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SUMMER GROWTH OF *CHORDARIA FLAGELLIFORMIS* (O.F. Muell.) C. Ag.: PHYSIOLOGICAL STRATEGIES IN A NUTRIENT STRESSED ENVIRONMENT

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Abstract: The objective of this study was to determine the relative importance of mechanisms by which *Chordaria flagelliformis* (O.F. Muell.) C. Ag. maintains rapid summer growth in sea water of low nitrogen content. Growth and nutrient uptake kinetic measurements showed that a steady-state uptake of ammonium, urea, and nitrate at ambient concentrations could more than satisfy the demand for growth. This finding is exemplified by the low half-saturation constants for growth (K_s) on the three nitrogen sources estimated in culture under natural irradiance. Wind and tidally related nutrient inputs were found to be insignificant. The contribution of ammonia and urea regenerated from animal excretion, though potentially significant was most likely overshadowed by the steady-state uptake of nitrogen. It was also shown that the specific growth rate of plants is as dependent on the internal thallus nitrogen quota as it is on the external sea-water concentration. Field measurements showed a high tissue polymeric nitrogen concentration early in the growing season. With the proposed uncoupling between growth and uptake, this reserve was shown to be sufficient to account for growth throughout the month of May.

INTRODUCTION

Chordaria flagelliformis (O.F. Muell.) C. Ag. is a summer annual brown seaweed with a wide distribution in the northern regions of the Atlantic (Munda, 1978). It is generally found in the lower eulittoral (*Chondrus crispus* Stackh. subzone) on the Atlantic coast of Nova Scotia. The annual periodicity of *Chordaria flagelliformis* along this coastline is somewhat enigmatic in that the macroscopic stage makes its appearance and flourishes during periods when ambient inorganic nitrogen (N) levels are depleted (Probyn, 1981). A number of studies along the northeast coast of North America have indicated that nutrient depletion during the summer might be so severe as to limit the growth of macroalgae (Buggeln, 1974; Topinka & Robbins, 1976; Chapman & Craigie, 1977; Neish *et al.*, 1977; Topinka, 1978; Hanisak, 1979a; Gagné *et al.*, 1982). In the terrestrial environment, annuals are found primarily on soils of intermediate to rich N content (Ellenberg, 1974, cited in Mattson, 1980). This nitrophilous nature of annuals, if applicable to seaweeds, is difficult to reconcile with the summer growth of *C. flagelliformis* in N-depleted waters.

C. flagelliformis is capable of absorbing low concentrations of ammonium, urea (Probyn & Chapman, 1982), and nitrate (Probyn, in prep.) with an efficiency exceeding that reported previously for macroalgae. The alga is also equipped to take up rapidly pulses of the two reduced N sources over the short term at rates that far exceed the

growth requirement (Probyn & Chapman, 1982). A similar potential for high transient uptake rates has been shown for the red alga *Gracilaria foliifera* (D'Elia & DeBoer, 1978). A recent view of the N nutrition of phytoplankton in oligotrophic oceanic waters emphasizes the short-term uptake capacities for ammonium and urea (McCarthy & Goldman, 1978; Horrigan & McCarthy, 1981). It is proposed that the rapid assimilation of pulses of ammonium or urea generated via animal excretion or biological degradation allow phytoplankton to grow at rates close to their maximal potential in severely N-impoverished waters (Goldman *et al.*, 1979). Possibly a similar pulse-related acquisition strategy is of importance to seaweed nutrition in N-depleted coastal waters.

This study is aimed at identifying the physiological attributes of *Chordaria flagelliformis* that permit its rapid growth during the summer, a period of N stress to a number of other seaweeds.

Methods

GROWTH MEASUREMENTS IN THE FIELD

Cranberry Cove (44°30′N : 63°55′W) on the Atlantic coast of Nova Scotia, Canada was chosen as the field site for the present study. A harvesting method was used to measure growth rate whereby 60 plants were hand collected on each sampling date ($\approx$ every 2 wk), returned to the laboratory on ice, and weighed immediately. A series of growth rates was calculated from biomass increments for pairs of plants between harvests: the largest at time 1 paired with the largest at time 2; the second largest at time 1 paired with the second largest at time 2, and so on (Hunt, 1978). All fresh weights were converted to dry weights from the relationship in Fig. 1. The corrected dry biomass changes over time were used in the calculation of the absolute growth rate (mg dry wt · day^{-1}) and the specific growth rate (day^{-1}).

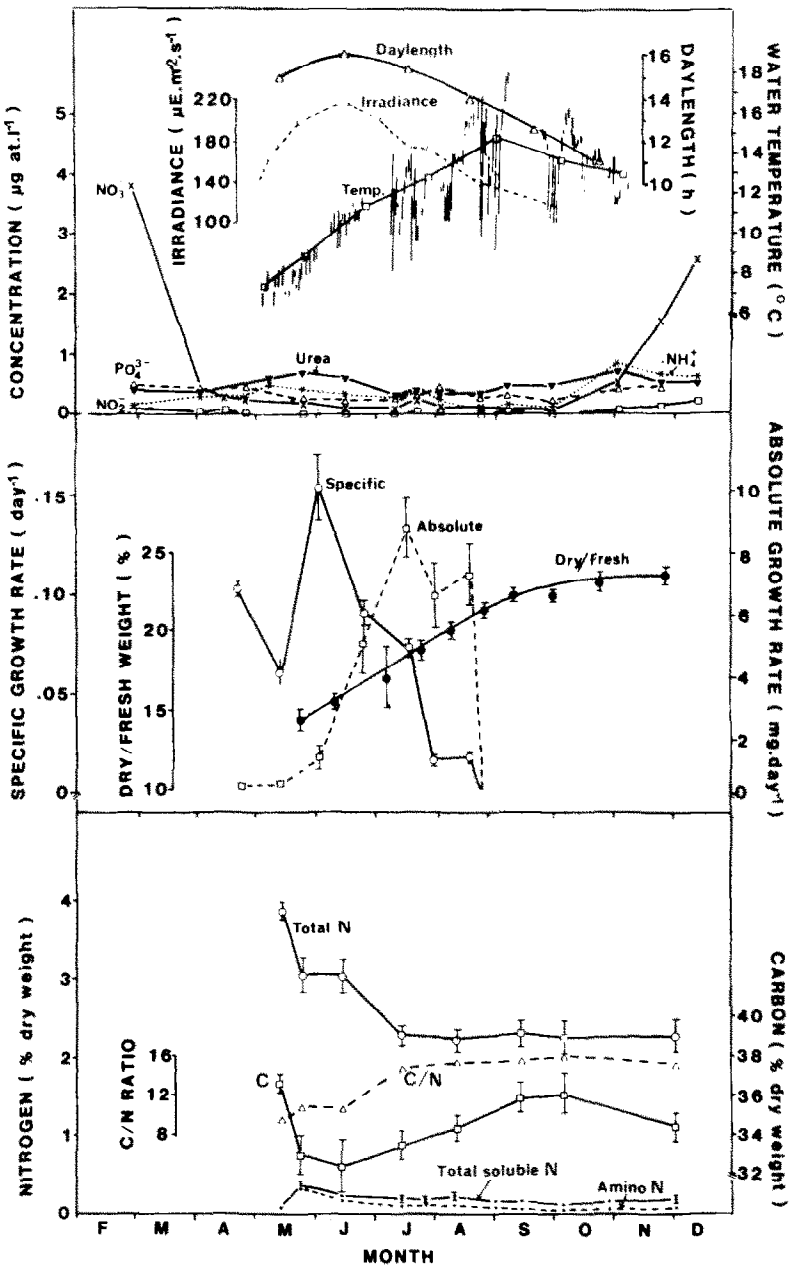

Fig. 1. Seasonal variation in nutrient concentrations, irradiance, temperature, daily temperature range (vertical lines) and daylength at Cranberry Cove in 1979–1980: the variation in absolute and specific growth rates, dry/fresh wt ratios, tissue concentrations of total C and N, C/N ratios and ethanol-soluble N (total and amino) for the growing season of *Chordaria flagelliformis* are also shown (means ± 95% confidence limits, $n = 5$).

IRRADIANCE AND TEMPERATURE

Irradiance was measured at a depth of 1 m on site with a Li-Cor Li-192s underwater quantum sensor. The quantum sensor was fixed onto a water-tight plastic housing containing a Li-Cor Li-500 integrator. Irradiance was integrated continuously throughout the summer with readings recorded $\approx$ every 2 wk. Shading of the sensor by fouling organisms could not be avoided, but was minimized by frequent cleaning of the light collecting surface.

Continuous records of water temperature at a depth of 1 m were provided by a Peabody-Ryan Model d-15 thermograph. The instrument operated continuously for 2 wk in the temperature range -5 to $+25\,^{\circ}C$. Occasional mechanical breakdowns explain the lack of data for certain periods in the summer. After calibration daily maximum and minimum temperatures as well as monthly means were estimated from the thermograph printout.

NUTRIENT ANALYSES

Three 1-litre water samples were collected approximately once every 2 wk, stored on ice in polyethylene containers, and returned immediately to the laboratory where they were either transfered to acid-cleaned borosilicate glass bottles (125 ml) for storage ($-18\,^{\circ}C$), or analysed immediately. As a rule ammonium determinations were performed on the day of collection. Samples for urea analysis generally were not stored for longer than 1–2 days. All sea-water samples, except those used for ammonium and urea determinations, were filtered through glass fibre filters (Whatman GF/C) prior to storage. Ammonium and urea samples were not filtered because the filters contained potentially contaminating amounts of both ammonium and urea. Unfiltered samples were corrected for turbidity.

Ammonium determinations were based on the phenol-hypochlorite method of Solórzano (1969) and phosphate on the procedure of Murphy & Riley (1962). More stable reagents for both of these methods were prepared according to Grasshoff (1976). Urea was measured by the diacetyl monoxime clinical procedure modified for application to sea water (Newell *et al.*, 1967). The concentration of dissolved nitrate was quantified as nitrite after reduction with a copper-hydrazine reagent (Strickland & Parsons, 1960). This method of nitrate determination was used because it was easily adapted to manual measurement on small (5 ml) samples. Total dissolved N was measured as nitrate after persulfate oxidation (Nydahl, 1978). The copper-hydrazine nitrate reduction method proved ineffective on persulfate oxidized sea-water samples. Consequently, the cadmium reduction method with the refinements suggested by Nydahl (1976) was used.

TISSUE ANALYSES

All plants intended for subsequent tissue analyses were stored in plastic bags on ice during transportation to the laboratory for immediate extraction. Fifteen plants were

weighed and then dried for 3 days in an oven at 60 °C and 2 days in a vacuum-sealed desiccator at room temperature for determination of dry wt/fresh wt ratios. Five replicate plants, desiccated as described above were ground to a fine, relatively homogeneous powder with a pestle and mortar and stored in a desiccator. The samples were used for total carbon and nitrogen determinations on a Hewlett-Packard 185B CHN analyser. Crude alcoholic tissue extracts (made up to 50 ml) were prepared by extracting ≈ 2 g wet wt of freshly collected material thrice with 15 ml of hot 80% ethanol (Chapman & Craigie, 1977). Extracts were stored at − 18 °C and subsequently used for total N and free-amino acid determinations. Total ethanol-soluble N was measured as ammonium after semi-micro Kjeldahl digestion (H_2SO_4-SeO_2 reagent) and distillation (Bremner, 1963). Samples for amino-acid measurements were evaporated under an air stream and redissolved in distilled water prior to analyses. Redissolved extracts were clarified before measurement of the ninhydrin positive compounds, mainly amino acids (Rosen, 1958).

EPIFAUNAL EXCRETION AND GRAZING

The potential for regeneration of nitrogen by the predominant animal epiphytes associated with *C. flagelliformis*, *Gammarellus angulosus* Rathke and *Littorina vincta* Montagu., was estimated as excretion rates for both ammonium and urea. Incubations were performed in the field as this method yielded substantially higher excretion rates than measured for animals maintained in the laboratory. Ratios of animal numbers to sea-water volume during incubations were $10 \cdot l^{-1}$ for *Gammarellus angulosus* and $50 \cdot l^{-1}$ for *Littorina vincta*. Excretion rates were measured as the increase in both ammonium and urea concentrations after 1 h. Concentrations were stable over this time period in the absence of animals. Incubations were performed on three occasions during late July and early August, 1981. The animals were dried at 60 °C for 2 days after experimentation and excretion rates were expressed on a dry weight basis. Using observed ratios of animal dry wt to *Chordaria flagelliformis* dry wt during late July and early August, the potential regeneration of N per g of plant material could be estimated.

The relative palatability of *C. flagelliformis* to these two invertebrate grazers was estimated according to the experimental protocol of Vadas (1977). Approximately equal amounts of pre-weighed portions of a number of macroalgal species known to occur in close proximity to *C. flagelliformis* in the field were used in these feeding preference studies. Feeding rates of the grazers for each algal species were expressed as a percentage of the total weight ingested after normalizing to equal initial weight and correction for photosynthetic and respiratory gains or losses measured in the absence of the potential grazers.

GROWTH KINETICS IN OUTDOOR TANK CULTURE

Growth experiments were conducted in outdoor continuous flow culture systems at the National Research Council of Canada Seaweed Experimental Station, Sandy Cove,

Nova Scotia. This system allowed measurement of growth rates of large plants at very high flow rates and under natural illumination. The experimental layout is shown in Fig. 2. The growth vessels were white plastic trays (60 cm × 40 cm × 10 cm) with an overflow pipe to give a functional volume of ≈20 l. Twelve 1 cm lengths of 1.25 cm diameter plastic pipe secured to the bottom of each tray served to hold rubber stoppers plus attached thalli in place (Fig. 3). Fixing individual plants in position in this manner

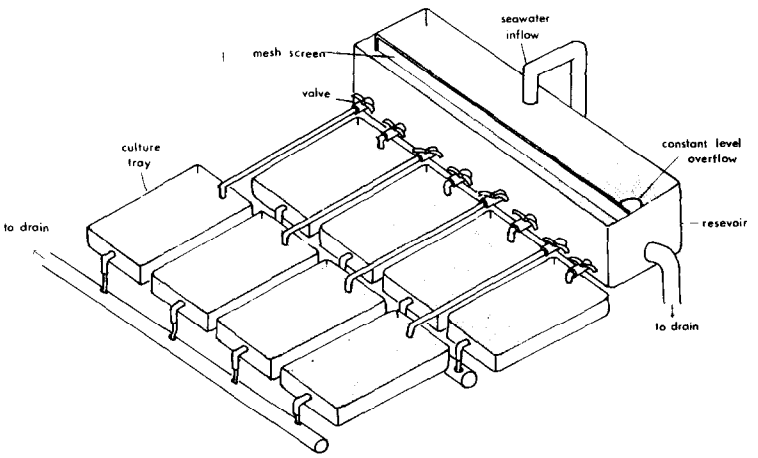

Fig. 2. Layout for rapid flushing outdoor cultivation experiments.

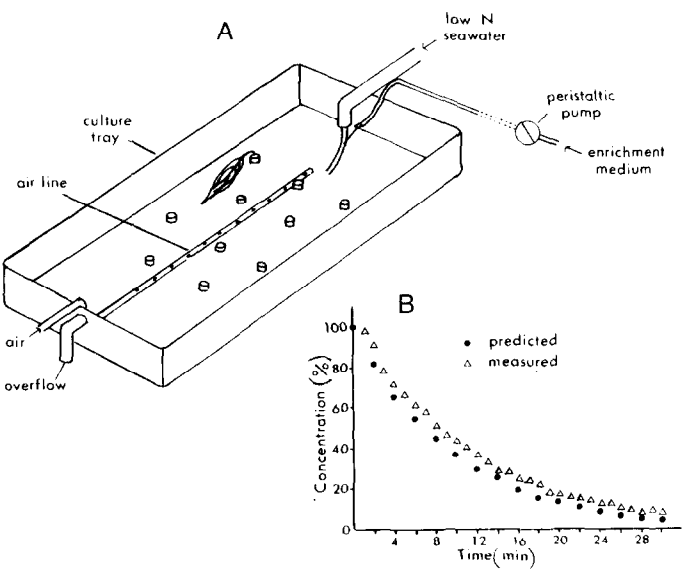

Fig. 3. Detail of culture tray in Fig. 2 (A) and graph (B) showing the predicted and experimentally determined rates of dilution of dye in the culture tray: predicted rate from $C_f = C_0 e^{-rt}$, where C_f = final dye concentration, C_0 = initial dye concentration, t = time and r = dilution rate.

effectively eliminated mutual shading of the plants and maximized water motion relative to the plant surface.

Low N sea water (ambient concentrations for August) was pumped to a constant level reservoir above the culture trays and filtered through a 1-mm mesh screen. Flow rates to the culture trays were adjusted to $\approx 2\,l \cdot min^{-1}$ by means of plastic valves. Flow rates were checked and readjusted, if necessary, on alternate days. These flow rates amounted to a flushing rate of 144 culture tray volumes $\cdot$ day^{-1}. An air line cemented to the bottom of each tray facilitated gas exchange and mixing. Dye studies revealed that this arrangement produced almost complete mixing within each culture tray. This is illustrated in Fig. 3 where the dilution of dye within a culture tray measured at the effluent end, closely paralleled the expected exponential dilution assuming complete and instantaneous mixing. Fifteen nutrient regimens were provided to plants by enriching sea water flowing to each culture tray. Nutrient medium (NH_4Cl, $NaNO_3$ or urea dissolved in distilled water) was held in 20-l glass carboys and supplied continuously to the culture trays by a peristaltic pump. Supply rates (≈ 1 ml $\cdot$ min^{-1}) and reservoir concentrations were calculated to give the desired range of inflow concentrations (0–40 μg at. N $\cdot$ l^{-1}). Phosphate (K_2HPO_4) was included to give an inflow concentration of 3 μg at. P $\cdot$ l^{-1} for all treatments.

The daily integrated irradiance at the surface was used to provide estimates of underwater irradiance in the culture trays after correcting for attenuation at 4 cm water depth. Experiments were performed during the latter part of August, a period when the irradiance was almost always above growth saturating levels, but not inhibitory. Preliminary investigations showed that shading of the culture trays would have been necessary during June and July to prevent bleaching of the thalli by the high irradiance levels. Daytime temperature readings were taken twice daily and were found to range between 14 and 19 °C (mean 15.5 °C).

Each culture tray was supplied with 12 individual plants trimmed to ≈ 1 g fresh weight each. The experimental plants were starved for 1 wk before experimentation by providing only N-depleted sea water to each chamber. After starvation the plants were supplied with enriched sea water at five concentrations for each N source for 1 wk prior to growth measurements. A mean specific growth rate was calculated for two 3-day growth intervals after this acclimation period. Effluent nutrient concentrations were measured on three occasions and mean values determined. Specific growth rate in culture was assumed to describe a hyperbolic relationship with residual N concentration, analogous to the Michaelis-Menten function. The equation takes the form (Monod, 1949):

$$\mu = \mu_{max} \cdot S/(K_s + S),$$

where μ = specific growth rate (day^{-1}); μ_{max} = maximum value of μ, and K_s = half saturation constant for growth (μg at. N $\cdot$ l^{-1}). This equation has been shown to be applicable to nutrient limited growth of macroalgae in both batch (Gordon *et al.*, 1981) and flow through (Chapman *et al.*, 1978; DeBoer *et al.*, 1978) culture. The growth

parameters K_s and μ_{max} were estimated using a non-linear curve fitting program (Cleland, 1979).

Growth rate was also expressed as a function of the internal N content of the seaweed (the thallus N quota) according to the following threshold equation (Droop, 1968):

$$\mu = \mu_m(Q-q_0)/Q\,,$$

where Q = thallus N quota (% dry wt) and q_0 = the subsistence quota (% dry wt) the mean value of Q at a basal μ. The maximal growth rate μ_m differs from μ_{max} in that it refers to a growth rate at infinite internal, rather than external, N.

RESULTS

NATURAL HISTORY

Young sporophytes first became obvious in the field in April just after the spring phytoplankton bloom had stripped the surrounding waters of nitrate (Fig. 1). Sporophytes persisted until the fall–early winter by which time the population had almost completely disappeared. Interestingly, the disappearance corresponded with the replenishment of the dissolved nitrogenous nutrients through mixing processes in the fall (Fig. 1). Thus the macroscopic phase of *C. flagelliformis* completed its growth cycle during those months characterized by minimal concentrations of dissolved nitrogenous nutrients.

Following their appearance in April the young sporophytes underwent a period of slow biomass addition before displaying a rapid increase in absolute growth rate in late May to peak in mid July (Fig. 1). Mid to late summer was characterized by a decrease

TABLE I

The N and C assimilation rates for *Chordaria flagelliformis* over the growing season as estimated from the product of the specific growth rate and tissue C, and tissue N contents, respectively.

Date	Specific growth rate (day^{-1})	Carbon assimilation rate (mg C · g^{-1} dry wt · day^{-1})	Nitrogen assimilation rate (mg N · g^{-1} dry wt · day^{-1})
23 April–13 May	0.10	37.70*	3.97*
13 May–24 May	0.06	23.41	2.49
24 May–12 June	0.16	50.96	4.66
12 June–12 July	0.09	29.63	2.32
12 July–23 July	0.07	22.42	1.53
23 July–9 Aug.	0.01	3.91	0.25
9 Aug.–27 Aug.	0.01	6.79	0.43
27 Aug.–10 Sept.	0	0	0

* Estimated using mid-May values for C and N (see Fig. 13).

in the rate of biomass accrual and by late August–early September plants began to lose weight and length. Growth on a relative basis ($g \cdot g^{-1} \cdot day^{-1}$) showed a different pattern from that on an absolute basis. The mean specific growth rate (μ) peaked in the early part of June, ≈ 5 wk earlier in the growing season than the absolute growth rate (Fig. 1). The μ declined steadily from June to late August and became negative in late summer. These dry wt specific growth rates together with total carbon and nitrogen values (Fig. 1) were used to express growth in terms of C fixed and N assimilated per unit biomass (Table I).

AMBIENT NUTRIENT CONCENTRATIONS

The seasonal variations in the concentrations of the dissolved nutrients PO_4^{3-}, NH_4^+, NO_3^-, NO_2^- and urea for Cranberry Cove are shown in Fig. 1. Total dissolved N in excess of the nitrogenous nutrients is shown in Table II. This fraction, though

TABLE II

Sea-water concentrations of the major dissolved N fractions over the summer of 1979 at Cranberry Cove, Nova Scotia.

Date	Total dissolved N (μg at. $N \cdot l^{-1}$)	$NH_4^+ + NO_3^-$ + urea (μg at. $N \cdot l^{-1}$)	Other dissolved organic N (μg at. $N \cdot l^{-1}$)
24 April	11.1	1.8	9.3
25 May	9.0	1.4	7.6
12 June	7.1	1.1	6.0
12 July	6.9	0.8	6.1
25 July	10.2	1.2	9.0
6 August	6.8	0.8	6.0
21 August	7.6	0.6	6.9
10 September	7.1	0.8	6.4
2 October	6.7	0.7	6.1

constituting the highest proportion of the dissolved N, was not utilized by *C. flagelliformis* (unpubl. results). The seasonal pattern in dissolved inorganic N variation was similar to that reported earlier for the nearby St. Margaret's Bay (Platt & Irwin, 1968; Chapman & Craigie, 1977; Gagné *et al.*, 1982). There was a sharp drop in inorganic N levels in the spring followed by a period of 6–7 months during which concentrations were consistently low. Concentrations of the dissolved nutrients, especially nitrate increased rapidly in the late fall reaching a maximum in mid-winter. The mean inorganic nitrogenous nutrient concentrations for the growing season of *C. flagelliformis*, April–September, were nitrite ≈ 0.03 μg at. $N \cdot l^{-1}$; nitrate ≈ 0.15 μg at. $N \cdot l^{-1}$, and ammonium 0.29 μg at. $N \cdot l^{-1}$. Most of the dissolved N was present in the organic fraction of which urea comprised only a small fraction ($\approx 7\%$). Nonetheless, urea at a mean concentration of 0.57 μg at. $N \cdot l^{-1}$ for the growing season was quantitatively more important than

any of the inorganic N nutrient sources. The total dissolved nitrogenous nutrient concentration decreased from spring to fall (Table II) and was strongly negatively correlated with the absolute growth rate ($r = -0.91$) over the growing season. Growth on a weight-specific basis revealed no such correlation with the ambient N concentration. Dissolved inorganic phosphate concentrations were similar to those in earlier reports for St. Margaret's Bay (Chapman & Craigie, 1977; Gagné *et al.*, 1982). Daily nutrient variations were measured by analyzing ammonium, urea, nitrate (plus nitrite) and

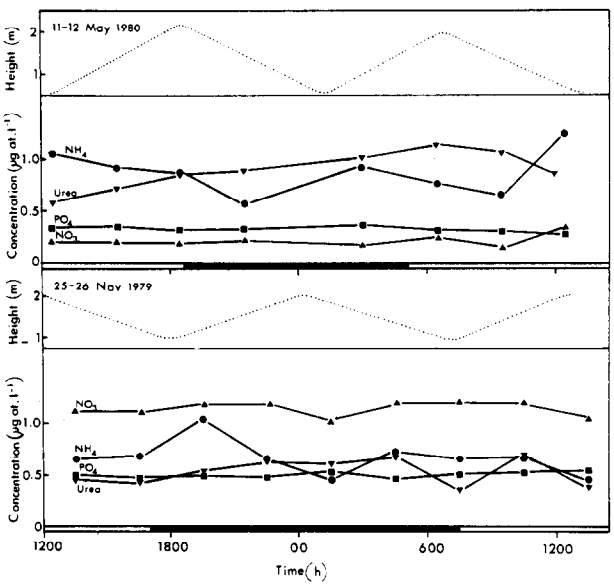

Fig. 4. Daily variation in tidal height, ammonium, urea, nitrate and phosphate concentrations during two 24-h periods at Cranberry Cove.

phosphate every 3 h through two 24-h periods. The results are shown in Fig. 4 with photoperiod and tidal cycles. Ammonium and urea concentrations showed the greatest daily variation (≈ 0.5 μg at. $N \cdot l^{-1}$) in this study.

LIGHT AND TEMPERATURE

The seasonal variation in the integrated irradiance between 400 and 700 nm at a depth of ≈ 1 m, the mean monthly daylength, the mean monthly water temperatures and daily water temperature ranges are shown in Fig. 1. Irradiance increased rapidly in the month of May to reach a maximum ($215\ \mu E \cdot m^{-2} \cdot s^{-1}$) in mid-June, closely paralleling the daylength. The μ of *C. flagelliformis* (Fig. 1) followed the light curve quite closely from mid-May onwards so that the two are significantly positively correlated ($r = 0.91$). The mean monthly water temperature at Cranberry Cove increased

throughout the growing season and reached a maximum in August of ≈ 15 °C (Fig. 1). This pattern was similar to that found for St. Margaret's Bay (Gagné *et al.*, 1982).

TISSUE ANALYSES

Total nitrogen and carbon

Variation in the total N and C concentration of *C. flagelliformis* over the growing season are shown in Fig. 1. Total N was highest in May and then decreased to a minimum in mid-July, coinciding with the period of maximum biomass addition, and remained relatively stable for the remainder of the summer. A similar pattern in total N concentration has been demonstrated for the summer annual kelp *Nereocystis leutkeana* on the west coast of Canada (Whyte & Englar, 1975). Total C reached a minimum in June and then increased steadily up to October. The total C concentration was relatively stable in comparison with total N, decreasing only 10% early in the growing season in contrast to the 43% decrease in N content. The seasonal range in C/N ratio (9.5–16.1) was within the range measured for field collected intertidal (Niell, 1976; Hanisak, 1979a) and subtidal (Mann, 1972a) seaweeds.

Ethanol-soluble nitrogen

The seasonal variation in total ethanol soluble organic N and α-amino N (glycine equivalents) exhibited similar patterns (Fig. 1). There was a rapid build-up of total ethanol-soluble organic N within the tissues of the young sporophytes up until late May when the maximum of 0.43% of the dry wt was achieved. The amount of N in the soluble fraction was only a small proportion (8.8 ± SE = 1.4%) of the total N content of the plants, the majority of the N being bound in a polymeric fraction. Free amino acids comprised the major portion of the soluble N fraction over much of the growing season (Fig. 1), similar to the findings with *Macrocystis pyrifera* in culture (Wheeler & North, 1980) and in the field (Wheeler & North, 1981). Both the total soluble N content ($r = 0.92$) and free α-amino N content ($r = 0.91$) were significantly correlated with μ, but showed no relation to absolute growth rate.

NUTRIENT EXCRETION AND GRAZING

Feeding preference studies with *Littorina vincta* and *Gammarellus angulosus* (Table III) indicated that when sufficient alternate food sources were available, *Chordaria flagelliformis* was likely to be only minimally grazed by these two invertebrates. This low palatability of *C. flagelliformis* for the gastropod is in agreement with an earlier report (Lubchenco, 1978). Both animals were demonstrated to excrete ammonium and urea (Table IV). *Gammarellus angulosus* provided quantitatively a more important source of N than *Littorina vincta*, though excretion rates for the amphipod were found to vary quite substantially between individuals. Expressed in terms of N regenerated per unit

weight of *Chordaria flagelliformis*, *Littorina vincta* supplied only $\approx 11\%$ of that supplied by *Gammarellus angulosus*.

TABLE III

Results of three separate feeding preference studies with the amphipod *Gammarellus angulosus* and the gastropod *Lacuna vincta*: the amount of food ingested was normalized to equal initial weight before percentage consumed was calculated.

Food species	Percent of total food eaten by *Gammarellus angulosus*		
	I	II	III
Alaria esculenta (L.) Grev.	43	53	45
Palmaria palmata (L.) O. Küntze	13	6	25
Fucus vesiculosus	17	4	18
Ulva sp.	15	15	7
Chondrus crispus	8	15	4
Chordaria flagelliformis	3	6	2
	Percent of total food eaten by *Littorina vincta*		
	I	II	III
Saccorhiza dermatodea (Pyl.) J. Ag.	26	31	34
Alaria esculenta	17	21	19
Scytosiphon lomentaria	10	19	12
Desmarestia aculeata (L.) Lamour	20	7	17
Ulva sp.	13	8	10
Chondrus crispus	5	6	7
Palmaria palmata	8	7	5
Chordaria flagelliformis	2	0	2

TABLE IV

Summary of excretion rates for *Gammarellus angulosus* and *Lacuna vincta* measured on three or four occasions in late July–early August: ratios of plant biomass to animal biomass/numbers are also included for this period; these results were used in the calculation of a mean regeneration rate of NH_4^+ and urea per unit dry biomass of *Chordaria flagelliformis*.

	Excretion rate	
	NH_4^+ ($\mu g\ N \cdot g^{-1}$ dry wt $\cdot h^{-1}$) ± SE	Urea ($\mu g\ N \cdot g^{-1}$ dry wt $\cdot h^{-1}$) ± SE
Gammarellus angulosus		
Expt. I	216.8 ± 64.2	751.3 ± 207.3 ($n = 5$)
II	94.3 ± 41.0	207.7 ± 75.1 ($n = 5$)
III	237.3 ± 69.5	76.0 ± 9.5 ($n = 5$)
(A) Mean	182.8 ± 36.4	345.0 ± 131.5
(B) Ratios (dry wt): 14.73 ± 3.31 mg *Gammarellus* $\cdot g^{-1}$ *Chordaria* ($n = 31$)		
Regeneration rate (AB/1000): NH_4^+	64.6	$\mu g\ N \cdot g^{-1}$ *Chordaria* $\cdot$ day^{-1}
Urea	122.0	
Total	186.5	

	Excretion rate	
	NH_4^+ (g N $\cdot$ snail$^{-1} \cdot$ day^{-1}) ± SE	Urea (g N $\cdot$ snail$^{-1} \cdot$ day^{-1}) ± SE
Littorina vincta		
Expt. I	0.37 ± 0.12	0.25 ± 0.11 ($n = 7$)
II	0.39 ± 0.12	0.30 ± 0.08 ($n = 5$)
III	0.49 ± 0.15	0.18 ± 0.10 ($n = 5$)
IV	0.67 ± 0.31	0.11 ± 0.05 ($n = 5$)
(A) Mean	0.48 ± 0.21	0.21 ± 0.09
(B) Ratios: 34.92 ± 3.83 snails $\cdot g^{-1}$ *Chordaria* ($n = 39$)		
Regeneration rate (AB/1000): NH_4^+	12.9	g N $\cdot g^{-1}$ *Chordaria* $\cdot$ day^{-1}
Urea	7.3	
Total	20.3	

GROWTH KINETICS

External nitrogen

Growth saturation was achieved at ≈ 3–$5\ \mu g$ at. $N \cdot l^{-1}$ for all three N sources (Fig. 5). Nitrogenous nutrient enrichment between 5 and 30 μg at. $N \cdot l^{-1}$ had no stimulatory or inhibitory effect on growth rate. In contrast to a previous report of the growth of young sporophytes in laboratory (slow-flushing) culture (Probyn, 1981), there was no significant difference between the three sources of N ($F = 2.76$, $P > 0.05$). The growth data for the plants on unenriched sea water were not included in the calculation of the kinetic parameters. Residual N concentrations were low to

undetectable for this treatment and hence could not be measured with confidence. Inclusion of this single datum point in the calculations had a very large effect on the value of K_s for all three nutrient sources, biasing estimates towards extremely low

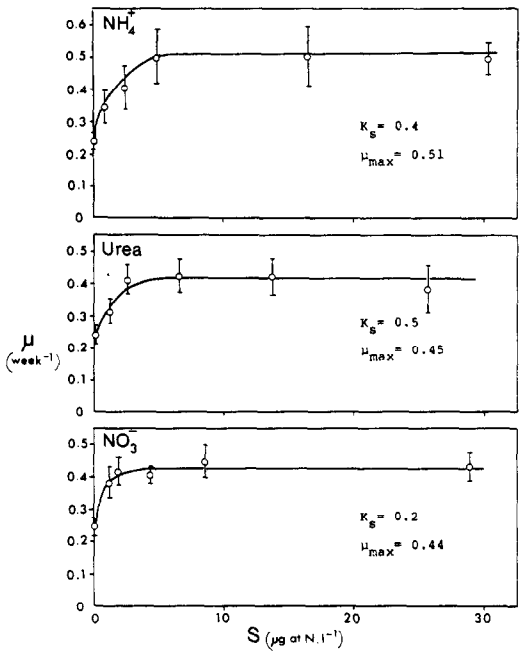

Fig. 5. Specific growth rate of *Chordaria flagelliformis* as a function of the residual nitrogenous nutrient concentration (S) for ammonium, urea and nitrate grown plants.

values. The estimated K_s values for the three N sources were: 0.4 μg at. N · l^{-1} (SE = 0.1) for ammonium; 0.5 μg at. N · l^{-1} (SE = 0.2) for urea; and 0.2 μg at. N · l^{-1} (SE = 0.1) for nitrate. These figures are presented for comparison with a number of other seaweeds in Table V. The K_s values found for *Chordaria flagelliformis* are amongst the lowest reported for seaweeds.

Internal nitrogen

Growth of *C. flagelliformis* in tank culture could be expressed in terms of N-status of the thallus. A plot of μ against Q (thallus N quota) described a threshold response for all three nutrient sources (Fig. 6). The critical N concentrations (C_n) values of Q below which μ was N limited, were calculated directly from these plots. The C_n values differed between N sources amounting to (on a dry wt basis) 1.5% for urea and 0.9% for nitrate (Table VI). The free amino content of these experimental plants was strongly correlated with Q for all three N sources (r = 0.98). Consequently, it is not surprising to find a similar hyperbolic relationship between μ and α-amino N content. The

TABLE V

The growth parameters K_s and μ_{max} for a number of macroalgae: the ratio μ_{max}/K_s provides a measure of the slope of the hyperbola at low ($<K_s$) substratum concentrations.

Species	N source	Growth parameters: K_s (± SE) μg at. N·l^{-1}	Growth parameters: μ_{max} (± SE) (wk^{-1})	Growth parameters: μ_{max}/K_s	References
Rhodophyceae					DeBoer *et al.*, 1978
Gracilaria foliifera	NO_3^-	0.4 (0.1)	0.69 (0.08)	1.73	
	NH_4^+	0.2 (0.1)	0.90 (0.10)	4.50	
Neoagardhiella baileyi	NO_3^-	0.2 (0.1)	0.74 (0.11)	3.70	
	NH_4^+	0.2 (0.2)	1.19 (0.09)	5.95	
	Urea	0.2 (0.1)	0.48 (0.06)	2.40	
Chlorophyceae					
Ulva	NO_3^-	<1.0	–	–	Lapointe & Tenore, 1981
Phaeophyceae					
Laminaria saccharina	NO_3^-	1.4	1.26	0.90	Chapman *et al.*, 1978
L. longicruris (Atlantic)	NO_3^-	1.8 (0.2)	1.79 (0.04)	1.02	Espinoza & Chapman, 1983
L. longicrurus (Fundy)	NO_3^-	2.9 (0.4)	1.53 (0.05)	0.53	
Chordaria flagelliformis					Probyn, 1981*
Laboratory culture	NO_3^-	0.5 (0.3)	0.21 (0.01)	0.43	
	NH_3	2.1 (0.8)	0.58 (0.05)	0.28	
	Urea	1.7 (0.1)	0.27 (0.04)	0.16	This study
Tank culture	NO_3^-	0.2 (0.1)	0.44 (0.01)	2.20	
	NH_4^+	0.4 (0.1)	0.54 (0.02)	1.35	
	Urea	0.5 (0.2)	0.45 (0.02)	0.90	

* Uptake parameters recalculated using a non-linear curve fitting program (Cleland, 1979).

subsistence quota (q_0) or N content below which μ was zero was estimated from a linear derivative of the Droop equation. Correlation coefficients for these regressions of μQ and Q (Fig. 6 inset) were typically high for ammonium and nitrate grown plants. For urea grown plants μQ at high Q values deviated from the linear relationship such that

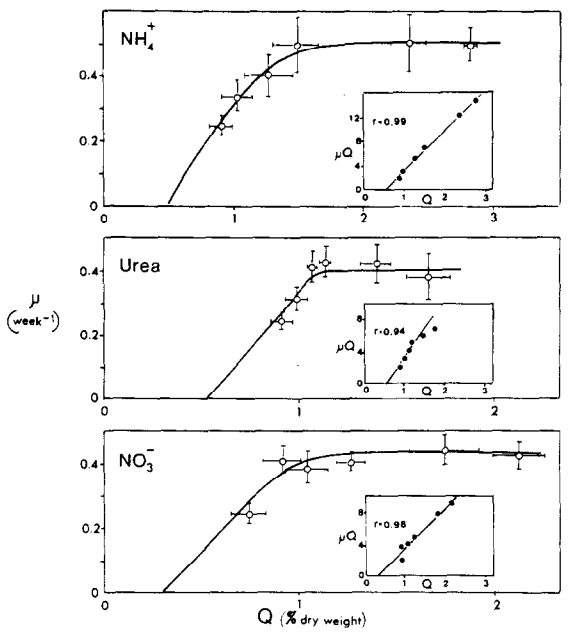

Fig. 6. The relationship between specific growth rate and thallus quota (Q) for ammonium, urea and nitrate grown *Chordaria flagelliformis* (means ± 95% confidence limits, n = 10 for Q and n = 12 for specific growth rate): the inset to each figure shows the linear derivative of the Droop (1968) equation.

TABLE VI

Estimates of the critical N concentrations (C_n) and subsistance quotas (q_0) for a number of macroalgae: the q_0 values in the present study were calculated from a linear derivative of the Droop (1968) equation; all other q_0 and C_n values were estimated directly from the μ vs. Q plots.

Species	N source	C_n % dry wt	q_0 % dry wt	References
Codium fragile	NO_3^-	1.9	0.8	Hanisak, 1979a
Laminaria saccharina	NO_3^-	1.9	1.3	Chapman *et al.*, 1978
Macrocystis pyrifera	NO_3^-	*	0.7	Wheeler & North, 1980
Chordaria flagelliformis	NH_4^+	1.5	0.5	This study
	Urea	1.1	0.5	
	NO_3^-	0.9	0.3	
Cladophora albida (Huds.) Kütz.	NO_3^- + NH_4^-	2.1	1.2	Gordon *et al.*, 1981

* Linear relationship between μ and Q over the experimental range in Q.

TABLE VII

The potential contribution of the polymeric N reserve (total N − [C_n + free amino N]) and free amino N (glycine equivalents), to the N requirement for growth ($\mu \times C_n$) of *Chordaria flagelliformis*: a C_n corresponding to the maximum measured in culture (15 mg N · g^{-1}) was used; all results are expressed on a dry wt basis.

	A	B			C		
Date	Growth requirement (mg N · g^{-1} · day^{-1})	Polymeric N reserve (mg N · g^{-1})	Rate of decline in polymeric fraction (mg N · g^{-1} · day^{-1})	α-amino N (mg N · g^{-1})	Rate of decline in α-amino N (mg N · g^{-1} · day^{-1})	B/A %	C/A %
13 May		25.55		2.10			
13 May–24 May	0.96		0.90			93.8	
24 May		15.65		2.49			
24 May–12 June	2.33				0.08		3.4
12 June		17.17		4.66			
12 June–12 July	1.34		0.23		0.03	17.2	2.2
12 July		10.17		2.32			
12 July–23 July	1.06		0.05			4.7	
23 July		9.58		1.53			
23 July–9 Aug.	0.17				0.02		11.8
9 Aug.		10.73		0.25			
9 Aug.–27 Aug.	0.29		0.02		0.02	6.9	6.9
27 Aug.		10.35		0.43			

q_0 was biased towards a low value. A q_0 calculated using all of the data points was much lower than one would expect from extrapolation of Fig. 6. Consequently the datum point corresponding to the highest Q value was not included in the calculation of q_0. Subsistence quotas are presented in Table VI for comparison with a few other macroalgae.

The potential contribution of reserve N to growth was calculated by comparing the rate of decline in storage N with the specific N assimilation rate. The growth demand in this instance was calculated from the μ and the maximum C_n and the reserve fraction was regarded as N in excess of the C_n. The reserve was split into a polymeric and α-amino fraction. These results summarized in Table VII indicate that growth early in May could be almost entirely through the utilization of internal N.

Discussion

NATURAL HISTORY

The specific growth rate (μ) or "efficiency index" is an important physiological measurement, providing an indication of the efficiency with which a plant or stage in a plant's life can, for a particular outlay of material, procure resources for growth (Blackman, 1919). Absolute growth rate, on the other hand, is more ecologically relevant. Growth rates of seaweeds in the field have traditionally been expressed on an absolute basis with relatively few investigations of μ. The maximum mean μ of 0.16 (day^{-1}) recorded in this field study translates to a doubling time, on a dry wt basis, of ≈ 4 days. Other field studies have estimated doubling times of 3–4 days for *Ulva lactuca*, 6–9 days for *Fucus vesiculosus* and *Chondrus crispus* (Kanwisher, 1966) and a spring minimum of 8 days for *Iridea cordata* (Hansen, 1977). Bearing in mind that μ is markedly size dependent, it is not surprising that the larger kelp species display long doubling times. Minimal doubling times for a number of laminarian fronds can be calculated to range between 26–130 days (Mann, 1972b; Kain, 1976; Lüning, 1979). These findings suggest that *Chordaria flagelliformis* exhibits a relatively high physiological growth rate characteristic of early colonisers (i.e. opportunists or ruderals) of available space (Murray & Littler, 1978; Sousa, 1979). It should be remembered that comparisons between species can only be made with confidence if μ is determined under controlled conditions with presumably no environmental variable limiting growth.

Littler & Littler (1980) have presented evidence for a functional form hypothesis for seaweeds by which physiological attributes can be correlated with thallus form. This theory differs from the more traditional life-form approach (i.e. incorporation of life history characteristics) in that it correlates important morphological traits with biological function. Accordingly the finely branched construction of *C. flagelliformis* and resultant high surface area/volume ratio, typical of opportunistic species, favors a high productivity (Littler & Murray, 1974; Littler, 1981). The maximum net productivity of *C. flagelliformis*, in the area of 2.1 mg $C \cdot g^{-1}$ dry $wt \cdot h^{-1}$ (Table I), calculated from μ

and C content, is near the high end of the range found by Littler (1980) from short term oxygen evolution experiments on a number of similarly finely-branched alga. The in situ productivity rates for the Baltic summer annual brown algal species *Scytosiphon lomentaria* and *Dictyosiphon foeniculaceus* are somewhat higher, ranging from 1.6 to 3.0 mg $C \cdot g^{-1}$ dry $wt \cdot h^{-1}$, and 4.2 to 8.8 mg $C \cdot g^{-1}$ dry $wt \cdot h^{-1}$, respectively (Wallentinus, 1978). Taking into account the seasonal periodicity of *Chordaria flagelliformis*, its high per plant productivity results in it being approximately as productive on a unit area basis as Nova Scotian kelps during the summer months (Rice & Chapman, 1982).

SOLUBLE NITROGEN RESERVES

The growth strategies of a number of perennial seaweed species, particularly at temperate latitudes, involve the storage and subsequent mobilization of soluble reserve material (Mann *et al.*, 1980). Opportunistic species on the other hand, can be expected to channel their resources into sustaining high growth rates for the short, favourable growing period. Accumulation of ethanol-soluble N constitutes an important adaptation for perennial seaweeds that experience marked seasonal fluctuations in dissolved N nutrient availability. *Laminaria longicruris* plants that experience extreme nitrogenous nutrient depleted conditions for much of the summer accumulate nitrate up to 2% of dry wt during the winter (Chapman & Craigie, 1977). *Chondrus crispus* subject to similar seasonal nutrient fluctuations stores the dipeptide L-citrullinyl-L-arginine, reaching levels (in terms of N) up to 2.9% of dry wt (Laycock & Craigie, 1977). It appears that both of these internal N pools function in a similar way to support growth in the spring when ambient nutrient levels are low. Where nutrients are plentiful throughout the year, or seasonal depletion less extreme, accumulation of soluble tissue N is less important (Anderson *et al.*, 1981; Gagné *et al.*, 1982). The comparatively low ethanol-soluble N concentrations of *Chordaria flagelliformis* (0.1–0.4% of dry wt, Fig. 3) indicates that, typical of opportunistic species, newly absorbed N is directed into maintaining a high rate of biomass accretion with little emphasis on the storage of N in the ethanol-soluble fraction. Rosenberg & Ramus (1982) have experimentally verified the contrasting N storage strategies of a competitor, such as *Gracilaria foliifera*, and an opportunist, such as *Ulva* sp. When cultured under similar conditions of natural irradiance, the soluble N reserve reached a maximum of $\approx 1\%$ of dry wt in *Gracilaria foliifera* and 0.5% in *Ulva* sp. Whereas the opportunist channels its resources into maintaining high rates of growth, the competitor accumulates N until conditions are favourable for growth.

STEADY VERSUS EPISODIC NUTRIENT SUPPLY

Defining adaptation in the present context as the suite of physiological attributes that maximize N acquisition at environmental concentrations, then *Chordaria flagelliformis* is well adapted to absorb the low ammonium, urea (Probyn & Chapman, 1982) and nitrate (Probyn, in prep.) concentrations prevalent during the summer. The steady-state

approach offers a plausible argument for explaining simultaneous high growth rates and a depleted residual nutrient concentration. Recently the applicability of this approach to phytoplankton nutrition has been challenged (Jannasch, 1974) with emphasis being placed rather on the temporal and spatial variability of a limiting resource (Harris, 1980). A corollary to this idea, originally expanded on by McCarthy & Goldman (1978) and Goldman *et al.* (1979), is that present techniques of nutrient analysis integrate information on scales that are too large to detect changes of physiological significance to a phytoplankton cell. It is tempting to apply these phytoplankton-related concepts to seaweed nutrition, especially in light of the high transient ammonium and urea uptake rates that we have demonstrated for *C. flagelliformis*, and the high ammonium uptake rates demonstrated in *Gracilaria foliifera* by D'Elia & DeBoer (1978). However, it is necessary to take into account the appropriate differences in scale between the two groups of organisms. Whereas extant techniques for micronutrient analysis may be too coarse for relevance in the environmental scale of phytoplankton, the techniques may be more appropriate at the environmental scale of importance to seaweeds.

The generalized uptake curves for *Chordaria flagelliformis* at a steady and at a pulsed nutrient supply are shown in Fig. 7. It is evident that only at concentrations above $\approx 6\ \mu g$ at. $N \cdot l^{-1}$ for urea and $1\ \mu g$ at. $N \cdot l^{-1}$ for ammonium are the transient uptake rates in excess of those predicted at steady state. For nitrate relatively high ($> 20\ \mu g$ at. $N \cdot l^{-1}$), essentially non-ecological, episodes in concentration would be

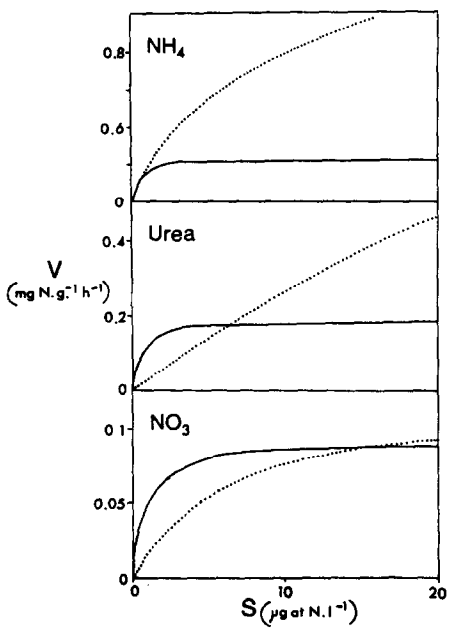

Fig. 7. Generalized curves for transient (dotted line) and apparent steady-state (solid line) uptake of various N species by *Chordaria flagelliformis*: curves drawn from Probyn & Chapman (1982) and Probyn (in prep.).

required for transient uptake to exceed that predicted at steady state. Measurements of diel fluctuations in nutrient availability at Cranberry Cove, our study site, indicated relatively stable nutrient concentrations (Fig. 4). In contrast, Rosenberg (1981) demonstrated that in the Newport River estuary ammonium concentration can fluctuate between 1 μg at. N $\cdot$ l^{-1} and $\approx$3 μg at. N $\cdot$ l^{-1} daily. Occasional storms at Cranberry Cove accompanied by strong offshore winds have been shown (unpubl. data) to be followed by elevated ammonium concentrations as high as 4 μg at. N $\cdot$ l^{-1}, which could persist for a day or two. Such storms were, however, too infrequent during the summer to have been of major ecological significance to the N nutrition of *C. flagelliformis*.

Another potential source of pulsed nutrient supply is regeneration by animal epiphytes. Kautsky & Wallentinus (1980) have shown that N and P regeneration rates by mussels were in excess of the seaweed requirement in the Baltic. They propose that excretion from mussels might explain why many of the Baltic red and brown seaweeds extend their growth maxima through the summer making use of improved light conditions, while the surrounding water mass is depleted of mineral nutrients. Such a tight nutrient cycle would imply a close physical association between the nutrient regenerating animals and the seaweeds. *Chordaria flagelliformis*, because of its finely branched construction, provides a suitable growth form for the support of large numbers of animals. Wieser (1952) demonstrated that dense tuft-like seaweeds contained larger invertebrate populations than the more leaf-like forms. Mature *C. flagelliformis* plants (late July onwards) were colonized mainly by populations of *Gammarellus angulosus* and *Littorina vincta* which were apparently not feeding directly on their host (Table III). During the latter part of July–early August, the period of high absolute growth rate for *Chordaria flagelliformis*, the excretion rates of these animals, in terms of ammonium and urea regenerated per unit biomass of host plant (Table IV) could account, potentially, for 12–45% of the N requirement in the field (see N assimilation rate, Table I). Such figures are, however, likely over-estimates because of the rapid dispersion of nutrient microzones by molecular diffusion (Jackson, 1980). The highly wave-exposed nature of areas colonized by *C. flagelliformis* would further promote spatial homogeneity in nutrient distribution, reducing the potential for regenerative flux from animals as an important N source.

It appears then that nutrient pulsing through wind or tidally induced mixing processes, or through animal excretion provides a relatively minor contribution towards the growth requirement of *C. flagelliformis* at least during May–June when the μ was maximal. Using the uptake parameters K_m and V_{max} at steady nutrient supply (Probyn & Chapman, 1982; Probyn, in prep.), one can predict uptake rates for the period of maximum μ in the field (using the mean nitrogenous nutrient concentrations for this period, late May–June). After correcting for a reduction in ammonium and urea uptake in the dark (Probyn & Chapman, 1982), the following rates would be possible at the indicated concentrations assuming a light/dark cycle of 16/8 h: ammonium (0.40 μg at. N $\cdot$ l^{-1}) – 2.05 mg N $\cdot$ g^{-1} dry wt $\cdot$ day^{-1}, urea (0.67 μg at. N $\cdot$ l^{-1}) – 2.51 mg N $\cdot$ g^{-1} dry wt $\cdot$ day^{-1}, nitrate (0.16 μg at. N $\cdot$ l^{-1}) – 0.36 mg N $\cdot$ g^{-1}

dry wt · day^{-1}. Assuming that all three nitrogen sources are taken up simultaneously, nutrient uptake could account for growth of 4.92 mg N · g^{-1} dry wt · day^{-1}. Consulting Table I, it can be seen that the predicted uptake rates are sufficient to satisfy the maximum N demand (i.e. during June). Gerard (1982a) has similarly predicted that in situ uptake rates at the generally low ambient nitrate and ammonium concentrations along the southern Californian coast are sufficient to support typical *Macrocystis pyrifera* growth rates.

Using the above uptake rates and concentrations it is possible to calculate an index of the relative preference for each of the three nutrients. The relative preference indices calculated according to McCarthy *et al.* (1977) are 0.8 for ammonium, 1.1 for urea, and 1.9 for nitrate. The values close to unity for ammonium and urea reflect uptake rates that are equitable with availability. The relative preference index in excess of unity for nitrate indicates that, even though the above calculations predict this nutrient contributes little to the combined uptake of N, it is the marginally prefered substrate relative to the other two. It should be noted in this context that extrapolation from uptake in the laboratory to growth in the field is fraught with problems and should be interpreted with caution.

GROWTH–EXTERNAL NITROGEN CONCENTRATION

To date very few studies have been performed on seaweeds relating growth performance on different sources of N over a wide concentration range. Most of the investigations of seaweed nutrition have been concerned with the effect of different fertilizing regimens on the growth rate and yield of commercially important seaweeds, with little reference to growth strategy in the wild.

It was shown in a previous study (Probyn, 1981) that ammonium was the superior N source for the growth of *Chordaria flagelliformis* in laboratory culture with low culture medium turnover rates. However, when plants were grown in outdoor culture with rapid flushing, growth rates were similar on all three N sources. Because of the rapid flushing, we believe that the outdoor cultures are a more realistic approximation of field conditions than the laboratory culture experiments. The ability of *C. flagelliformis* to utilize ammonium, nitrate and urea with approximately equal capacity (μ_{max}) would provide a competitive advantage over seaweeds which can utilize only one or two of these sources. The fact that urea is quantitatively more important than both ammonium and nitrate in the waters of Cranberry Cove during the summer months suggests an unprecedented importance of this organic substrate to the N nutrition of a seaweed in the wild.

The above discussion is concerned with maximal growth rates at high (non-ecological) nutrient concentrations, and consequently, might be misleading when applied to the natural situation in the wild. The ratio μ_{max}/K_s (Healey, 1980) is used as a measure of the efficiency with which sub-growth saturating concentrations are assimilated. Tank culture experiments revealed that nitrate ($\mu_{max}/K_s = 2.2$) is a more effective N source

for *C. flagelliformis* than either ammonium (μ_{max}/K_s = 1.35) or urea (μ_{max}/K_s = 0.9) at low concentrations (Table V). Ammonium, on the other hand, appears to constitute a more satisfactory N source at subgrowth saturating concentrations for the red alga *Gracilaria foliifera* and *Neoagardhiella baileyi* Harvey ex Kützing (Table V). The efficiency with which growth limiting concentrations of the three N sources are utilized displays a trend which is inversely related to the relative abundance of these N sources during the growing season of *Chordaria flagelliformis*. Urea, quantitatively the most important source, is the least efficiently utilized at ambient nutrient concentrations. In contrast, nitrate, which is present only in very low concentrations throughout the summer, is the most efficiently utilized. These observations suggest that substrate utilization efficiency, estimated as μ_{max}/K_s, reflects a number of physiological attributes that tend to compensate for the relative abundance of a particular N source. Bearing in mind the previously mentioned relative preference for nitrate transport it is tempting to propose that at environmental concentrations all three sources of N contribute similarly to growth, or at least that the differences between individual source contributions are not as marked as predicted from steady state uptake kinetics.

GROWTH – INTERNAL NITROGEN

The little information that is available on the relationship between growth rate and internal nutrient concentration of seaweeds generally indicate a typical threshold response (Chapman *et al.*, 1978; Hanisak, 1979a). One study with *Macrocystis pyrifera* has shown a positive linear relationship between Q and μ in nitrate limited batch and flow through cultures (Wheeler & North, 1980).

The relationship between yield and plant nutrient content has been known for some time in higher plants and has proved an extremely useful tool in agriculture. Central to the application of this relationship to plants in the field is the "critical nutrient concentration" (C_n). Internal nutrient concentrations in excess of this level indicate luxury consumption. The critical nutrient concept has important applications to the field of seaweed aquaculture. It is well documented for seaweeds that when N limits growth, carbohydrate synthesis predominates resulting in high polysaccharide levels (Neish & Shacklock, 1971; Dawes *et al.*, 1974; Chapman & Craigie, 1977). Because of this inverse relationship between carbohydrate content and N content, Neish *et al.* (1977) concluded that the production of carrageenan by *Chondrus crispus* could be increased by a period of N deficiency after N sufficient growth. DeBoer (1978) was able to maximise both growth rate and carageenan content in *Neogardhiella baileyi* by maintaining his cultures at external concentrations that just barely saturated growth. In other words, maintaining tissue N at close to the C_n would result in the maximum yield of this commercially important carbohydrate.

The C_n of *Chordaria flagelliformis* appears to be dependent on the N source, being lowest for nitrate grown plants and highest for ammonium grown plants. These findings reflect the previously mentioned efficiency of nitrate utilization based on K_s values. The

low C_n of nitrate grown *C. flagelliformis* relative to perennial seaweeds (Table VI) might represent an important adaptation to growth in nutrient poor areas. The benefits would be two fold. First, maximum growth rates can be maintained at relatively low internal N concentrations, and secondly, this will allow more scope for the luxury accumulation of N. It is, however, difficult to apply this kind of reasoning to the field where ammonium, nitrate and urea are all likely to contribute towards an effective C_n.

Implicit in the relationship between μ and Q is that the potential of a body of water for supporting maximal growth rates is likely to depend as much on the nutrient already inside the thallus as that supplied by current uptake. It should be remembered in this context that both the internal (Droop) and external (Monod) models predict the same results under steady state conditions i.e. when concentration dependent uptake is in equilibrium with the internal Q related pool (Goldman, 1977; DiToro, 1979). The Droop equation is advantageous in that it depicts the relationship between uptake and growth, or rather the progressive uncoupling between the two as μ increases, leading to luxury consumption. Because of this phenomenon, measurement of internal nutrient pools might give a better indication of fertility of a given habitat than measurement of nutrients in the water. Using the algae as integrators of N availability accommodates the dynamics of nutrient turnover and avoids complications arising from the inadequacy of present analytical methods in detecting extremely low environmental N concentrations. Comparing the experimentally determined C_n values (Table VI) with the field situation, where Q never falls below 2.2% of dry wt (Fig. 1) establishes that the plants are N sufficient in the field throughout the growing season. In fact if we take the effective C_n in the field as the maximum measured experimentally, (1.5% of dry wt for ammonium grown plants), it is obvious that *C. flagelliformis* accumulates N substantially in excess of that required to maintain maximum growth. It appears that the rapid initial increase in μ in May is the result of the utilization of this excess N which is bound predominantly in the polymeric fraction (Table VII). The relatively small potential contribution from the amino N is in agreement with the findings of Gerard (1982b) who showed that *Macrocystis pyrifera*, when transferred to a low N environment, maintains growth mainly through the utilization of reserve N other than free amino acids.

Another important N status related measure is the subsistence quota (q_0) or minimal cellular N content required to maintain a basal growth rate. Comparing q_0 for nitrate grown *C. flagelliformis* with that of nitrate grown *Codium fragile*, *Macrocystis pyrifera*, and *Laminaria saccharina* (Table VI) again suggests an advantage of the annual species over the perennials in a low N environment. The relatively low q_0 for *Chordaria flagelliformis* indicates that it can maintain a positive μ at much lower internal N levels than the other species. However, since Q in the field is always in excess of C_n (for *C. flagelliformis*), it is reasonable to conclude that q_0 has little ecological significance in the present study. Hanisak (1979a) showed that for *Codium fragile* in northeastern U.S.A. Q falls well below C_n in the summer approaching values as low as its q_0. *Macrocystis pyrifera* growing off the coast of southern California shows similar seasonal variation in Q with summer values falling close to q_0 (Wheeler & North, 1981). At thallus

quotas below C_n the q_0 becomes an important parameter determining the lower limit of Q for survival. Since survival (i.e. the ability to grow at a rate exceeding tissue loss through grazing, senescence, etc) of unfavourable or stressful periods over the annual cycle is fundamental to the perennial growth strategy, it would be a significant advantage to a species subjected to seasonal N stress to possess a low q_0. The lower q_0 for *Macrocystis pyrifera* and *Codium fragile* compared to *Laminaria saccharina* can be related to differences in the degree of N availability in each species' habitat. The summer inorganic N concentrations off the coast of California (Wheeler & North, 1981) and off Rhode Island (Hanisak, 1979b) can drop to 1–2 μg at. N $\cdot$ l^{-1}, whereas off Helgoland in North Sea, where *L. saccharina* was studied, the total inorganic N concentrations never fell below 20 μg at. N $\cdot$ l^{-1} (Harms & Hagmeier, 1976).

A SUMMARY OF SEASONAL GROWTH IN *CHORDARIA FLAGELLIFORMIS*

The N-related adaptations of *C. flagelliformis* can best be discussed with reference to the phase in its growing season. The phases recognized in the present study are regarded as typical of annual plants (Scaife & Smith, 1973).

Phase I: (May–early June). This phase can last for a few days to several weeks depending on the N status and size of plants. During this phase *C. flagelliformis* relies mainly on N reserves (polymeric) with little effect of external supply (uptake) on growth. Through utilization of internal N the plants, by virtue of their small size, are able to exploit the increasingly favourable light conditions and attain maximal μ. Growth and uptake of N are uncoupled and μ is negatively correlated with Q. This can be regarded as the physiologically important phase when the plants achieve maximal "working efficiency".

Phase II: (early June–mid-July). During this phase the internal nutrient status parallels μ. Cellular equilibrium is achieved such that Q is in dynamic balance with external N supply. It would appear that a steady-state uptake rate at mean ambient nitrogenous nutrient concentrations is sufficient to meet the plants N demands. In this respect the extremely high efficiency with which low concentrations of all three N sources are used (low K_s) is of the utmost importance. Episodic phenomena are regarded as relatively unimportant to the N nutrition of *C. flagelliformis*. A significant contribution from excretion by animal epiphytes is possibly only ever achieved from the latter part of this phase onwards. The fall in μ reflects the decreasing irradiance in the field. Ecologically this is the more important period in the growing season as the plants display a rapid increase in absolute growth rate and attain maximal standing crop.

Phase III: (mid-July–Sept.). Well nourished *C. flagelliformis* forms a canopy as μ continues to decline and absolute growth rate begins to fall because of self-shading and decreasing ambient irradiance. The thallus N quota (Q) remains stable and independent of μ as the dynamic equilibrium is disrupted, presumably a result of uptake now exceeding growth. Population senescence is well underway by the end of August when the plants display a loss of tissue.

ACKNOWLEDGEMENTS

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