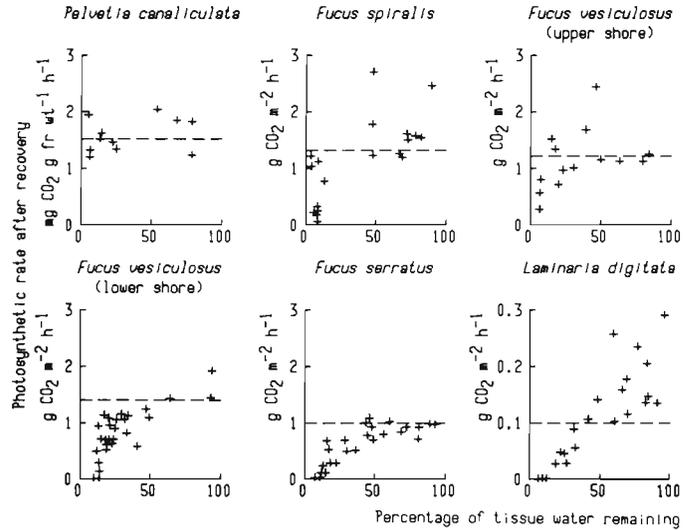


Fig. 4. Maximum rate of CO₂-uptake (measured by IRGA at 10°C and 550 μmol m⁻² s⁻¹) by emerged thalli of different species, which had previously been dried to various tissue water contents and then had been re-soaked for at least 2 h. The mean photosynthetic rate for fresh thalli of each species is indicated by a horizontal broken line

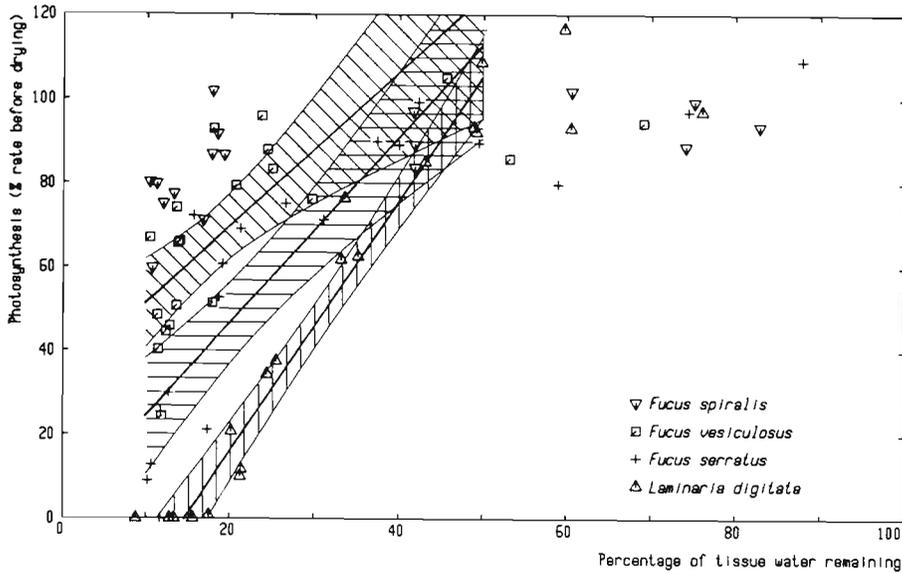


Fig. 5. Net photosynthesis (measured by O₂-electrode at 15°C and 500 μmol m⁻² s⁻¹) of submersed discs or thallus segments from 4 species, following complete recovery from drying treatments which had reduced the tissue water content to different extents. Photosynthesis is expressed as a percentage of the photosynthetic rate of the disc or thallus segment before drying. Linear regressions of photosynthesis on tissue water remaining (for values of the latter between 10 and 50%), together with their 95% confidence zones (hatched areas), are shown for *Fucus vesiculosus* (diagonal hatching), *F. serratus* (horizontal hatching) and *Laminaria digitata* (vertical hatching), but the regression for *F. spiralis* was not significant at $p = 0.05$

This 'recovered rate' of photosynthesis was then compared with the photosynthetic rate of fresh thalli to obtain a measure of the extent, or the completeness, of recovery from desiccation (see Hypothesis 3, p. 302). These experiments were conducted both with Irish material (Fig. 4), whose recovered photosynthesis was taken to be the maximum rate of CO₂-uptake recorded after a re-soaked plant was placed in the experimental chamber, and with Helgoland material (Fig. 5), whose O₂-output was measured continuously after re-immersion, until a steady rate was obtained. In spite of the major differences in detail between the 2 experimental techniques, and the environmental differences between the 2 collecting sites, the pattern of the results is similar in both sets of data.

The species which always occupies the uppermost

position on Irish shores, *Pelvetia canaliculata*, showed almost complete recovery of photosynthesis from even the most severe drying treatments (Fig. 4). In one plant, the tissue water content was reduced to 4% of its initial value, but photosynthesis was comparable with that in fresh plants within 2 h of re-immersion. Photosynthesis in *Fucus spiralis* also recovered to within 20 to 25% of that in fresh plants, provided that at least 10% of the initial tissue water remained (Figs. 4 and 5). All species were air-dry at about this water content under the drying conditions used for the Helgoland experiments (Fig. 5) and, for *F. spiralis*, there was no significant correlation between the extent of recovery of photosynthesis and the tissue water content after drying. However, more severe drying was achieved in the IRGA experiments, and *F. spiralis* did not always

recover completely when more than 90 % of the initial water content had been lost (Fig. 4). The results for the species from the opposite end of the zonation, *Laminaria digitata*, show a complete contrast. In both Irish (Fig. 4) and Helgoland (Fig. 5) material, plants which had lost more than 40 to 50 % of their initial water content failed to recover their original photosynthetic rate and, if the water content was reduced to less than 20 % of the initial value, net photosynthesis remained negative (e.g. Fig. 3) or zero. The remaining two species, *F. vesiculosus* and *F. serratus*, which occupy an intermediate position in the zonation, showed an intermediate ability to recover from drying treatments of a given severity (Figs. 4 and 5), and plants of *F. vesiculosus* from an upper shore population in Ireland showed better recovery than those from a population lower on the shore (Fig. 4). The linear regression of percentage recovery of photosynthesis on the percentage of tissue water remaining (results obtained when this parameter was >50 % were not included in the regression calculations) was non-significant for *F. spiralis* (Fig. 5) but was significant ($p < 0.01$) for the other 3 species examined in the Helgoland experiments. The regression lines for these 3 species are shown in Fig. 5, together with 95 % confidence zones. These species show significant differences in their ability to recover from severe drying treatments, and these results provide clear support for Hypothesis 3 (p. 302).

DISCUSSION

An increase in the photosynthetic rate of fucoids during the early stages of drying (Fig. 1a, d) was first reported as long ago as 1937 by Stocker and Holdheide. Their observations have since been confirmed for a wide range of intertidal algae, including species of *Ulva*, *Porphyra* and *Iridaea* (Johnson et al., 1974; Brinkhuis et al., 1976; Quadir et al., 1979), but not previously for a species from the Laminariales (Fig. 1b). Stocker and Holdheide (1937) suggested that a thin film of water over the surface of freshly emersed thalli might inhibit CO₂ diffusion from the air into the thallus, and this explanation has yet to be either confirmed or improved upon. A gradual decline in respiration rate during drying (Fig. 1c) is also well documented for fucoids (Kanwisher, 1957; Quadir et al., 1979), but it may be significant that, in at least 2 sublittoral species (*Iridaea cordata*, Quadir et al., 1979; *Laminaria digitata*, this investigation), respiration did not decline during emersion. Another significant result from the present study of photosynthesis during emersion is that the rate of photosynthesis does not decline over a long period if the thallus does not dry out

(Fig. 1d). This indicates that emersion is not, in itself, detrimental for photosynthesis. In some recent experiments with artificial tidal regimes (e.g. Schonbeck and Norton, 1979b), intertidal algae have been exposed to 100 % humidity during the emersion periods. The differences in growth rate that were observed between species from different zones cannot, therefore, be attributed to differential effects of emersion on either drying or photosynthesis, and the rate of nutrient uptake during short periods of submersion may well be a critical factor for the growth of plants on the upper part of the shore.

The evidence obtained in the present investigation that the photosynthetic apparatus of species from the upper shore is no more resistant to water loss than that in species from the lower shore (Fig. 2) is again supported by the early work of Stocker and Holdheide (1937). These authors also measured water loss at the same time as photosynthesis in 3 species of *Fucus*, and they concluded that the relationship between photosynthetic rate and water content is similar in all 3 species. Wiltens et al. (1978) studied the effects of desiccation on photosynthesis in 10 intertidal algae from British Columbia by *in vivo* determinations of the induction of chlorophyll fluorescence. The changes in the induction pattern that occurred with dehydration were similar in all species, regardless of their natural growth zone on the shore, although the precise water content at which specific changes occurred varied from species to species. They concluded, however, that the most significant difference between desiccation-tolerant and desiccation-sensitive species was in the extent of the reversibility of these changes on rehydration, rather than in the changes occurring during dehydration. As far as we are aware, no other comparative studies of the relationship between water content and photosynthetic rate have been conducted with marine algae. All of the available evidence, therefore, supports the present results in suggesting that Hypothesis 1 (p. 302) should be rejected.

There also appears to be no evidence that contradicts our conclusion – on the basis of the results presented in Fig. 3 – that there are no major differences between species in the rate at which photosynthesis recovers after a period of emersion. Kaltwasser (1938) followed the time-course of recovery of photosynthesis after drying in *Fucus vesiculosus*, *F. serratus* and *Laminaria digitata* from the Baltic Sea, and Schramm (1968) conducted similar experiments with *F. vesiculosus* from the same site. All of these results are similar to those in Fig. 3 in that recovery was normally complete within 2 to 3 h of re-immersion, and the photosynthetic rate then remained constant for the duration of the experiment (up to 4 d). The restoration of the normal pattern of fluorescence induction after rehydration also

required about 2 h in desiccation-tolerant species (Wiltens et al., 1978). It appears, therefore, that recovery is not a gradual, long-term process, but that the photosynthetic apparatus of desiccation-sensitive species must be irreversibly damaged during severe dehydration.

The third hypothesis that was tested in the present investigation was that species from the upper shore exhibit a greater ability to recover from a given degree of desiccation than species from lower on the shore. This hypothesis receives clear support from the results illustrated in Figs. 4 and 5. Kaltwasser (1938) also showed that *Fucus vesiculosus* from the Baltic Sea could recover more completely from severe desiccation than either *F. serratus* or *Laminaria digitata*. However, he could not detect the difference between the latter 2 species that was observed in this investigation, and *F. vesiculosus* appeared to be more tolerant of extreme desiccation than is indicated by the present results. These differences are probably related to the different habitats occupied by these species in the Baltic Sea, compared with Helgoland and the Irish Sea. *F. serratus* is entirely sublittoral in the Baltic Sea and occupies essentially the same vertical zone as *L. digitata*. *Pelvetia canaliculata* and *F. spiralis* are absent, and *F. vesiculosus* is the only large brown alga that is found extensively in the narrow intertidal zone. In this site, it is often emersed for much longer periods (i.e. several tidal cycles) than this species ever experiences in Helgoland or Ireland (Schramm, 1968). Japanese species of *Porphyra*, *Ulva*, *Gelidium* and *Zostera* also show differential recovery from severe desiccation (Ogata and Matsui, 1965) but, again, the species investigated do not form such a clear and well documented ecological series as *L. digitata* and the fucoids on the shores of N.W. Europe. Wiltens et al. (1978) concluded from their fluorescence induction studies that the critical difference between desiccation-tolerant and desiccation-sensitive species lay in the extent of their recovery from severe desiccation, but it was not possible for them to quantify this difference, or to demonstrate a series of increasing capacity for recovery from sublittoral to upper shore species.

Our conclusion that critical differences exist in the ability of different species to recover from desiccation is, therefore, by no means new. However, the present results provide better evidence than was previously available for a correlation between this ability and the typical position of each species on the shore. The clear rejection of Hypotheses 1 and 2 will also permit future work to be concentrated on the mechanism which enables desiccation-tolerant species to prevent irreparable damage to their photosynthetic apparatus during emersion. The recent studies of fluorescence induction in relation to desiccation in various marine

algae (e.g. Wiltens et al., 1978; Fork and Öquist, 1981) suggest that it will soon be necessary to search for biophysical, rather than physiological, causes of intertidal zonation.

Acknowledgements. We wish to thank Dr. R. N. Govier for his assistance in designing and setting up the IRGA-system used in this investigation, and Dr. K. Lüning for making the oxygen-electrode system available to us. The experimental work in Helgoland was made possible by the award of a Research Fellowship from the Humboldt Foundation to M. J. D., and this assistance and the hospitality of the 'Biologische Anstalt Helgoland' are gratefully acknowledged.

LITERATURE CITED

- Baker, S. M. (1909). On the causes of the zoning of brown seaweeds on the seashore. *New Phytol.* 8: 196–202
- Biebl, R. (1962). Seaweeds. In: Lewin, R. A. (ed.) *Physiology and biochemistry of algae*. Academic Press, New York, pp. 799–815
- Brinkhuis, B. H., Tempel, N. R., Jones, R. F. (1976). Photosynthesis and respiration of exposed salt-marsh fucoids. *Mar. Biol.* 34: 349–359
- Chapman, A. R. O. (1974). The ecology of macroscopic marine algae. *A. Rev. Ecol. Syst.* 5: 65–80
- Chapman, V. J. (1966). The physiological ecology of some New Zealand seaweeds. *Proc. Int. Seaweed Symp.* 5: 29–54
- Connell, J. H. (1961). The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42: 710–723
- Doty, M. S., Archer, J. (1950). An experimental test of the tide factor hypothesis. *Am. J. Bot.* 37: 458–464
- Dromgoole, F. I. (1980). Desiccation resistance of intertidal and subtidal algae. *Botanica mar.* 23: 149–159
- Fork, D. C., Öquist, G. (1981). The effects of desiccation on excitation energy transfer at physiological temperatures between the two photosystems of the red alga *Porphyra perforata*. *Z. Pflanzenphysiol.* 104: 385–393
- Johnson, W. S., Gigon, A., Gulmon, S. L., Mooney, H. A. (1974). Comparative photosynthetic capacities of intertidal algae under exposed and submerged conditions. *Ecology* 55: 450–453
- Kaltwasser, J. (1938). Assimilation und Atmung von Submersen als Ausdruck ihrer Entquellungsresistenz. *Protoplasma* 29: 498–535
- Kanwisher, J. (1957). Freezing and drying in intertidal algae. *Biol. Bull. mar. biol. Lab., Woods Hole* 113: 275–285
- Kornmann, P., Sahling, P.-H. (1977). Meeresalgen von Helgoland. *Benthische Grün-, Braun- und Rotalgen*. *Helgoländer wiss. Meeresunters.* 29: 1–289
- Kristensen, I. (1968). Surf influence on the thallus of fucoids and the rate of desiccation. *Sarsia* 34: 69–82
- Lüning, K. (1980). Critical levels of light and temperature regulating the gametogenesis of three *Laminaria* spp. (Phaeophyceae). *J. Phycol.* 16: 1–15
- Ogata, E., Matsui, T. (1965). Photosynthesis in several marine plants of Japan as affected by salinity, drying and pH, with attention to their growth habitats. *Botanica mar.* 7/8: 199–217
- Quadir, A., Harrison, P. J., DeWreede, R. E. (1979). The effects of emersion and submergence on the photosynthesis and respiration of marine macrophytes. *Phycologia* 18: 83–88

- Schonbeck, M., Norton, T. A. (1978). Factors controlling the upper limits of furoid algae on the shore. *J. exp. mar. Biol. Ecol.* 31: 303-313
- Schonbeck, M. W., Norton, T. A. (1979a). An investigation of drought avoidance in intertidal furoid algae. *Botanica mar.* 22: 133-144
- Schonbeck, M., Norton, T. A. (1979b). The effects of brief periodic submergence on intertidal furoid algae. *Estuar. coast. mar. Sci.* 8: 205-211
- Schonbeck, M. W., Norton, T. A. (1980). Factors controlling the lower limits of furoid algae on the shore. *J. exp. mar. Biol. Ecol.* 43: 131-150
- Schramm, W. (1968). Ökologisch-physiologische Untersuchungen zur Austrocknungs- und Temperaturresistenz an *Fucus vesiculosus* L. der westlichen Ostsee. *Int. Revue ges. Hydrobiol.* 53: 469-510
- Stocker, O., Holdheide, W. (1937). Die Assimilation Helgoländer Gezeitenalgen während der Ebbezeit. *Z. Bot.* 32: 1-59
- Wiltens, J., Schreiber, U., Vidaver, W. (1978). Chlorophyll fluorescence induction: an indicator of photosynthetic activity in marine algae undergoing desiccation. *Can. J. Bot.* 56: 2787-2794
- Zaneveld, J. S. (1937). The littoral zonation of some Fucoaceae in relation to desiccation. *J. Ecol.* 25: 431-468
- Zaneveld, J. S. (1969). Factors controlling the delimitation of littoral benthic marine algal zonation. *Am. Zool.* 9: 367-391

This paper was submitted to the editor; it was accepted for printing on March 9, 1982