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NUTRIENT UPTAKE AND GROWTH KINETICS IN BROWN SEAWEEDS: RESPONSE TO CONTINUOUS AND SINGLE ADDITIONS OF AMMONIUM

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Abstract: The brown seaweeds *Fucus distichus* Linnaeus subsp. *edentatus* (de la Pylaie) Powell, a perennial, and *Chordaria flagelliformis* (O. F. Mueller) C. Agardh, a summer annual, were grown in continuous-flow greenhouse cultures. In winter, the growth of *Fucus distichus* ($\mu = 0.01 \cdot day^{-1}$) in culture was not stimulated by added ammonium. Nitrogen in excess of the growth requirement was accumulated in the thallus (1.34–2.18% N by dry wt, depending on the N-loading). In summer, the growth of both species in continuous cultures was stimulated by added ammonium. *Chordaria flagelliformis* showed higher rates of both growth ($\mu_{max} = 0.109 \cdot day^{-1}$) and ammonium uptake ($V_{max} = 23.2$ μmol $NH_4^+ \cdot h^{-1} \cdot g$ dry wt^{-1}) than *Fucus distichus* ($\mu_{max} = 0.074 \cdot day^{-1}$, $V_{max} = 13.9$ μmol $NH_4^+ \cdot h^{-1} \cdot g$ dry wt^{-1}). Calculated nitrogen subsistence quotas were similar in the two species (0.7% N in *Chordaria*, 0.6% N in *Fucus*). In those continuous cultures which did not receive added ammonium, *Chordaria* stored less nitrogen in excess of the subsistence quota than *Fucus*, although both species accumulated nitrogen at increased N-loading. Transient uptake rates were measured in response to single additions of ammonium. At any given initial concentration, short-term (30 min) uptake rates were a decreasing function of the thallus nitrogen quota and were higher for *Chordaria* than for *Fucus*. In N-depleted plants, short-term ammonium uptake rates exceeded both the uptake rates predicted from continuous cultures and the nitrogen requirements for growth. *Chordaria flagelliformis*, in particular, is able to scavenge efficiently low ambient N-nutrient concentrations and to sequester rapidly transient ammonium pulses. In comparison with *Fucus distichus*, *Chordaria flagelliformis* appears to be better adapted to short-term fluctuations in nutrient availability (on a scale of minutes to hours). Their N-storage capability allows both of these seaweeds to buffer the effect of fluctuations in external N-nutrient concentrations on their growth rates over periods of days to several weeks.

INTRODUCTION

Nitrogen limitation of phytoplankton production during at least part of the year is frequently observed in the temperate coastal marine environment (Ryther & Dunstan, 1971). Recent evidence suggests that this generalization also applies to seaweeds since fluctuations in ambient inorganic nitrogen can result in corresponding fluctuations of tissue nitrogen and growth rate (LaPointe & Ryther, 1979; Topinka & Robbins, 1976). Along the Atlantic coast of Nova Scotia, nitrogen has been shown to limit the growth

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of the red seaweeds *Chondrus crispus* (Neish *et al.*, 1977) and *Palmaria palmata* (Morgan *et al.*, 1980) as well as that of the kelp *Laminaria longicruris* (Chapman & Craigie, 1977).

The coastal waters in the vicinity of St. Margaret's Bay, Nova Scotia, show a seasonal variation in inorganic N-nutrient concentration, with a maximum of ≈ 6 μg-at. NO_3^--N $\cdot l^{-1}$ in winter and a minimum of ≈ 1 μg-at. N $\cdot l^{-1}$ (mostly as NH_4^+) in the spring–summer months (Chapman & Craigie, 1977). This presumably reflects the pattern of N-nutrient availability, although this assessment also depends on the (unknown) rates of nutrient supply from marine and terrestrial sources. Many perennial seaweeds are able to mitigate spring–summer N-nutrient limitation by utilizing tissue nitrogen reserves accumulated during the winter when nitrate is readily available. Chapman & Craigie (1977) have shown that *L. longicruris* growing in St. Margaret's Bay is able to draw on this tissue reserve in order to sustain high growth rates into the summer months. A similar seasonal variation in tissue nitrogen (maximum in winter, minimum in summer) has been observed in the red seaweed *Chondrus crispus* (Laycock *et al.*, 1981), suggesting that nitrogen reserves in this species may also serve to reduce the impact of seasonal nitrogen limitation.

This is not, however, possible for all seaweeds. A number of spring–summer annuals appear as macrothalli during periods when ambient inorganic nitrogen approaches undetectable levels. Consequently, they are unable to draw upon nitrogen reserves accumulated in the winter. Despite this, many of these species exhibit rapid growth rates and attain significant standing crops.

In Nova Scotian waters, the period of severe nitrogen limitation may only be relieved for brief periods by N-nutrient peaks associated with storms (Probyn, 1982), offshore upwelling (Garrett & Loucks, 1976), or excretion by epifauna (Probyn, 1982). Collectively, these N-enrichment events embrace a wide range of environmental scales in both space (cm^3 to km^3) and time (seconds to days). In the laboratory, transient additions of the limiting N-nutrient to diatoms grown in continuous culture have been shown to cause a short-term uncoupling between uptake and growth (Eppley & Renger, 1974; McCarthy & Goldman, 1979). Over the ensuing interval, the algal cells were able to assimilate the limiting nutrient (NH_4^+ or NO_3^-) at rates greatly exceeding the nitrogen requirement for growth. This difference was greatest in N-depleted cells and provides a short-term counterpart to the seasonal nitrogen reserve accumulated by perennial seaweeds. These observations led Conway & Harrison (1977) to propose that species with a greater potential for such "surge" uptake would be at a competitive advantage in an environment where the limiting nutrient became available on a sporadic basis.

The foregoing considerations gave rise to two possible explanations for the rapid growth rates realized by summer annuals under conditions of low to undetectable ambient nitrogen concentrations. First, these species may be more efficient at steady-state nutrient uptake than perennial seaweeds. This would involve adjusting the values of the steady-state kinetic conditions for uptake and growth (high maximum rates, low half-saturation constants). An alternative, but not mutually exclusive hypothesis, is that the summer annuals may be better adapted to take advantage of transient peaks in

nutrient availability than the perennials. This would involve an enhanced potential for surge uptake under N-limitation relative to the perennials.

The object of this study was to test these two hypotheses using the brown seaweeds *Fucus distichus* Linnaeus subsp. *edentatus* (de la Pylaie) Powell (= *Fucus evanescens* C. Agardh; Rice, 1983) as a representative perennial and *Chordaria flagelliformis* (O. F. Mueller) C. Agardh as a representative summer annual. Both species occur as macroscopic diploid plants in the lower intertidal to upper subtidal zone in moderately exposed locations along the open coastline of Nova Scotia. The bilaterally branched, flattened fronds of *Fucus distichus* have a distinct midrib and are organized into three cellular layers. Individual plants persist throughout the winter when they are subject to freezing temperatures and ice cover at low tide. *Chordaria flagelliformis* is somewhat smaller and consists of a finely branched cylindrical axis organized into two cellular layers. This species first appears in April, after the spring phytoplankton bloom has depleted the ambient sea water of inorganic nitrogen (Probyn & Chapman, 1983). Growth rates reach a peak from May to July, although, by the autumn to early winter, the plants have virtually disappeared (Probyn & Chapman, 1983).

Materials and Methods

CONTINUOUS-FLOW CULTURE SYSTEM

Seaweeds for experimental use were collected from the lower rocky intertidal zone of Fink (= Sandy) Cove (44°28′N : 63°33.4′W) near St. Margaret's Bay, Nova Scotia. In winter (December), only *Fucus distichus* subsp. *edentatus* was collected since *Chordaria flagelliformis* macrothalli were not present. Summer (June and July) collections included both species. Individual thalli of *C. flagelliformis* and apical segments of *Fucus distichus* weighing ≈ 1 g fresh wt per piece were cultured in a modified version of the continuous-flow culture system illustrated in Enright (1979). The culture chambers consisted of PVC pipes (28.4 cm I.D., 30.4 cm O.D.) sectioned longitudinally and divided by 3-mm thick Plexiglas partitions into 21-cm long compartments each of capacity 4.6 l. Mixing was provided by compressed air which entered along the bottom through small holes drilled in an airline consisting of a half-section of 2.5-cm diameter PVC pipe cemented to the outside bottom of the tank. Each compartment also had a non-clogging overflow drain.

The growth chambers were located in a glass greenhouse at the National Research Council of Canada Seaweed Experimental Station, Sandy Cove. Ambient sea water was pumped from the cove and filtered to 1 μm before flowing into a holding tank (equipped with an overflow) located adjacent to the culture chambers. The flow of sea water from the holding tank to the culture chambers at a rate of ≈ 2000 ml $\cdot$ h^{-1} (flushing rate = 10.8 chamber-volumes per day) was regulated by a high-volume peristaltic pump (Cole-Parmer Instrument Co. Masterflex). Autoclaved nutrient media containing a fixed amount of P (as $NaH_2PO_4 \cdot H_2O$) and variable N (as NH_4Cl) in deionized water were supplied continuously to the appropriate compartments from 20-l plastic carboys, via

a low-volume peristaltic pump, at a rate of ≈ 1 ml $\cdot$ min^{-1}. This yielded inflow concentrations in the compartments of 5 μg-at. PO_4^{3-}-P $\cdot l^{-1}$ and 0–21 μg-at. NH_4^+-N $\cdot l^{-1}$ (winter experiment) or 0–72 μg-at. NH_4^+-N $\cdot l^{-1}$ (summer experiments), in addition to background nutrient levels (negligible in the summer, ≈ 6 μg-at. NO_3^--N $\cdot l^{-1}$ in the winter).

In the greenhouse, the seaweeds were exposed to natural daylight. Water temperature was monitored using a Peabody-Ryan Model D-15 bathythermograph which was placed in a compartment by itself. In the winter, the temperature ranged from 8–10 °C with little diel variation. In the summer, the culture chambers were cooled by partial immersion in large rectangular fibreglass tanks provided with a separate recirculating flow of refrigerated water. Summer temperatures ranged from 13 °C at night to 18 °C during the day, which is within the range the plants would experience in the field at this time of year (Probyn & Chapman, 1983).

NUTRIENT UPTAKE AND GROWTH IN CONTINUOUS CULTURE

Each culture compartment was stocked with nine individual thalli of either species. These experimental plants were initially acclimated by providing only non-N-enriched (ambient) sea water to the chambers. Following this treatment, the plants were supplied with enriched sea water and residual inorganic N concentrations in the culture compartments were monitored on a daily basis. The initial decline in residual N concentration was rapid, followed by a very slow decline as the plants approached steady state (within 1 to 2 days). Higher residual N concentrations corresponded to increased N-loading (= concentration $\times$ flow rate $\div$ plant biomass). A true steady state could not be obtained using this system since there was no "washout" of plant biomass as in a chemostat.

The uptake rate, V, in continuous culture was determined from the following equation (modified from Rhee, 1980):

$$V = \frac{f(S_i - S)}{w}, \tag{1}$$

where f = flow rate ($l \cdot h^{-1}$), w = weight of seaweed (g), and S_i and S are the inflow and residual inorganic N concentrations (μg-at. N $\cdot l^{-1}$), respectively.

Water samples for nutrient analysis were filtered (Gelman GF/C, 1.2 μm pore size) and either frozen at -18 °C (nitrate samples) or analysed immediately (ammonium samples; DeGobbis, 1973). Ammonium was measured using the phenol hypochlorite method (Koroleff, 1970). Nitrate was determined according to the method of Strickland & Parsons (1960). The figures for nitrate include very low to negligible levels of nitrite.

Since the V vs. S plots fitted a rectangular hyperbola, the Michaelis–Menten kinetic parameters V_{max} (maximum uptake rate) and K_m (half-saturation constant for uptake) were determined using an iterative, non-linear curve-fitting programme (Bliss & James, 1966). This programme also provided 95% confidence intervals (95% C.I.).

Growth rates were measured over 4-day intervals after the plants had been exposed to enriched sea water for at least 5 days. Individuals of *F. distichus* were recognized by punching small holes near the base of each plant. Growth rates of *Chordaria flagelliformis* were calculated from biomass increments for pairs of plants: the largest at time 0 paired with the largest at time t; the second largest at time 0 paired with the second largest at time t, etc. (Probyn & Chapman, 1983).

Specific growth rates, μ (in units of day^{-1}), were then calculated as:

$$\mu = \frac{\ln (w_t/w_0)}{t}, \tag{2}$$

(Hunt, 1978) where w_0 is the initial individual biomass (blotted fresh weight) and w_t is the biomass at t = 4 days. As for nutrient uptake, the plots of μ vs. S fitted a rectangular hyperbola. The Monod kinetic parameters μ_{max} (maximum growth rate) and K_s (half-saturation constant for growth) were calculated as before using the curve-fitting programme.

Experiments were run for at least 9 days in enriched sea water. At the conclusion of this period, the seaweeds were removed from continuous culture and reweighed. Some individuals were used for dry weight determinations while others were placed in plastic Whirlpak bags and stored frozen at − 18 °C for subsequent tissue analysis. Samples for CHN analysis (n = 3) were placed in serum bottles and lyophilized. The individual plants were then ground to a fine powder in a ball mill and stored in a desiccator. Total carbon and nitrogen were determined on a Perkin-Elmer Model 240B Elemental Analyzer. Dry weights (n = 5) were determined after desiccation for 3 days at 60 °C and storage in a desiccator at room temperature for 1 day.

In summer, the growth rate could be expressed as a hyperbolic function of the internal N content of the seaweeds according to the threshold equation of Droop (1968):

$$\mu = \frac{\mu_m (Q - q_0)}{Q}, \tag{3}$$

where Q = thallus nutrient quota (% N by dry wt) and μ_m = maximum growth rate. A μQ vs. Q linear transformation of this expression was used to estimate q_0, the subsistence quota (the value of Q when μ = 0). μ_m in the Droop formulation differs from μ_{max} in the Monod expression in that μ_m represents the maximum growth rate at infinite internal N whereas μ_{max} represents the maximum growth rate at infinite external N.

RESPONSE TO A SINGLE ADDITION OF AMMONIUM

At the conclusion of the summer experiments, individual plants weighing ≈200 mg dry wt were removed from continuous culture, blotted, and placed in glass beakers containing 1 litre of filtered (Gelman GF/C) sea water which had been spiked to different initial concentrations (5, 10, 20, 40, or 80 μg-at. NH_4^+-N · l^{-1}) with NH_4Cl. Mixing was provided by magnetic stir bars which were separated from the experimental

plants by a fibreglass screen at the bottom of each beaker. A standard mixing rate was obtained by using six-place magnetic stirring units (Lab-Line Instruments, Inc. Multi-Magnestir).

All incubations were carried out at 15 °C under 175 $\mu E \cdot m^{-2} \cdot s^{-1}$ (measured with a Li-Cor Model LI-185 quantum light sensor) provided by a bank of four "cool-white" fluorescent tubes (Sylvania F48T12-CW-VHO). It is not known whether inorganic N uptake was saturated at this irradiance, although Hanisak & Harlin (1978) reported saturation of ammonium uptake by the green seaweed *Codium fragile* subsp. *tomentosoides* at only 7 $\mu E \cdot m^{-2} \cdot s^{-1}$.

Uptake was monitored as the disappearance of ammonium in water samples taken at 0, 15, and 30 min. Ammonium concentrations and seaweed dry weights were determined as described above. Uptake rates expressed as μg-at. $N \cdot h^{-1} \cdot g$ dry wt^{-1} were normalized to the internal N content to obtain specific uptake rates in units of h^{-1}. The concentration of dissolved inorganic N in the unspiked sea water was negligible. No change in inorganic N concentration was observed in the absence of thalli.

RESULTS

NUTRIENT UPTAKE AND GROWTH IN CONTINUOUS GREENHOUSE CULTURES: WINTER EXPERIMENT

In winter, background levels of NO_3^- in the ambient sea water were ≈ 6 μg-at.NO_3^--$N \cdot l^{-1}$. Nitrate uptake rates of *Fucus distichus* remained constant at ≈ 0.7 μmol

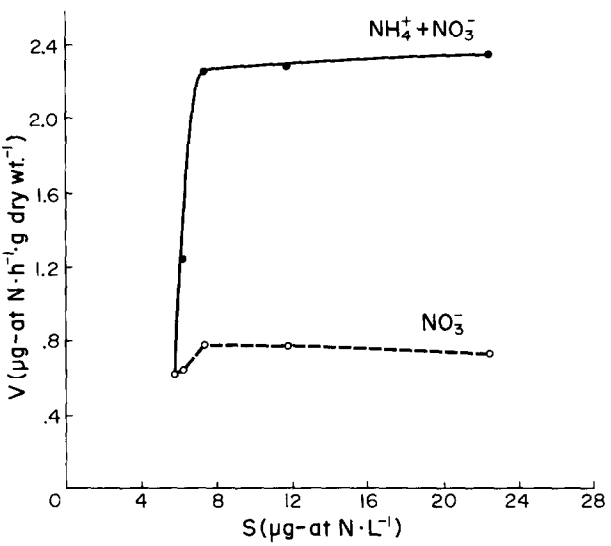

Fig. 1. Winter (December) uptake rates (V) of inorganic nitrogen by *Fucus distichus* in continuous greenhouse cultures over a range of residual inorganic N concentrations (S): ○, NO_3^- uptake; ●, total inorganic N (NO_3^- + NH_4^+) uptake; curves were fitted by eye.

$NO_3^- \cdot h^{-1} \cdot g$ dry wt^{-1} over a range of added ammonium loading (Fig. 1). Ammonium uptake reached saturating rates of ≈ 1.6 μmol $NH_4^+ \cdot h^{-1} \cdot g$ dry wt^{-1} (Fig. 1) at a residual inorganic N concentration of 7.33 μg-at.$N \cdot l^{-1}$ (2.48 μg-at. NH_4^+ -$N \cdot l^{-1}$ + 4.85 μg-at. NO_3^--$N \cdot l^{-1}$). No attempt was made to fit the ammonium uptake data to the Michaelis–Menten expression due to the simultaneous presence of background nitrate. The maximum total inorganic N uptake rate measured in culture was 2.34 μg-at. $N \cdot h^{-1} \cdot g$ dry wt^{-1} at saturation (Fig. 1).

Despite higher uptake rates with increased ammonium loading, the growth rate of *F. distichus* remained constant at $\approx 0.01 \cdot day^{-1}$ (Table I). Thus, in winter, growth in the continuous cultures was not limited by N availability. With increased ammonium loading, the plants accumulated N in the thallus, resulting in a decrease in the C : N ratio (Table I). Although the N content did not reach saturation, measured thallus N quotas varied from 1.34 to 2.18% N (Table I).

TABLE I

Winter (December) N-loading (background NO_3^- + added NH_4^+), specific growth rates (μ, mean values ± 95% C.I.), N content (dry weight basis; mean values ± SD, $n = 3$), and C:N ratios (by weight; mean values ± SD, $n = 3$) for *Fucus distichus* in continuous greenhouse cultures.

N loading (μg-at. $N \cdot h^{-1} \cdot g$ dry wt^{-1})	μ (day^{-1})	% N	C:N
3.2	0.010 ± 0.003	1.34 ± 0.05	26.1 ± 0.9
4.2	0.008 ± 0.001	1.69 ± 0.02	20.9 ± 0.3
6.2	0.008 ± 0.002	1.98 ± 0.17	17.4 ± 1.9
8.1	0.009 ± 0.002	1.84 ± 0.10	19.3 ± 1.2
13.6	0.010 ± 0.002	2.18 ± 0.20	16.0 ± 1.9

UPTAKE AND GROWTH IN CONTINUOUS GREENHOUSE CULTURES: SUMMER EXPERIMENTS

In summer, ammonium loading was increased in order to compensate for higher expected growth rates (Table II). Uptake and growth rates were measured in separate experiments in June and July, respectively, well after background nitrate concentrations had dropped to low summer levels. Growth rates in both species were higher with increased N-loading (Fig. 2). Thus, in contrast to the winter experiment, growth in continuous cultures in the summer was responsive to added N.

The July growth data for both species (Fig. 2) gave a good fit to a rectangular hyperbola (Table III). μ_{max} for *Chordaria flagelliformis* was higher than μ_{max} for *Fucus distichus* (Table III, $P < 0.05$). This difference would have been even more pronounced if entire *F. distichus* thalli had been used instead of apical segments. Trimming the plants in this manner effectively increased the proportion of meristematic to non-meristematic tissue, resulting in higher specific growth rates. The K_s values for the two species were not significantly different (Table III, $P > 0.05$).

TABLE II

N-loading (added NH_4^+, negligible background N) for two summer experiments with *Chordaria flagelliformis* and *Fucus distichus* grown in continuous greenhouse cultures.

N loading (μg-at. $N \cdot h^{-1} \cdot g$ dry wt^{-1})			
June		July	
Chordaria	*Fucus*	*Chordaria*	*Fucus*
2.7	2.5	0.8	1.6
6.2	4.0	2.2	5.5
7.7	5.6	7.8	10.3
20.2	19.5	15.3	24.9
24.5	36.9	37.7	41.9
43.3	47.7	68.9	81.2

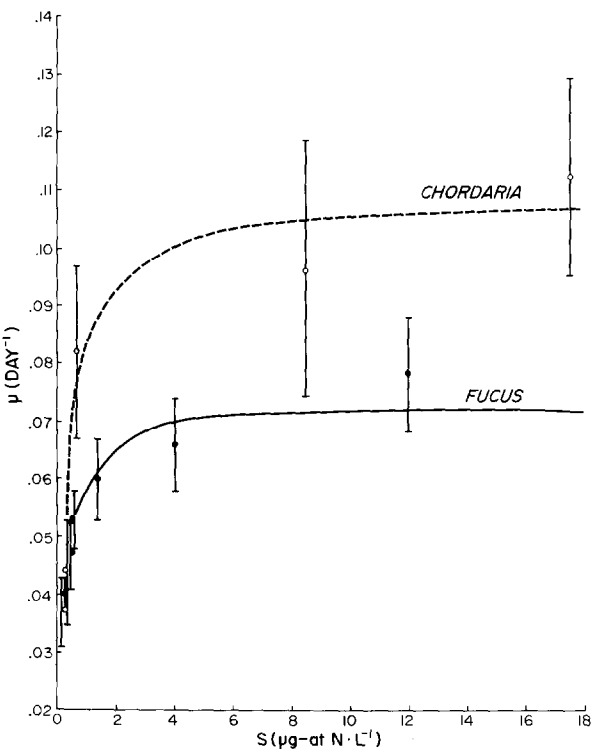

Fig. 2. Specific growth rates (μ, mean values ± 95% C.I.) in the summer (July) for *Chordaria flagelliformis* and *Fucus distichus* in continuous greenhouse cultures over a range of residual ammonium concentrations (S): curves were fitted using the Monod expression; ○, *C. flagelliformis*; ●, *F. distichus*.

TABLE III

Calculated kinetic parameters for growth by ammonium-limited *Chordaria flagelliformis* and *Fucus distichus* in continuous greenhouse cultures: figures in parentheses represent 95% C.I.

Species	μ_{max} (day^{-1})	K_s ($\mu M\ NH_4^+$)	μ_{max}/K_s
C. flagelliformis	0.109 (0.091–0.126)	0.31 (0.13–0.54)	0.35 (0.19–0.78)
F. distichus	0.074 (0.067–0.081)	0.24 (0.15–0.36)	0.30 (0.20–0.48)

Healey (1980) has argued that the initial slope of the μ vs. S curve is the best index for comparing the nutrient use efficiency of species at low ambient nutrient concentrations. For data described by the Monod expression, the initial slope is equal to μ_{max}/K_s. Although the calculated initial slope of the μ vs. S curve was slightly higher for *Chordaria flagelliformis* than for *Fucus distichus*, this difference was not significant (Table III, $P > 0.05$).

The June ammonium uptake data for plants grown in continuous cultures (Fig. 3) fitted the Michaelis–Menten expression (Table IV). As for μ_{max}, V_{max} for *Chordaria flagelliformis* exceeded V_{max} for *Fucus distichus* (Table IV; Student's t-test, $P < 0.01$). Maximum measured uptake rates (NH_4^+ only) of *F. distichus* in the summer exceeded

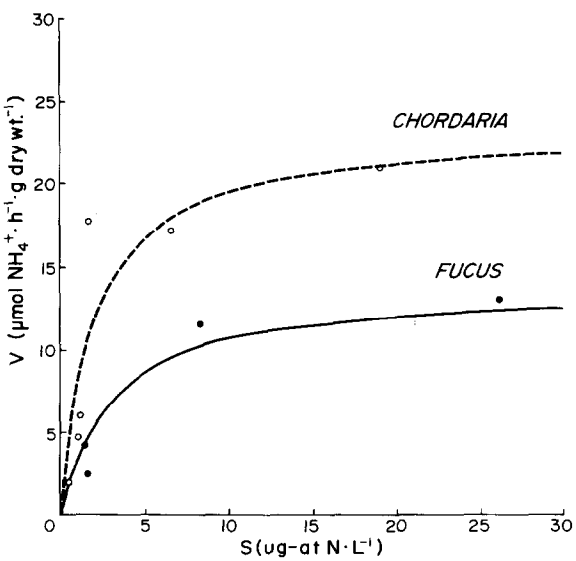

Fig. 3. Summer (June) ammonium uptake rates (V) in *Chordaria flagelliformis* and *Fucus distichus* in continuous greenhouse cultures over a range of residual ammonium concentrations (S): curves were fitted using the Michaelis-Menten expression; ○, *C. flagelliformis*; ●, *F. distichus*.

TABLE IV

Calculated kinetic parameters for ammonium uptake by *Chordaria flagelliformis* and *Fucus distichus* in continuous greenhouse cultures: figures in parentheses represent 95% C.I.

Species	V_{max} (μmol $NH_4^+ \cdot h^{-1} \cdot$ g dry wt^{-1})	K_m (μM NH_4^+)	V_{max}/K_m
C. flagelliformis	23.2 (13.0–33.3)	1.86 (0.01–5.81)	12.4 (1.3–89.5)
F. distichus	13.9 (10.0–17.8)	3.61 (0.23–8.81)	3.8 (1.2–22.9)

the maximum uptake rate ($NO_3^- + NH_4^+$) of winter plants by a factor of six (cf. Figs. 1 and 3). *Chordaria flagelliformis* also showed a lower value for K_m and a higher initial slope than *Fucus distichus* (Table IV). These differences were, however, not significant due to the scatter of the data points at residual ammonium concentrations of < 1.7 μM (Fig. 3, Table IV). Growth and thallus N contents were not determined for the June experiment due to a breakdown in the temperature control system.

In both species, the half-saturation constants for growth (K_s) were less than the half-saturation constants for uptake (K_m). This is in agreement with the phytoplankton chemostat theory (Droop, 1973). Part of this difference may also have been due to the growth of epiphytic diatoms on the walls of the culture chambers by the time of the last seaweed growth measurement.

As in the winter experiment, the tissue N content (thallus N quota) was higher in both species at increased N-loading, resulting in a decrease in the C : N ratio (Table V). The range in % N was somewhat greater in *Chordaria flagelliformis* (0.82–4.02% N) than in *Fucus distichus* (1.05–2.87% N, Table V), although saturation of the tissue N contents in continuous cultures was not observed (Fig. 4). The increase in tissue N was

TABLE V

Per cent N (by dry weight), C:N ratios (by weight), and dry weight (as a percentage of fresh weight) for *Chordaria flagelliformis* and *Fucus distichus* grown in continuous greenhouse cultures: % N and C:N are mean values ± SD ($n = 3$); % dry weight are mean values ± 95% C.I. ($n = 5$).

C. flagelliformis			*F. distichus*		
% N	C:N	% dry wt	% N	C:N	% dry wt
0.82 ± 0.10	42.2 ± 6.1	20.7 ± 1.1	1.05 ± 0.13	34.5 ± 3.7	20.3 ± 0.8
1.17 ± 0.09	29.3 ± 2.7	19.8 ± 1.1	1.11 ± 0.09	31.9 ± 1.8	22.0 ± 2.2
1.63 ± 0.25	22.5 ± 3.4	20.8 ± 1.3	1.32 ± 0.14	28.2 ± 2.8	22.0 ± 1.2
3.18 ± 0.21	11.8 ± 0.9	19.0 ± 1.9	2.06 ± 0.27	18.1 ± 2.2	20.2 ± 1.8
3.24 ± 0.26	11.4 ± 0.3	18.0 ± 1.0	2.47 ± 0.18	15.3 ± 0.8	19.7 ± 2.0
4.02 ± 0.27	9.1 ± 0.6	17.6 ± 1.8	2.87 ± 0.17	13.3 ± 0.9	17.6 ± 0.6

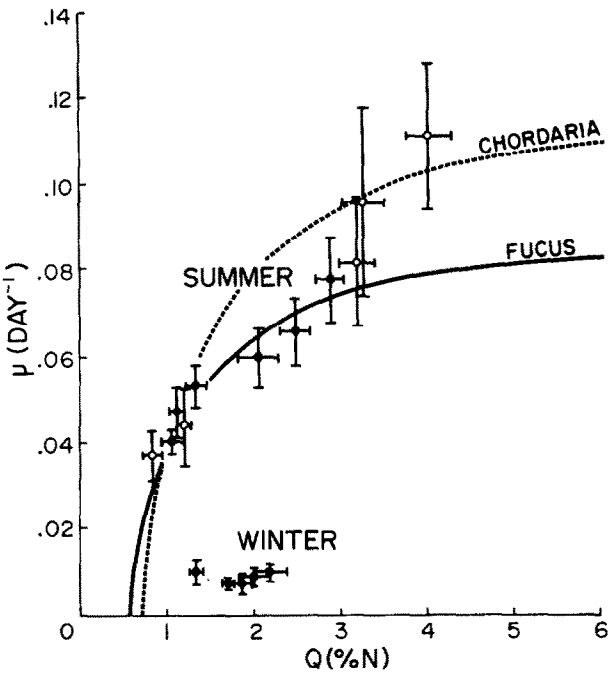

Fig. 4. Specific growth rates (μ) as a function of thallus N quota (Q) for *Chordaria flagelliformis* and *Fucus distichus* in continuous greenhouse cultures: winter (December) and summer (July) experiments; curves for summer experiments were fitted using the Droop expression; μ, mean values ± 95% C.I.; Q, mean values ± SD (n = 3); ●, *F. distichus*; ○, *C. flagelliformis* (summer only).

accompanied by a decrease in the tissue density, as per cent dry wt (Table V; $r^2 = 0.83$, $P < 0.01$ for *Chordaria flagelliformis*; $r^2 = 0.72$, $P < 0.05$ for *Fucus distichus*). In *F. distichus*, the specific growth rate was an increasing function of the thallus N quota in summer, but not in winter (Fig. 4).

The plots of μ vs. Q gave a good fit to the Droop equation (Fig. 4; $r^2 = 0.96$ for the μQ vs. Q linear transformation). The calculated N subsistence quotas were similar in the two species: 0.7% N in *Chordaria flagelliformis* and 0.6% N in *Fucus distichus* (Fig. 4). In both cases, the calculated values of μ_m, the maximum growth rate at infinite internal N, were somewhat higher than μ_{max} (Table III), the maximum growth rate at infinite external N (0.125 compared with $0.109 \cdot day^{-1}$ for *Chordaria flagelliformis*, 0.092 compared with $0.074 \cdot day^{-1}$ for *Fucus distichus*; cf. Figs. 2 and 4). Since the growth rate in continuous culture cannot be greater than μ_{max}, μ_m must be regarded as more of an abstraction than μ_{max} (Droop, 1973).

COMPARISON WITH FIELD-COLLECTED PLANTS

The calculated N subsistence quotas may be compared with the thallus N quotas in plants which were collected in August in the rocky intertidal zone. Field-collected

Chordaria flagelliformis had ≈2.2% N (Probyn & Chapman, 1983) while *Fucus distichus* had 1.2 ± 0.2% N (mean value ± 95% C.I., n = 9). For both species, these N contents were well above the calculated subsistence quotas, but still within the range of N limitation in culture, as indicated by the plots of μ vs. Q in Fig. 4. The lower N content in field-collected *F. distichus* suggested that this species may be more N-stressed than *Chordaria flagelliformis* at this time of year. The N content and C:N ratios of *Fucus distichus* did not show significant variation within three microhabitats from which it was collected, although there was a tendency for N content to increase in plants from the low intertidal zone (Table VI; one-way ANOVA, $P < 0.05$).

TABLE VI

Per cent N (by dry weight) and C:N ratios (by weight) in *Fucus distichus* collected in August from different microhabitats in the rocky intertidal zone at Cranberry Cove (44°30'N:63°55'W), near St. Margaret's Bay, Nova Scotia: mean values ± SD (n = 3).

Microhabitat	% N	C:N
Tide-pool, high intertidal	1.16 ± 0.13	34.3 ± 3.7
Tide-pool, mid-intertidal	1.01 ± 0.19	39.8 ± 9.5
Exposed, low intertidal	1.56 ± 0.24	22.2 ± 2.9

RESPONSE TO A SINGLE ADDITION OF AMMONIUM

Transient (non-steady-state) uptake rates were measured in response to single additions of ammonium up to 5, 10, 20, 40, or 80 μg-at. NH_4^+-N·l^{-1}. At 5 μg-at. NH_4^+-N·l^{-1}, the decrease in ammonium over 30 min ranged from 5–60% of the initial concentration for *Chordaria flagelliformis* and 5–25% for *Fucus distichus*, with the highest depletion percentages corresponding to thalli with the lowest N contents. Transient uptake rates at an initial concentration of 5 μg-at. NH_4^+-N·l^{-1} were a decreasing function of the thallus N quota (Q) in both species (Fig. 5). Measured uptake rates in *Chordaria flagelliformis* exceeded those in *Fucus distichus* over a range of thallus N contents (Fig. 5). This difference was observed whether the uptake rates plotted represented the highest 15-min rates or the lower 30-min rates shown in Fig. 5. For plants of both species with low N contents, the 30-min uptake rates were much higher than uptake rates measured in continuous cultures over a similar range of residual ammonium concentrations (cf. Figs. 3 and 5).

Normalizing these uptake data to the thallus N content yielded a specific rate (v_5) in units of h^{-1}. This allowed a direct comparison of uptake and growth rates in units of time^{-1}. In Fig. 6, the lower growth curves (shown as a single curve for clarity) are equivalent to the rates of ammonium uptake adequate to meet the N requirements for growth at the time the plants were removed from continuous culture. The upper uptake curves represent the transient (30-min) ammonium assimilation rates which were

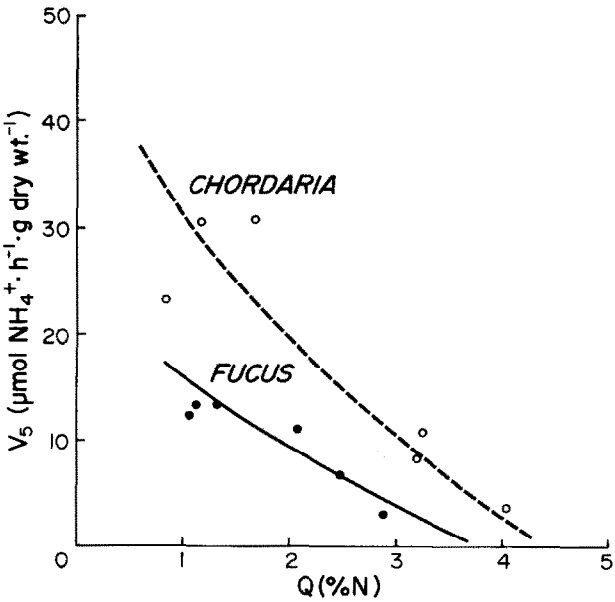

Fig. 5. Short-term (30-min) uptake rates (V_S) at an initial concentration of 5 µg-at. NH_4^+-N·l^{-1} as a function of the thallus N quota (Q) for *Chordaria flagelliformis* and *Fucus distichus*: ○, *C. flagelliformis*; ●, *F. distichus*; curves were fitted by eye.

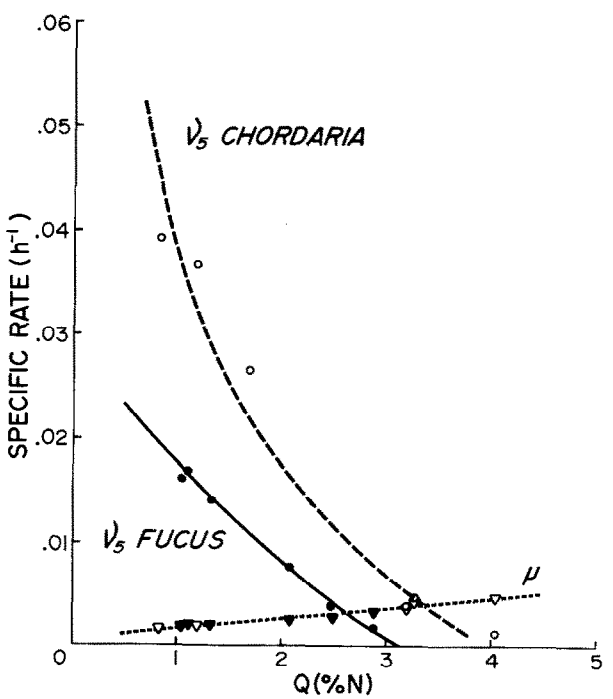

Fig. 6. Specific rates of ammonium uptake (v_S) and growth (μ) for *Chordaria flagelliformis* and *Fucus distichus* as a function of the thallus N quota (Q) attained after growth in continuous cultures: short-term (30-min) uptake data re-plotted from Fig. 5; summer growth data from continuous cultures re-plotted from Fig. 4; for clarity, only a single growth curve is shown; ○, *C. flagelliformis* uptake; ●, *F. distichus* uptake; ▽, *C. flagelliformis* growth; ▼, *F. distichus* growth; curves were fitted by eye.

actually measured. The excess of uptake over the amount required for growth represented a metabolic imbalance which was presumably accumulated as a N reserve.

As in Fig. 5, the specific uptake rates (v_5) at an initial concentration of 5 μg-at. NH_4^+-N · l^{-1} were a decreasing function of thallus N quota in both species. The higher uptake rates measured in *Chordaria flagelliformis* became even more pronounced when these data were normalized to thallus N content (cf. slopes in Figs. 5 and 6). Since the growth requirements for both species were similar when expressed in units of h^{-1} (Fig. 6), this meant that *C. flagelliformis* was able to accumulate a larger N reserve than *Fucus distichus* over the time-course of the experiment. In both species, plants with low N contents showed a correspondingly greater capability for excess ammonium consumption (Fig. 6). Thirty-min uptake in plants with very high thallus N quotas was inadequate to meet the growth requirement (Fig. 6).

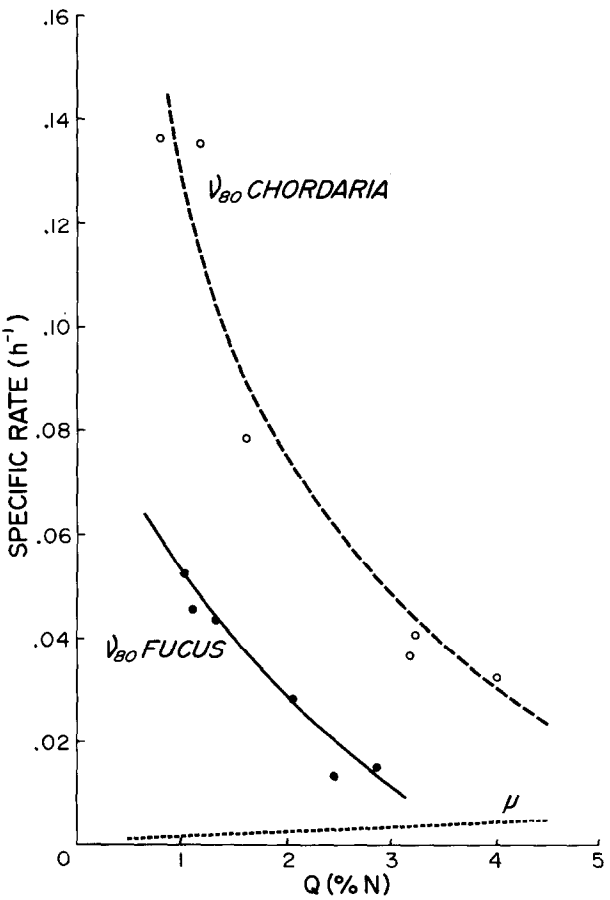

Fig. 7. Specific rates of growth (μ) and short-term (30-min) ammonium uptake (v_{80}) at an initial concentration of 80 μg-at. NH_4^+-N · l^{-1} for *Chordaria flagelliformis* and *Fucus distichus* as a function of thallus N quota (Q): growth data re-plotted from Fig. 6; see legend to Fig. 6 for further explanation.

A concentration of 5 μg-at. NH_4^+-N $\cdot l^{-1}$ represents a realistic level to which seaweeds might be exposed during a storm in the vicinity of St. Margaret's Bay (Probyn, 1982). 80 μg-at. NH_4^+-N $\cdot l^{-1}$, at the upper end of the range of initial concentrations used, is well above what the seaweeds would be exposed to in their natural environment. At this concentration, the per cent decrease in ammonium over 30 min ranged from 10–13% for *Chordaria flagelliformis* and 3–6% for *Fucus distichus*. Measured short-term uptake rates were higher than at 5 μg-at. NH_4^+-N $\cdot l^{-1}$, whether these rates were for 30 min (cf. Figs. 6 and 7) or the highest 15-min rates. The remarkable ability of *Chordaria flagelliformis* to accumulate rapidly N reserves in excess of the growth requirement was again apparent (Fig. 7). For both species, at 80 μg-at. NH_4^+-N $\cdot l^{-1}$, even the plants with the highest thallus N quotas were able to assimilate ammonium at rates exceeding the specific growth rate (Fig. 7).

When expressed in terms of μmol $NH_4^+ \cdot h^{-1} \cdot g$ dry wt^{-1}, measured 30-min uptake rates at 80 μg-at. NH_4^+-N $\cdot l^{-1}$ exceeded the V_{max} calculated from continuous cultures (Table IV) by factors of 3.4–4.8 in *C. flagelliformis* and 1.7–3.0 in *Fucus distichus*, depending on the thallus N content. Since 80 μg-at. NH_4^+-N $\cdot l^{-1}$ was insufficient to saturate short-term ammonium uptake in either species, the results at initial concentrations of 10, 20, and 40 μg-at. NH_4^+-N $\cdot l^{-1}$ were intermediate between Figs. 6 and 7 and are therefore not shown.

Discussion

During winter conditions of decreased temperature and light, growth in *F. distichus* proceeded at a slow rate. Although growth in continuous cultures was not stimulated by added ammonium (Table I), increased N-nutrient availability resulted in increased N accumulation within the thallus. The response of *F. distichus* to a given external N-loading was not a simple function of the thallus N content. Summer and winter plants with identical N contents ranging from 1.11–2.18% N exhibited different inorganic N uptake rates (cf. Figs. 1 and 3). The higher uptake rates measured in the summer may merely reflect temperature and light dependence. Topinka (1978) found a Q_{10} value (between 5 and 10 °C) of 1.8 for short-term ammonium uptake by *F. spiralis*. The six-fold increase in maximum inorganic N uptake rates between 9 °C (winter) and $\approx$ 15 °C (summer) for *F. distichus* in continuous greenhouse cultures suggests, however, that temperature dependence was not the only metabolic factor involved. The relationship between uptake rate and light intensity in *Fucus* spp. has not been investigated, although ammonium uptake in *Codium fragile* was found to saturate at intensities far less than natural daylight (Hanisak & Harlin, 1978).

Although winter growth in *Fucus distichus* was not stimulated by added N, added ammonium has been found to stimulate winter growth in the green seaweed *Ulva lactuca* L. grown in continuous greenhouse cultures under the same conditions (unpubl. data). The growth rate of *Laminaria longicruris* in St. Margaret's Bay has also been

found to increase in the winter along with nitrate levels in the ambient sea water (Chapman & Craigie, 1977).

During the winter, both *L. longicruris* and *Fucus distichus* were able to accumulate N reserves within the thallus. In the kelp, much of this reserve N was in the form of nitrate (Chapman & Craigie, 1977) whereas inorganic N is not accumulated to a significant extent in either *Fucus* spp. (Black, 1949; Macpherson & Young, 1952; Smith & Young, 1953) or *Chordaria flagelliformis* (Probyn, 1982). Almost all of the tissue N in these species is in the form of organic N.

The Droop equation (3) relating growth rate to the internal N content can be integrated over time to yield an estimate of the length of time that an alga would be capable of maintaining a positive growth rate in the absence of any external sources of N. Assuming that the subsistence quota is similar in summer and winter plants, the winter N reserves accumulated by *Fucus distichus* were sufficient to maintain steadily decreasing growth rates in excess of the winter rate of $0.01 \cdot day^{-1}$ for ≈ 25 days in plants which did not receive added ammonium, or up to 34 days in plants with the highest winter N contents measured (2.18% N). These N reserves would yield increases in biomass by factors of 2.2 and 3.7, respectively. While not sufficient to last as long as in *Laminaria longicruris* (Chapman & Craigie, 1977), these N reserves are still significant.

In the summer, the growth of both *Fucus distichus* and *Chordaria flagelliformis* in continuous cultures was strongly N-limited (Figs. 2 and 4). The range in N content in *Fucus distichus* (1.05–2.87% N) was similar to the N contents of *F. spiralis* (1.48–2.85% N) grown in ammonium-enriched outdoor continuous cultures (Topinka & Robbins, 1976). Macpherson & Young (1952) found a seasonal variation of 1.6–3.5% N in *Fucus* spp. collected in the vicinity of Halifax, Nova Scotia. For *Chordaria flagelliformis*, the range in N content (0.82–4.02% N) exceeded both the seasonal variation (May–November) in field-collected plants (2.2–3.9% N; Probyn & Chapman, 1983) and the range in N content for plants grown in ammonium-enriched outdoor continuous-flow cultures (0.9–2.8% N; Probyn, 1982). The calculated subsistence quota for ammonium-limited *C. flagelliformis* (0.7% N) was similar to the value of 0.5% N reported by Probyn & Chapman (1983). The high N contents of field-collected seaweeds, when compared with plants grown in continuous-flow cultures with no added ammonium, probably reflects the higher flushing rates of water over the plant surface in their natural environment. This results in a high rate of N-loading, even at very low ambient concentrations.

Probyn & Chapman (1983) reported saturation of summer growth of *C. flagelliformis* at a thallus quota of 1.5% N. In the present study, growth failed to saturate even at an N content of 4.02%, suggesting N limitation over the entire range of ammonium loading in culture. Direct comparisons between the two studies may be somewhat misleading since Probyn & Chapman (1983) used a different continuous-flow culture apparatus and a much higher flow rate ($2000 \text{ ml} \cdot \text{min}^{-1}$ or 144 culture volumes per day compared with $2000 \text{ ml} \cdot \text{h}^{-1}$ or 10.8 culture volumes per day in the present study). The resulting range in ammonium loading exceeded that in the present study by over an order of magnitude.

Such high flow rates are more representative of the conditions the plants would experience in the natural environment. The use of the present results as a criterion for the existence of N-limitation in natural populations of *C. flagelliformis* or *Fucus distichus* must therefore be viewed cautiously. *Macrocystis pyrifera* grown in continuous-flow laboratory cultures also failed to show saturation of growth up to a thallus N quota of 3.35% (Wheeler & North, 1980).

The ability to accumulate N reserves is not restricted to perennial seaweeds. In summer plants of *Fucus distichus*, tissue N in excess of the subsistence quota was sufficient to maintain growth rates in excess of $0.01 \cdot day^{-1}$ for ≈ 20 days in plants which received no added ammonium, or up to 37 days in N-enriched plants. In terms of biomass, this would yield increases by factors of 1.8 in unenriched plants, or up to 4.8 in N-enriched plants. With no added ammonium, the N accumulated by *Chordaria flagelliformis* was only sufficient to maintain growth rates above $0.01 \cdot day^{-1}$ for 4 days, while N-enriched plants could accumulate sufficient reserves to grow for up to a month (equivalent to a biomass increment by factors of 1.1–5.6). Thus both *Fucus distichus* and *Chordaria flagelliformis* showed similar capacities for N storage with ammonium enrichment. The high growth rates realized by *C. flagelliformis*, together with the limited size of the N reserve in plants which did not receive added ammonium, emphasize the importance of efficient N-nutrient uptake in this species.

The μ_{max} for *C. flagelliformis* ($0.109 \cdot day^{-1}$) was somewhat higher than the maximum growth rate of $0.077 \cdot day^{-1}$ reported by Probyn & Chapman (1983). This may be partly due to the fact that they carried out their study at the end of the summer, after the specific growth rate in natural populations of *C. flagelliformis* had already decreased from its May-July maximum (Probyn & Chapman, 1983). Thus, the initial physiological state of the plants used to stock their continuous-flow cultures may have differed from the present study. The calculated half-saturation constant for growth (K_s = 0.31 μM NH_4^+) was close to Probyn & Chapman's (1983) value of 0.4 μM NH_4^+. No comparable growth kinetics data are available for *Fucus distichus*.

The increased tissue density in plants which did not receive added ammonium (Table V) may reflect the accumulation of carbohydrate reserves (Chapman & Lindley, 1980). An inverse relationship between carbohydrates and tissue N has been demonstrated both in culture studies (Neish *et al.*, 1977) and in natural populations of a number of seaweeds, including *Fucus* spp. (Black, 1949; Macpherson & Young, 1952; Zavodnik, 1973). Nitrate fertilization of a kelp bed in the summer resulted in increased tissue N and growth rates while drastically reducing reserve laminarin (Chapman & Craigie, 1977).

The V_{max} for ammonium uptake by *Chordaria flagelliformis* in continuous cultures (23.2 μmol $NH_4^+ \cdot h^{-1} \cdot$ g dry wt^{-1}) was reasonably close to the value of 17.6 μmol $NH_4^+ \cdot h^{-1} \cdot$ g dry wt^{-1} reported by Probyn & Chapman (1982) for plants grown in laboratory culture. The K_m (1.86 μM NH_4^+), although higher, was not significantly different from their value of 0.6 μM NH_4^+ at the 5% level (Table IV). In this case, as well, direct comparisons are difficult since the continuous-flow apparatus used by

Probyn & Chapman (1982) was located indoors and had a comparatively low flow rate (180 ml · h^{-1} or 1.44 culture volumes per day). Other differences included temperature, light source and intensity, and the acclimation period. Topinka's (1978) ammonium uptake data for *Fucus spiralis* cannot be used for comparison with *F. distichus* since the nutrient was not supplied continuously.

By virtue of its high initial slope (= V_{max}/K_m) for N-nutrient uptake in continuous culture (Fig. 3), *Chordaria flagelliformis* is well adapted to scavenge efficiently the extremely low N-nutrient concentrations which prevail during the spring and summer. In plants which did not receive any added ammonium, this N was presumably channelled directly into rapid growth rather than being accumulated in the thallus. Consequently, unenriched *C. flagelliformis* had a N content which was closer (by a factor of 4) to the subsistence quota (cf. Table V and Fig. 4) than was the case for *Fucus distichus*. Probyn & Chapman (1983) have noted that natural populations of *Chordaria flagelliformis* accumulated considerably less reserve carbohydrate (as mannitol) than a number of other brown algae, including *Fucus* spp. (Black, 1949; Macpherson & Young, 1952) and *Laminaria longicruris* (Chapman & Craigie, 1978). As N-loading was increased, however, *Chordaria flagelliformis* could accumulate a significant N reserve in addition to increasing its growth rate. This is especially important early in the growing season of *C. flagelliformis* (Probyn & Chapman, 1983).

In both *Fucus distichus* and *Chordaria flagelliformis*, the kinetics for short-term (30 min) ammonium uptake differed markedly from the uptake kinetics for plants growing in continuous-flow cultures. Probyn & Chapman (1982), using field-collected *C. flagelliformis*, fitted their results to the Michaelis-Menten expression. Comparing these results to the "true" kinetic parameters determined in continuous-flow laboratory cultures, they concluded that the short-term experiments tended to over-estimate the K_m and V_{max} by an order of magnitude. The results of the present study (for both species) support this conclusion.

Uptake rates in excess of the rates predicted from continuous culture experiments were indicative of uncoupling between uptake and growth. This is in agreement with the earlier findings for diatoms grown in chemostats with variable N-loading (Eppley & Renger, 1974; McCarthy & Goldman, 1979). Such high uptake rates, were they to be sustained, would support growth rates greatly exceeding the μ_{max} values calculated for *Fucus distichus* and *Chordaria flagelliformis* (Table III).

Although 30-min incubations were used for purposes of comparison (Figs. 5, 6 and 7), ammonium uptake during this interval was not linear. Non-linear time-course uptake of ammonium has also been observed in phytoplankton (Goldman *et al.*, 1981). In the present study, uptake over the second 15 min frequently exceeded uptake over the first 15 min. In both species, the initial lag in uptake rates tended to occur in N-enriched plants. The highest 15-min rates actually measured were 134 μmol $NH_4^+ \cdot h^{-1} \cdot$ g dry wt^{-1} for *C. flagelliformis* (Q = 1.17% N) and 68 μmol $NH_4^+ \cdot h^{-1} \cdot$ g dry wt^{-1} for *Fucus distichus* (Q = 1.11% N). Probyn & Chapman (1982) found a V_{max} of 145 μmol $NH_4^+ \cdot h^{-1} \cdot$ g dry wt^{-1} for short-term uptake by field-collected *Chordaria flagelliformis*

($Q \geqslant 2.2\%$ N). Topinka (1978) reported a short-term V_{max} of 35 μmol $NH_4^+ \cdot h^{-1} \cdot g$ dry wt^{-1} for field-collected *Fucus spiralis* of unknown N content. Comparisons are complicated by the different thallus N quotas and incubation times involved. Transient uptake rates measured at saturation in plants with N contents approaching their subsistence quota would presumably represent the maximum capacity of the permease involved.

Short-term ammonium uptake was a decreasing function of the thallus N quota in both *F. distichus* and *Chordaria flagelliformis* (Figs. 5, 6 and 7). D'Elia & DeBoer (1978), working with the red seaweeds *Neoagardhiella baileyi* and *Gracilaria foliifera* found that short-term ammonium uptake increased with increasing C : N ratio up to a critical ratio, after which it became constant. This could be explained by feedback regulation of ammonium uptake through the build-up of some internal nitrogenous metabolite, such as amino acids (Dortch, 1982).

In addition to its ability to scavenge low ambient N-nutrient levels in continuous-flow cultures, *Chordaria flagelliformis* also demonstrated an impressive capability for short-term excess ammonium consumption (Figs. 6 and 7). This would enable *C. flagelliformis* (and, to a lesser extent, *Fucus distichus*) to sequester rapidly short-term pulses of elevated ammonium concentrations which might arise due to storms or epifaunal excretion. In this respect, it is interesting to note that the intersection of the curves for growth and specific uptake rate at an initial concentration of 5 μg-at. NH_4^+-$N \cdot l^{-1}$ (v_5; Fig. 6) occurred at thallus N quotas of $\approx 3.4\%$ N for *Chordaria flagelliformis* and 2.6% N for *Fucus distichus*. These N contents corresponded to those that would be obtained at a steady residual concentration of 5 μg-at. NH_4^+-$N \cdot l^{-1}$ (in a summer experiment; cf. Figs. 2 and 4). If, in general, the external concentration threshold for excess N-nutrient consumption corresponds to low background levels in the natural environment, then even relatively slight perturbations in nutrient concentrations could be important.

Much theoretical attention in algal ecology has recently been focused on the rôle of temporal fluctuations in limiting light and nutrients (e.g. Harris, 1980). For example, at a fixed N-loading of natural phytoplankton communities in outdoor cultures, Turpin & Harrison (1979) found that the frequency of addition of the limiting nutrient (ammonium) determined the outcome of interspecific competition. They proposed that prolonged periods of low nutrient availability would favour efficient uptake at low nutrient concentrations, while fluctuating nutrient availability would favour species with the capability for rapid short-term uptake.

With regard to the present study, *F. distichus* appears to be adapted to longer term (seasonal) fluctuations in nutrient availability. Its perennial habit and relatively slow biomass turnover rate (i.e. the number of times an individual renews its tissue in the course of a year) favour an important rôle for storage of reserve N. These N reserves can subsequently be mobilized when other conditions for growth (e.g. temperature and light) become more favourable. *Chordaria flagelliformis*, on the other hand, appears to be adapted to short-term fluctuations in nutrient availability (on a scale of minutes or hours). Its summer annual habit precludes winter N accumulation and its susceptibility

to tissue loss from wave action and scouring (Probyn, 1982) increases the likelihood of losing any previously constituted N reserves. These factors would tend to favour growth at the expense of storage under conditions of N stress. *C. flagelliformis* will, however, accumulate N reserves if N-nutrients are readily available. Their N-storage capability allows both of these seaweeds to buffer the effect of fluctuations in external N-nutrient concentrations on their growth rates over periods of days to several weeks.

While it is tempting to suggest that these considerations may be generally applicable to perennial and annual seaweeds, there is at present a paucity of comparative studies. *C. flagelliformis* and *Fucus distichus* differ with respect to a number of characteristics, in addition to their nutrient uptake and growth kinetics. These include development time (faster in *Chordaria flagelliformis*), thallus morphology (more complex in *Fucus distichus*), reproduction (sporangia distributed over the entire thallus in *Chordaria flagelliformis* compared with specialized receptacles in *Fucus distichus*), and life span (months compared with years). These category-specific morphological and physiological attributes have been elegantly summarized in a functional-form model by Littler & Littler (1980, their tables 1 and 2). They distinguished between opportunistic and persistent forms, representing the extremes along an ecological continuum. On the basis of this model, *Chordaria flagelliformis* would be placed in the opportunistic category while *Fucus distichus* would be classified as a persistent form. Opportunistic species are rapid colonizers with high photosynthetic and growth rates (Littler & Littler, 1980; Littler & Arnold, 1982). Since they are generally competitively inferior to the longer-lived perennials (Lubchenco, 1978), these species depend on efficient utilization of potentially limiting resources in order to sustain high growth and turnover rates. Thus, the scale of environmental fluctuations to which a species is adapted will be fundamental in any ecological classification of this type.

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