Contribution of air and water to the carbon balance of *Fucus spiralis*

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ABSTRACT: A model was used to calculate the rate of carbon exchange by *Fucus spiralis* L. in the field. The model combines laboratory measurements of the effect of photon irradiance, desiccation and temperature on photosynthesis and respiration in air and water, with a simulation of changes in tidal level over a lunar month, received photon irradiance for different coastal water types and field-measured coefficients of water loss (D). The model predicts field growth rates of 1.3 and 2.1 % (mol C mol^{-1} C d^{-1}) in April and 2.1 and 4.8 % in July for the highest and lowest values of D, respectively. These values are in general agreement with published estimates of growth rates for *F. spiralis* in the field and laboratory. The net production per tide is very variable, even under the regular diurnal changes in photon irradiance used in the model. This is a result mainly of the length of time spent in light and dark per tide, but partly a response to whether *F. spiralis* is in air or water around midday, and whether maximal production is possible in air or water, which will depend largely on the value of D. The value of D was the major influence on total net production, and the relative contribution of air and water Under Jerlov's 'coastal 7' water type, net production when D was the lowest measured in the field was 1.6 and 2.3 times greater than that when D was the highest measured in the field for April and July respectively, but only 0.63 for April, and 0.53 for July, of that possible if desiccation was absent. In April, water contributed between 49 and 55 % of the total net production for Jerlov's 'coastal 13' and 'coastal 1' water types when D was the lowest, and 82 and 84 % for these water types when D was the highest measured in the field. Similar values for July are 23 and 28 % when D was low and 56 and 63 % when D was high. The effect of different coastal water types on total production was fairly small. Under field values of D, spring tides were between 1.85 and 2.3 times more productive than neap tides for both months. Production was calculated assuming *F. spiralis* was present at higher and lower positions on the shore. Under all conditions, except for the extreme case of no water loss, production decreased markedly higher up the shore, and increased down the shore, with maximal production between 1 and 3 m lower depending on conditions. These calculations reinforce the suggestions that the position of *F. spiralis* on the shore is not determined by carbon balance per se.

INTRODUCTION

Marine macroalgae which grow exposed in the inter-tidal region of the seashore spend, by definition, part of the time in air and part in water. They therefore experience 2 very different environments for photosynthesis and growth (Maberly & Spence 1989). In particular, the aerial environment presents problems of water loss, nutrient uptake for haptophytes, and possibly high light levels, while the aquatic environment poses problems of lower light levels and possibly a restricted supply of inorganic carbon given the low rate of diffu-sion of CO_2 in water. For intertidal species, the timing of exposure to air and water interacts with the timing of exposure to light and dark to produce a very variable environment for photosynthesis and respiration. Air frequently is thought to be the less favourable of the 2 environments for photosynthesis and growth of many intertidal macroalgae. Thus, for example, desiccation in air is thought to be an important environmental factor which restricts the upshore extension of many species (Schonbeck & Norton 1978). Laboratory measurements of net photosynthesis have shown, however, that for some species at least, rates may be greater in air than in water (e.g. *Fucus distichus*, Johnson et al. 1974, Quadir et al. 1979; *Endocladia muricata*, *Porphyra perforata*, and *Iridaea flacca*, Johnson et al. 1974). These data were obtained under limited, or in

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the absence of, desiccation and so represent the potential for rapid photosynthesis in air. Desiccation in the field could markedly reduce the rates, and thus reduce the importance of air to the carbon-balance of intertidal macroalgae.

In the absence of any direct measurements of the relative importance of air and water in the overall carbon balance of an intertidal species, an alternative approach has been to combine laboratory measurements of the response of the alga to relevant environmental conditions, with field measurements of these variables over time using a model. Thus, Beer & Eshel (1983) combined information on the effect of water content on the rate of photosynthesis with rates of water loss in the field for *Ulva* sp. on one day to estimate the extent to which desiccation in air would reduce rates of photosynthesis in the field assuming light saturation. Oates (1985) calculated production during daylight in air and water for the saccate Phaeophyta *Colpomenia peregrina*, by multiplying the number of hours in each medium by the light-saturated rate. Thalli of this species lose little water in air because they have access to retained water, and so it was not necessary to take the effect of desiccation into account. A similar approach was used by Oates (1986) for another saccate species, *Halosaccion americanum*.

Fucus spiralis L. is an upper-shore intertidal alga which, like the bulk of intertidal species, is not saccate. The effects of photon irradiance, temperature and water loss on rates of photosynthesis and respiration in air and water have been described by Madsen & Maberly (1990). These data give an opportunity to model the relative importance of air and water in the carbon balance of this species, and the relative effects of desiccation in air and light attenuation underwater on productivity.

MATERIALS AND METHODS

Rates of water loss in the field. Apices of *Fucus spiralis* of similar appearance and a length of about 5 cm were collected from the field site at the Hind Rock, St. Andrews, UK (50° 20' N, 2° 47' W) the previous day. They were allowed to hydrate fully in aerated seawater for at least 12 h at 15 °C and 200 μmol m^{-2} s^{-1} (PAR, 400 to 700 nm) under a 16 h day. On 6 occasions in July 1987, 20 apices were laid out on the Hind Rock, just above the level at which *F. spiralis* is found. Every 20 min for 200 min, 2 apices were collected, placed in plastic bags and kept in the dark. At the same time, measurements were made of the air temperature and relative humidity immediately above the apices using wet and dry bulbs in a ventilated psychrometer. Thallus temperature was measured using a copper-constantan thermocouple

connected to a meter. A solarimeter, 1.7 km away from the shore, recorded integrated values of total Jm^{-2} every 30 min. These values were converted to photon irradiance, PAR, using an empirical factor of 1.983 μmol m^{-2} s^{-1} (PAR)/Jm^{-2} (total) determined by direct comparison, under a range of sky conditions, between the solarimeter and the quantum sensor used in the determination of photon irradiance in the photosynthesis experiments (Madsen & Maberly 1990).

On return to the laboratory the apices were weighed to determine their 'desiccated weight' and placed in aerated seawater for at least 12 h as before, to fully hydrate before being re-weighed to determine their 'fully-hydrated weight'. The apices were dried at 80 °C for 24 h and weighed to determine their dry weight. Percent water content was determined from:

$$W\% = \frac{(\text{desiccated weight} - \text{dry weight})}{(\text{fully-hydrated weight} - \text{dry weight})} \times 100 \quad (1)$$

Description of the model. Equations and data which described tide height, available light, rates of water loss and rates of photosynthesis and respiration of *Fucus spiralis* were incorporated into a programme, written in Basic, which ran on a micro-computer. The physiological data were collected in May and June, and calculations were made for adjacent months. April was chosen as a month where air and water temperature were both low, and in July both were high.

Tide height and time: The model assumes that 57 tides occur within a lunar synodic month of 29.531 d, and that each tide has an equal duration of 12.432 h. The sequence was located in time by starting at low water for the spring tide following a full moon. The average time of water for this tide for the appropriate standard port of Leith corrected for the nearest secondary port. 'Anstruther Easter' (24 km around the coast from St. Andrews), is at 21:30 h.

For each of the 57 tides, the height of the low and high water was determined from the mean of 3 lunar months (between January and March 1985) for Leith. This therefore took into account inter alia the fact that the low water in the afternoon is lower than that in the morning. The height of mean high water of spring and neap tides, mean low water of spring and neap tides and mean tidal level calculated by the model differed by between 0.03 and 0.08 m from the mean values for Leith given in the Admiralty Tide Tables (1984).

During each tide, tidal level (referred to Chart Datum) was calculated 48 times at an interval of 0.259 h, using the spring and neap tide curves for Leith. It was assumed that tides intermediate between spring and neap had linearly intermediate tidal curves. The height of *Fucus spiralis* at the Hind Rock was located to tidal level by surveying to a benchmark 0.4 km away

The mid-point of the *F. spiralis* zone occurred at 4.41 m above Chart Datum.

Light: When *Fucus spiralis* is underwater, the surface irradiance will be reduced. Surface reflection was assumed to equal 10 % and attenuation coefficients (K) for 7 wavelengths at 50 nm intervals between 400 and 700 nm for coastal water types 1, 3, 5, 7 and 9 were obtained from Jerlov (1976); values in Dring (1987) were used for the extrapolated coastal water types 11 and 13.

For each of the 7 wavelengths, the partial daily irradiance (I_p) was calculated from:

$$I_p = e^{(log_e (0.9\ I_\Sigma^0/7)\ -\ Kz)} \tag{2}$$

where I_Σ^0, the daily irradiance at the surface, was assumed to comprise all wavelengths between 400 and 700 nm equally, so that the daily irradiance at depth z, I_Σ^z was calculated from the sum of these values.

The photon irradiance received by *Fucus spiralis* at any time over the average day (I_t) was calculated from the average daily irradiance (I_Σ) which equalled I_Σ^0 when *F. spiralis* was in air and I_Σ^z when in water, the daylength (λ) and the time from noon (t), following the approach in Maberly (1985):

$$I_t = (I_\Sigma/\lambda)\ (1 + cos\ (2\pi t/\lambda)) \tag{3}$$

Fifteen-year average values of surface daily irradiance for April and July were obtained from a solarimeter at Invergowrie, Dundee, about 22 km away. These values were converted to PAR as described above.

Photosynthesis and respiration in air: Rates of net photosynthesis in the light (P) and respiration in the dark (R), in air, were calculated using the equations and data in Madsen & Maberly (1990) for assumed constant air temperatures of 10 and 20 °C for April and July respectively. Data from the Meteorological Office, Edinburgh, for Leuchars (7 km away) between 1974 and 1980 show that mean night-time temperatures were 1.6 and 2.1 °C below respective daily averages for April and July. Mean daytime temperatures were 1.0 and 0.9 °C above the respective daily averages for the same months. This diurnal variation in temperature was not taken into account in the model.

The rate of gross photosynthesis (P^{gross}) as a function of photon irradiance was described by the Smith (1936) equation:

$$P^{gross} = P_{max}^{gross}\ \alpha I_t / (P_{max}^{gross^2} + (\alpha I_t)^2)^{1/2} \tag{4}$$

where P_{max}^{gross} is the maximum rate of gross photosynthesis at light saturation and α is the initial slope of P against I.

The percent water content (W%) at any time (min) since the plants emerged into air (t_E) is a function of the coefficient of water loss (D):

$$W\% = 100\ e^{-(Dt_E)} \tag{5}$$

The proportional reduction in the rates of net photosynthesis (P_w) and respiration (R_w) by reduced water content was described by equations in Madsen & Maberly (1990):

$$P_w = (1.5\ W\% - 23.6)/100 \tag{6}$$

$$R_w = (1.09\ W\% - 2.4)/100 \tag{7}$$

These equations were modified so that P_w and R_w did not exceed 1.0.

The rate of net photosynthesis (P) at a given water content was calculated from:

$$P = (P^{gross}\ P_w) - (R\ R_w) \tag{8}$$

Photosynthesis and respiration in water: Rates of net photosynthesis in the light and respiration in the dark were calculated using the equations of Madsen & Maberly (1990) for an assumed constant temperature of 10 °C in April and 15 °C in July. The effect of light on gross photosynthesis was described by the Smith (1936) equation (Eq. 4).

On return to water following desiccation in air, photosynthesis took up to 35 min to reach maximum rates (Madsen & Maberly 1990). The proportion of net photosynthesis during recovery (P_r) to maximum rates at a time (min) since re-submergence (t_s) was described by:

$$P_r = (1 - P_w)\ (1 - e^{-0.0961\ t_s}) + P_w \tag{9}$$

The similar proportion of recovery of respiration rate (R_r) was not measured, but was assumed to follow a similar pattern:

$$R_r = (1 - R_w)\ (1 - e^{-0.0961\ t_s}) + R_w \tag{10}$$

When t_s was greater than 35 min, P_r and R_r equal 1. The rate of net photosynthesis in water was calculated from:

$$P = (P^{gross}\ P_r) - (R\ R_r) \tag{11}$$

RESULTS

Rates of water loss

Percent water content (W%) followed an exponential decrease with time of exposure (data not shown). Linear regressions were performed on log_e W% against time (min) in order to determine the coefficients of water loss (D) with units log_e min^{-1}. There was a 4-fold variation in D over the 6 occasions when measurements were made (Table 1). The highest and lowest values of D were used in the model to delineate the likely extremes of D to be found in the field.

Table 1 *Fucus spiralis*. Rates of water loss in the field. Water loss parameters determined by linear regression. Dates ordered in increasing rate of water loss. W%: percent water content; D: coefficient of water loss

Date	Time (h)	Average conditions at the site				Linear regression		
		Temperature (°C)		$\bar{x}$ PAR (μmol photon $m^{-2} s^{-1}$)	Relative humidity (%)	($W\% = b \exp^{-D \times minutes}$)		
		Air	Plant			b	$D \times 10^3$	r^2
15 Jul 87	14:10–17:31	15.1	15.7	549	92.4	105.3	2.54	0.79
14 Jul 87	9:55–13:25	16.6	17.6	831	87.1	116.1	4.77	0.84
16 Jul 87	13:41–17:01	16.2	18.3	735	79.3	95.4	5.14	0.55
21 Jul 87	13:31–16:51	16.8	22.3	1905	83.9	90.8	6.14	0.65
22 Jul 87	16:11–21:31	13.7	17.0	529	80.8	80.1	6.18	0.72
23 Jul 87	9:16–12:36	17.5	20.3	1155	72.6	122.8	10.96	0.95

Table 2. Summary of environmental and physiological data used in the model. R: respiration in the dark; P_{max}^{gross}: maximum rate of gross photosynthesis

	April	July
Environmental		
$\bar{x}$ Daylength (h)[a]	13.9	16.6
$\bar{x}$ Daily I_Σ (mol photon $m^{-2} d^{-1}$)[b]	24.42	31.48
$\bar{x}$ Air temperature (°C)[c]	7.2	14.4
$\bar{x}$ Water temperature (°C)[d]	8.4	15.8
Physiological		
R in water (μmol C g^{-1} DW h^{-1})[e]	4.3 (10° C)	5.6 (15° C)
R in air (μmol C g^{-1} DW h^{-1})[e]	9.4 (10° C)	27.6 (20° C)
P_{max}^{gross} in water (μmol C g^{-1} DW h^{-1})[e]	132 (10° C)	126 (15° C)
P_{max}^{gross} in air (μmol C g^{-1} DW h^{-1})[e]	88 (10° C)	255 (20° C)
α in water [μmol C g^{-1} DW h^{-1} (μmol photon $m^{-2} s^{-1}$)$^{-1}$][e]	0.78 (10° C)	0.63 (15° C)
α in air [μmol C g^{-1} DW h^{-1} (μmol photon $m^{-2} s^{-1}$)$^{-1}$][e]	0.35 (10° C)	0.80 (20° C)

[a] Determined from Smithsonian Meterological Tables (1951)
[b] Monthly average for 1968 to 1982 measured at Invergowrie, Dundee, in $J m^{-2}$ and converted to PAR (see text)
[c] Monthly average for 1951 to 1980 for St. Andrews from Meterological Office, Edinburgh
[d] Calculated from equation for St. Andrews in Drew (1983)
[e] From data in Madsen & Maberly (1990)

Results of the model

A summary of the environmental and physiological variables used in the model is given in Table 2. An example of the results from the model for 2 tides in July is shown in Fig. 1. The average depth of water above *Fucus spiralis* at high tide was 1.11 m for spring tides and 0.06 m for neap tides. In the example in Fig. 1 where the 2 tides were intermediate between spring and neap, the depths of water at high tide were 0.62 and 0.75 m. The average photon irradiance at noon in air was 1054 μmol $m^{-2} s^{-1}$ (PAR) in July, about half the maximum possible under a clear sky. Under the tidal regimes and Jerlov's 'coastal 7' water used in Fig. 1, submergence reduced the photon irradiance to between 51 and 56% of surface values at high tide.

When D was equivalent to the highest measured in the field, the water content of *Fucus spiralis* declined rapidly on entry into air (Fig. 1b). Under these condi-

tions, positive net photosynthesis was restricted to the 2.8 h immediately following emergence into air in the light and rates were less than half-maximal after only 1.7 h (Fig. 1a). In contrast, when D was equivalent to the lowest measured in the field, positive net photosynthesis would be possible for 12.1 h, and half-maximal rates reached after 4.7 h (Fig. 1a).

The net production per tide during the lunar month is very variable (Fig. 2) even under the regular diurnal changes in photon irradiance used in the model. This is a result mainly of the length of time spent in light and dark per tide, but partly a response to whether *Fucus spiralis* is in air or water around midday, and whether maximal production is possible in air or water, which will depend largely on the value of D. Tides 42 to 46 fail to cover *F. spiralis*, so even when D is low, net production will be impossible unless rehydration occurs by wave-splash, which was not taken into account in the model.
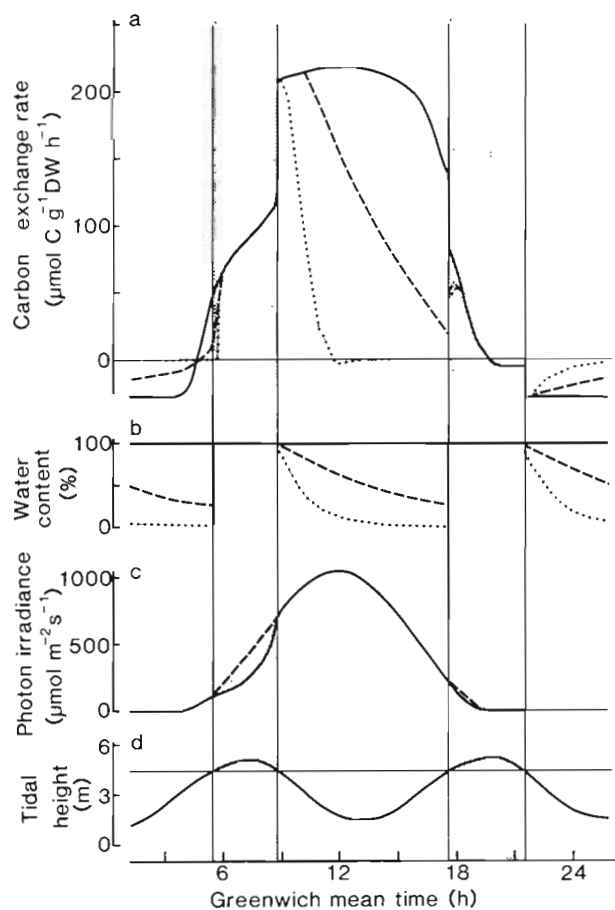
Fig. 1. Example of output from the model in July for the 9th and 10th tide after spring tides and 'coastal 7' water. Stippled area indicates time underwater. (a) Rates of carbon exchange for the highest ($10.96 \times 10^{-3} \log_e \min^{-1}$) (....) and lowest ($2.54 \times 10^{-3} \log_e \min^{-1}$) (-----) coefficients of water loss measured in the field, and also for no water loss (———). (b) Percent water content for the highest (....), lowest (-----) and no water loss (———). (c) Photon irradiance received (———) and also that at the surface (-----). (d) Tidal level. Horizontal line represents the position of *Fucus spiralis*

carbon gain during the day. Carbon gain in water is slightly affected by the rate of water loss, through its influence on recovery after an episode of desiccation.

Fig. 3a shows the effect of different coefficients of water loss on daily net production for the 2 extreme coastal water types. The clear 'coastal 1' water allows only slightly greater production than the extremely turbid 'coastal 13' water. In April, the percent contribution of water to the total daily net production ranged between 49 and 55 % for coastal 13 and 1 water types respectively when D was the lowest measured, and between 82 and 84 % when D was the highest measured in the field (Fig. 3b). In July, water contributed 23 and 28 % for coastal 13 and 1 water types respectively when D was the lowest measured, and 56 and 63 % when D was the highest measured in the field (Fig. 3b).

The contribution of air and water to the carbon balance will depend on the average rates of photosyn-
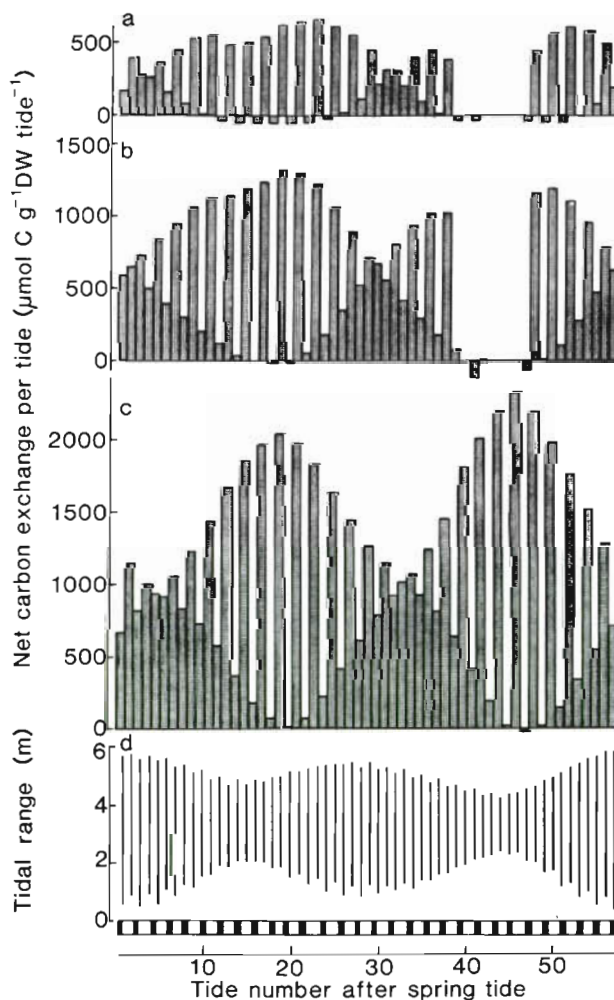

Fig. 2. Net production for each of the 57 tides during the lunar month. Calculated for July, a 'coastal 7' water type and 3 coefficients of water loss: (a) D = 10.96×10^{-3}; (b) D = 2.54×10^{-3}; (c) D = $0 \log_e \min^{-1}$ Tidal range (d) and the duration of dark and light periods are shown at the foot of the figure

The predicted carbon balance over the lunar month, expressed as the average daily carbon exchange, shows that in April, water is the major source of carbon when D is high, but air and water contribute about equally when D is low (Table 3). In July, water and air contribute about equally to the daily production when D is high, but air is most important when D is low. Net carbon gain in air was 4.5 and 4.8 times higher under low compared to high values of D for April and July respectively, and total net production was 1.6 and 2.3 times greater. If desiccation was absent, daily production would be substantially higher, particularly in July when high air temperatures allow potentially high rates of photosynthesis. Carbon loss at night is reduced when D is high, but this beneficial effect on the carbon balance is small compared to the adverse effect on

Table 3. *Fucus spiralis*. Average daily carbon exchange (μmol C g^{-1} DW d^{-1}) over a lunar month for the highest (10.96×10^{-3} log$_e$ min^{-1}) and lowest (2.54×10^{-3} log$_e$ min^{-1}) coefficients of water loss measured in the field, and also for no water loss. Calculated for 'coastal 7' water type

Environment	Period	April			July		
		Coefficient of water loss $\times$ 10^3 (log$_e$ min^{-1})					
		10.96	2.54	0.00	10.96	2.54	0.00
Water	Light	256	259	272	287	290	303
	Dark	−10	−11	−11	−9	−10	−10
	Net	246	248	261	278	280	293
Air	Light	56	255	555	196	858	1855
	Dark	−10	−36	−72	−21	−79	−157
	Net	46	219	483	175	779	1698
	TOTAL	292	467	744	453	1059	1991

thesis and the length of exposure to each medium. On average over the lunar month, *Fucus spiralis* spends 18.2 h in air compared to 5.8 h in water every 24 h (Table 4). Average rates of photosynthesis in water are greater than those in air under all possible coefficients of water loss in April. In July, average rates of photosynthesis in water are greater than or equal to those in air except for the hypothetical case of no water loss. The greater rates of photosynthesis in water in July occur despite the approximately 2-fold greater rates of net photosynthesis possible in air at light saturation in the absence of desiccation (Table 2).

The relative effect of tidal regime on production within the lunar month was determined by dividing the 57 tides equally into spring, mean and neap on the basis of the mean range of each tide (i.e. the mean of low water to high water and high water to low water). In the absence of desiccation, neap tides contribute a large proportion of the total production in July as rates of photosynthesis in air are potentially high (Table 5). For both months, however, even the lowest coefficient of water loss measured in the field reduced substantially the proportion of net production contributed by neap tides. Spring tides may be between 1.85 and 2.3 times more productive than neap tides under low and high coefficients of water loss respectively for the 2 months.

The degree to which ambient light saturates production was assessed by re-calculating production so that P^{gross} in Eq. (4) equalled the light-saturated rate, P$^{gross}_{max}$ for air and water as appropriate, during daylight hours. Production in water is 62 and 60 % of that possible if light was saturating for April and July respectively (data not shown). Production in air was 55 and 56 % of saturating values when D was high, and 64 and 61 % when D was low, for April and July respectively (data not shown).

The average carbon exchange over a lunar month was calculated for 3 coefficients of water loss, assuming
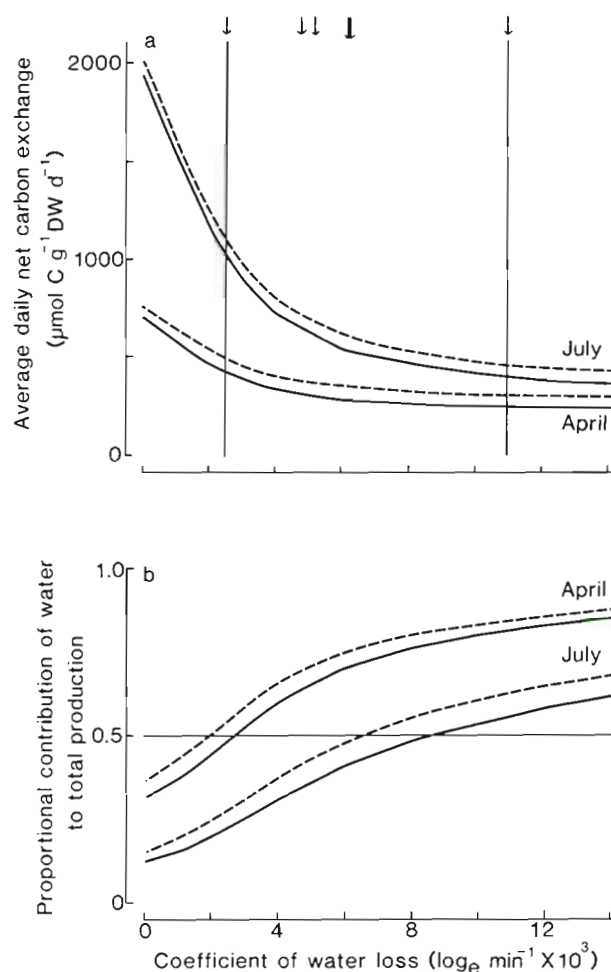

Fig. 3. *Fucus spiralis*. The effect of the coefficient of water loss (D) on: (a) total net production; (b) the contribution of water to total net production. Horizontal line indicates a contribution of 50 %. Calculated for April and July and 'coastal 1' (– – – –) and 'coastal 13' (——) water types. Vertical lines indicate the minimum and maximum values of D measured in the field: the other values are presented by vertical arrows

Table 4. *Fucus spiralis*. Average rate of carbon exchange (μmol C g^{-1} DW h^{-1}) over a lunar month for the highest (10.96×10^{-3} log$_e$ min^{-1}) and lowest (2.54×10^{-3} log$_e$ min^{-1}) coefficients of water loss measured in the field, and also for no water loss. Calculated for 'coastal 7' water type

Environ- ment	Period	Duration (h)		April			July		
		April	July	Coefficient of water loss $\times 10^3$ (log$_e$ min^{-1})					
				10.96	2.54	0.00	10.96	2.54	0.00
Water	Light	3.3	4.1	78	78	82	70	71	74
	Dark	2.5	1.7	−4	−4	−4	−5	−6	−6
Air	Light	10.5	12.5	5	24	53	16	69	148
	Dark	7.7	5.7	−1	−5	−9	−4	−14	−20

Table 5. *Fucus spiralis*. Percentage of total production over a lunar month contributed by spring, mean and neap tides for the highest (10.96×10^{-3} log$_e$ min^{-1}) and lowest (2.54×10^{-3} log$_e$ min^{-1}) coefficients of water loss measured in the field, and also for no water loss. Calculated for 'coastal 7' water type

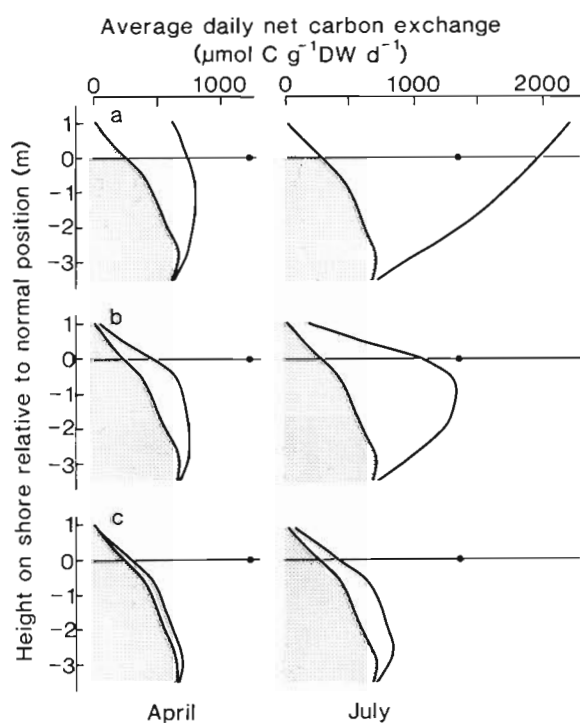| Tidal regime	April			July		
	Coefficient of water loss $\times 10^3$ (log$_e$ min^{-1})					
	10.96	2.54	0.00	10.96	2.54	0.00
Spring	43.8	42.0	36.2	44.7	40.9	32.4
Mean	34.8	35.5	31.6	35.9	37.0	31.2
Neap	21.4	22.5	32.2	29.4	22.1	36.4

Fig. 4. Effect of position on the shore on average daily net production in water (stippled area) and air (open area): total production is the sum of these 2 areas. Calculated for 'coastal 7' water and 3 coefficients of water loss: (a) D = 0; (b) D = 2.54×10^{-3}; (c) D = 10.96×10^{-3} log$_e$ min^{-1}. Horizontal line represents normal height of *Fucus spiralis*. Circles represent production possible if *F. spiralis* was in a pool at least 0.01 m below the water surface at its normal position on the shore

that *Fucus spiralis* was present higher and lower on the shore than normal. The model predicts that production would be greater under nearly all conditions if *F. spiralis* was present lower down the shore with maximal production between 1 and 3 m lower depending on conditions (Fig. 4). In contrast, production would be markedly reduced if *F. spiralis* were 0.5 or 1.0 m higher (Fig. 4). If *F. spiralis* was in a pool at its normal position and 0.01 m below the water surface at low tide, then production would be increased over that possible when exposed to air during the tidal cycle (Fig. 4). This assumes, however, that other factors such as carbon-depletion within the pool are not operating.

DISCUSSION

The calculated rates of carbon exchange based on the combination of laboratory and field data can be checked approximately by comparing literature values for the growth rate of *Fucus spiralis* with those calculated from the model. Niemeck & Mathiesen (1978) present data which were used to calculate growth rates of 0.2 % (g FW g^{-1} FW d^{-1}) in April and 0.4 % in July in the field in New Hampshire, USA. F. A. Brown (unpubl., cited in Dring 1982, p. 125) measured growth rates of 1.5 % (g FW g^{-1} FW d^{-1}) in September at Co. Down, Northern Ireland. In a laboratory experiment at 10 °C, a 16 h day and with seawater enriched with

nutrients, *F spiralis* had an average growth rate of 3.8 % (g FW g^{-1} FW d^{-1}) when continuously submerged (Schonbeck & Norton 1980). The carbon balance data calculated here for 'coastal 7' water (Table 3) combined with a measured organic carbon content (wet-oxidation method) of 26.4 % C g^{-1} DW give predicted growth rates of 1.3 to 2.1 % for April and 2.1 to 4.8 % for July under high and low coefficients of water loss respectively. These values are more or less within the range of measured growth rates, although higher than those measured in the field. This presumably is because the physiological measurements of Madsen & Maberly (1990) were made on active, apical pieces, and the model did not take into account biomass losses caused by factors such as attrition, grazing or gamete release, although the quantitative effect of these factors is not known.

Fucus spiralis is typically found towards the top of the zonation on rocky shores, beneath *Pelvetia canaliculata*. Unlike *Pelvetia* however, which is unable to tolerate continuous submergence (Rugg & Norton 1987), downward extension of *F. spiralis* appears to be prevented by competition with faster-growing species. Schonbeck & Norton (1980) found that *F. spiralis* had a greater linear growth rate when transplanted 0.85 m lower down the shore than when present at its normal position. The model predicts that production would be greater down to between 1 and 3 m lower, depending on conditions. The decline in production with declining height on the shore below this optimum position is a result of declining light availability. Like the model of Dring (1987), this model predicts a more or less linear decrease in light availability with declining height on the shore in the intertidal zone (data not shown). Net production would be markedly reduced if *F. spiralis* was higher up the shore than is normal. The fact that net production would still be possible suggests that the absence of *F. spiralis* from this zone could be explained by factors which affect survival such as periodic severe desiccation (Schonbeck & Norton 1978). The greater production found when *F. spiralis* is continually submerged was calculated without taking improved nutrient availability into account (Schonbeck & Norton 1979). Since the model predicts that net production would be possible throughout the intertidal region, the restricted distribution of *F. spiralis* in the field appears not to be the result of a restriction on carbon exchange per se.

The small effect of coastal water type on production is clearly a result of the shallow depth of water above *Fucus spiralis*, even at high tide. This contrasts with the results for macroalgae such as the Laminarians at the base of the intertidal or top of the subtidal where, using a model, Dring (1987) has shown that coastal water type has a large effect on available light and presumably on production.

Aerial leaves of amphibious freshwater macrophytes may increase productivity by giving these plants access to an environment of high light and constant availability of CO_2 without suffering from water stress (Maberly & Spence 1989). Saccate macroalgae such as *Colpomenia peregrina* have an internal reservoir of water which helps alleviate water loss and allows net photosynthesis to occur throughout the period of exposure to air (Oates 1985). Most intertidal macroalgae, however, are like *Fucus spiralis* in lacking means of restricting water loss or replacing lost water while in air. *F. spiralis* can photosynthesise more rapidly in air than in water at 15 to 20 °C in the absence of desiccation (Madsen & Maberly 1990), but in the field under most conditions water loss will reduce the rate of photosynthesis in air and may prevent photosynthesis for much of the daylight period. In the field, portions of thallus beneath overlying thalli may experience reduced water loss (Jones & Norton 1979). Although this may have important implications for survival, the effect on productivity will be fairly small because a dry thallus only transmits 2.3 % (n = 10; SD = 0.9 %) of photosynthetically active radiation.

The model emphasizes the large effect that the coefficient of water loss, D, has on production. Even low values of D reduce production considerably compared to the hypothetical case of no water loss. Thus the potentially high rates of photosynthesis in air when temperature is high are reduced dramatically by desiccation.

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