

## UPTAKE OF INORGANIC NITROGEN AND SEAWEED SURFACE AREA:VOLUME RATIOS

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### ABSTRACT

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Surge uptake of ammonium and nitrate by four intertidal seaweed species was examined under standard conditions (16.5 or 20°C, 72  $\mu\text{E m}^{-2} \text{s}^{-1}$ ), at both subsaturating and saturating initial nutrient concentrations. Uptake rates were positively correlated with the surface area:volume (SA:V) ratio of the thallus: *Ulva curvata* (Kützing) DeToni > *Fucus evanescens* C. Agardh  $\approx$  *Gracilaria tikvahiae* McLachlan > *Codium decorticateum* (Woodward) Howe. A positive correlation was also found for the relationship between SA:V and the initial slope of the curves of uptake rate vs. external concentration. These results support the predictions of an earlier functional-form model, and suggest the usefulness of the SA:V ratio as a comparative index of nutrient uptake capability in co-occurring seaweeds.

### INTRODUCTION

The recent identification of functional-form groups among seaweeds (Littler and Littler, 1980; Littler et al., 1983) has led to the emergence of testable general hypotheses about seaweed survival strategies. Based on a number of morphological, physiological and ecological attributes, Littler and Littler (1980, their Tables 1 and 2) distinguished between opportunistic and persistent strategies, representing the extremes along a continuum of possible strategies. Opportunistic forms were characterized by relatively simple (undifferentiated) thalli with a high surface area:volume (SA:V) ratio. Persistent forms, on the other hand, were differentiated both structurally and functionally and had a low SA:V ratio. The functional-form concept can be related to the survival strategies proposed by Grime (1979) for terrestrial plants. Accordingly, opportunistic species would correspond to terrestrial ruderals (R-strategists), whereas persistent species would include both competitive and stress-tolerant forms (C- and S-strategists, respectively, *sensu* Grime, 1979).

In view of concomitant physiological and ecological trade-offs, Littler and Littler (1980) predicted that opportunistic seaweeds should show both high net primary productivity and high rates of nutrient uptake, providing a potential for rapid growth. In contrast, persistent forms, by virtue of their investment in non-photosynthetic structural tissue, should show lower net productivity and nutrient uptake rates and, thus, slower growth. Several studies (e.g. Kanwisher, 1966; Littler, 1980) have borne out these predictions for the relationship between morphological form and photosynthetic capacity. To date, however, little comparative information is available on the relationship between morphological form and nutrient uptake rates. This study was undertaken in order to test this prediction of the Littler and Littler functional-form model for some seaweeds from the Atlantic coast of North America.

#### MATERIALS AND METHODS

The green seaweeds *Codium decorticaum* (Woodward) Howe and *Ulva curvata* (Kützting) DeToni and the red seaweed *Gracilaria tikvahiae* McLachlan (formerly identified as *G. foliifera* (Forsskål) Børgesen) were collected in December–January and April–June (1980) from the intertidal zone near Beaufort, North Carolina (34°43' N, 76°40' W). These waters are characterized by year-round low levels of available inorganic nitrogen ( $\text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+$ , annual mean = 0.82  $\mu\text{g-at. N l}^{-1}$ ; Thayer, 1974). The brown seaweed *Fucus evanescens* C. Agardh (formerly *F. distichus* Linnaeus subsp. *edentatus* (de la Pylaie) Powell) was collected in April (1982) from the intertidal zone of Cranberry Cove, on the Atlantic coast of Nova Scotia (44°30' N, 63°55' W). By this time, ambient inorganic N levels at this site had fallen from a seasonal winter maximum of > 6.0  $\mu\text{g-at. N l}^{-1}$  to low spring–summer levels of < 1.0  $\mu\text{g-at. N l}^{-1}$  (Probyn, 1982). Although the growth of algae at both sites may be seasonally limited by N availability (Thayer, 1974; Probyn, 1982), the identity of the growth-limiting resources at the time of the experiments was not determined.

The seaweeds were returned to the laboratory where apical vegetative portions of the thalli were cut with a razor blade to yield plants weighing ca. 150 mg dry weight for *U. curvata*, 250 mg for *G. tikvahiae*, 990 mg for *C. decorticaum* and 330 mg for *F. evanescens*. These plants were gently wiped with a Kimwipe and held in a flow-through seawater system (ambient seawater for Beaufort plants, low-N seawater collected the previous summer for *F. evanescens*). *U. curvata*, *G. tikvahiae* and *C. decorticaum* were used for uptake measurements the following day, whereas *F. evanescens* was held for several days (under  $105 \mu\text{E m}^{-2} \text{s}^{-1}$ ) in order to deplete its internal nitrogen reserves.

During uptake measurements, the plants were sandwiched between two pieces of  $9.0 \times 11.5$  cm wide-mesh (7 mm) plastic screening. This was done to prevent self-overlap and to hold the plants in an attached posi-

tion. The plants were suspended in glass beakers containing 1 l of filtered (Gelman GF/C, 1.2  $\mu\text{m}$  pore size) seawater which had been spiked up to the desired initial concentration with an aliquot from a concentrated stock solution of  $\text{NH}_4\text{Cl}$  or  $\text{NaNO}_3$ . The concentration of dissolved inorganic N in the unspiked seawater was negligible ( $<0.1 \mu\text{g-at. N l}^{-1}$ ). Mixing was provided by magnetic stir bars in each beaker.

All incubations were carried out between 10.00 and 16.00 h at 16.5°C (*F. evanescens*) or 20°C (all other species) under 72  $\mu\text{E m}^{-2} \text{s}^{-1}$  provided by "cool-white" fluorescent tubes (Sylvania F48T12-CW-VHO). This irradiance was above the photosynthetic light compensation point, but below saturation for all four species. It is not known whether inorganic N uptake was saturated at this irradiance, although Hanisak and Harlin (1978) reported that uptake by *Codium fragile* ssp. *tomentosoides* (van Goor) Silva saturated at 7–28  $\mu\text{E m}^{-2} \text{s}^{-1}$ , depending on the N source.

Uptake was monitored as the disappearance of ammonium or nitrate. Ammonium was determined using the phenol hypochlorite method (Solórzano, 1969), while nitrate and nitrite were analyzed according to the methods of Strickland and Parsons (1972). Incubation times were 20 or 30 min. Each uptake-rate measurement was carried out at least three, and usually six, times. No change in inorganic N concentration was observed in the absence of thalli.

Surface area:volume (SA:V) ratios were determined on at least five individuals of each species. Volumes were measured from the volume of seawater displaced in a graduated cylinder. Surface areas were determined by planimetry of traced outlines of the blotted seaweeds. Segments of *C. decorticutum* were assumed to approximate a cylinder. Seaweed dry weights were determined after desiccation for 24 h at 90°C.

## RESULTS AND DISCUSSION

Among the four species of seaweeds studied, *Ulva curvata* had the simplest thallus structure (sheetlike cellular bilayer composed entirely of photosynthetic tissue) and the highest SA:V ratio ( $165 \pm 16 \text{ cm}^2:\text{cm}^3$ ;  $\bar{x} \pm 95\%$  C.I.). Next in order of increasing morphological complexity and decreasing SA:V were *Fucus evanescens* (photosynthetic surface layer, underlain by non-photosynthetic cortex and medulla, SA:V =  $29.5 \pm 1.6 \text{ cm}^2:\text{cm}^3$ ) and *Gracilaria tikvahiae* (photosynthetic cortex surrounding a colourless parenchymatous medulla, SA:V =  $27.9 \pm 3.5 \text{ cm}^2:\text{cm}^3$ ). The difference in SA:V ratios between *F. evanescens* and *G. tikvahiae* was not statistically significant (Student's *t*-test,  $P > 0.05$ ). The species with the lowest SA:V ratio ( $8.9 \pm 0.3 \text{ cm}^2:\text{cm}^3$ ) was *Codium decorticutum*. The thallus of this species is coenocytic, comprising a surface layer of photosynthetic utricles surrounding a colourless medullary region. Both the photosynthetic capacity (Rosenberg and Ramus, 1982) and the light-saturated growth rates (Ramus and Rosenberg, 1980) of three of these species have been shown to be

correlated with the SA:V ratios: *U. curvata* > *G. tikvahiae* > *C. decortica-*  
*tum*.

The inorganic N uptake rates measured in this study represent transient responses to nutrient pulses ("surge uptake" sensu Conway et al., 1976). As such, they should be distinguished from acclimated (steady state) uptake rates measured in continuous culture (Probyn and Chapman, 1982).

Ammonium uptake rates at an initial concentration of  $10 \mu\text{M}$  ( $V_{10}^{\text{NH}_4^+}$ ) are shown in Fig. 1. This initial concentration is below saturation for all four species, and represents the highest concentration to which these seaweeds are likely to be exposed in the natural environment, either seasonally (in Nova Scotia) or during storms (in either area). Uptake rate was correlated with the SA:V ratio (Fig. 1;  $r^2 = 0.984$ ,  $P < 0.01$ ). A similar relationship between ammonium uptake rate and SA:V ratio was observed at an initial concentration of  $40 \mu\text{M}$  ( $V_{40}^{\text{NH}_4^+}$ , Fig. 2;  $r^2 = 0.963$ ,  $P < 0.05$ ). This initial concentration was above saturation for *C. decortica-*  
*tum* (Rosenberg and Paerl, 1981) and *G. tikvahiae* (Rosenberg, 1981), barely saturating for *U. curvata*, and below saturation for *F. evanescens* (unpublished data). At saturation, the maximum realizable uptake rate per unit of biomass would be expected to depend on the number of ion pump active sites and, thus, to a first approximation, on the SA:V ratio of the thallus.

Nitrate uptake rates were measured for *U. curvata* (high SA:V) and *G. tikvahiae* (lower SA:V). At an initial concentration of  $10 \mu\text{M}$  nitrate, the uptake rate of *U. curvata* exceeded that for *G. tikvahiae* (Table I).

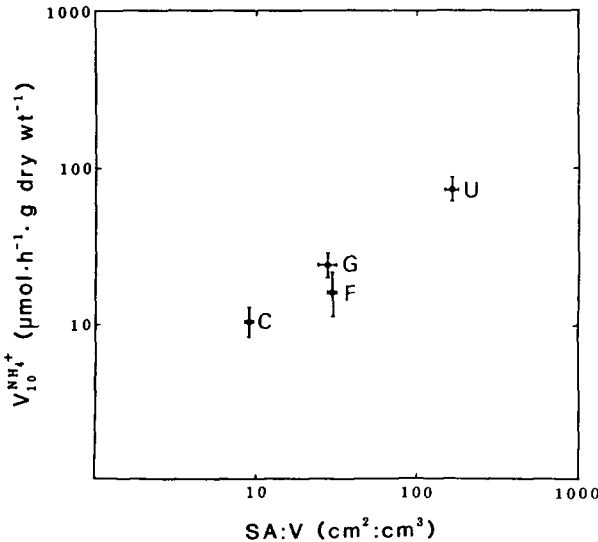


Fig. 1. Surge uptake of ammonium at an initial concentration of  $10 \mu\text{M}$  ( $V_{10}^{\text{NH}_4^+}$ ) as a function of seaweed SA:V ratios. C = *Codium decortica-*  
*tum*; G = *Gracilaria tikvahiae*; F = *Fucus evanescens*; U = *Ulva curvata*. Mean values  $\pm$  95% C.I.

A similar relationship was observed at 30  $\mu\text{M}$  nitrate (Table I), which was above saturation for both species. For both *U. curvata* and *G. tikvahiae*, uptake rates of ammonium at 10  $\mu\text{M}$  were higher than for nitrate at the same initial concentration. This probably reflects the increased energetic cost of reducing nitrate to ammonium within the cell via nitrate reductase (Syrett, 1981).

Healey (1980) has argued that the initial slope of the curve of uptake rate versus external nutrient concentration is the best index for comparing the uptake efficiency of a species at low ambient nutrient concentrations. Based on uptake rates for three species at initial ammonium concentrations  $\leq 5 \mu\text{M}$  (Rosenberg, 1981; Rosenberg and Paerl, 1981), the calculated initial slopes were 9.2  $\mu\text{mol NH}_4^+ \text{h}^{-1} \text{g dry wt.}^{-1} [\mu\text{mol NH}_4^+ \text{l}^{-1}]^{-1}$  for *U. curvata*, 2.2 for *G. tikvahiae* and 0.8 for *C. decorticum*. The ratio of these initial slopes, 11.9: 2.8: 1, was similar to the ratios of the SA:V

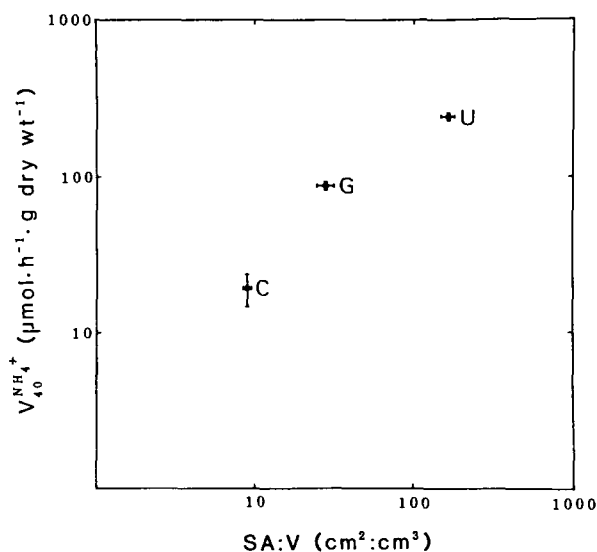


Fig. 2. Surge uptake of ammonium at an initial concentration of 40  $\mu\text{M}$  ( $V_{40}^{\text{NH}_4^+}$ ) as a function of seaweed SA:V ratios. Mean values  $\pm$  95% C.I.

TABLE I

Surge uptake of nitrate ( $\mu\text{mol NO}_3^- \text{h}^{-1} \text{g dry wt.}^{-1}$ ) at initial concentrations of 10  $\mu\text{M}$  ( $V_{10}^{\text{NO}_3^-}$ ) and 30  $\mu\text{M}$  ( $V_{30}^{\text{NO}_3^-}$ ) for *Ulva curvata* and *Gracilaria tikvahiae*. Mean values  $\pm$  95% C.I.

Species	SA:V	$V_{10}^{\text{NO}_3^-}$	$V_{30}^{\text{NO}_3^-}$
<i>U. curvata</i>	165	43.2 $\pm$ 3.7	65.4 $\pm$ 10.9
<i>G. tikvahiae</i>	27.9	3.1 $\pm$ 1.0	8.2 $\pm$ 4.2

values, 18.5: 3.1: 1 ( $r^2 = 0.998$ ,  $P < 0.05$ ). Similarly, for nitrate uptake, the initial slopes were  $7.0 \mu\text{mol NO}_3^- \text{ h}^{-1} \text{ g dry wt.}^{-1}$  [ $\mu\text{mol NO}_3^- \text{ l}^{-1}$ ] $^{-1}$  for *U. curvata* and 0.4 for *G. tikvahiae*.

Overall, the results support the predictions of the functional-form model of Littler and Littler (1980). The SA:V ratio was positively correlated with uptake rates of ammonium and nitrate and with the initial slope of the uptake curves. Similar results have been reported for phosphate uptake by several species of phytoplankton (Smith and Kalf, 1982). The only comparable data for seaweeds are those of Odum et al. (1958). They monitored uptake as the disappearance of  $^{32}\text{P}$ -phosphate from seawater in bottles containing the seaweeds. Although actual phosphate uptake rates and the external concentration required to saturate uptake were not determined, the rate of disappearance of radioactivity was found to be correlated with the calculated SA:V ratios of the thalli.

Thus, lower uptake rates seem to be associated with lower SA:V ratios and increasing structural complexity. This suggests that the development of structural complexity in persistent forms, while conferring advantages such as resistance to desiccation (Dromgoole, 1980), grazing (Littler et al., 1983) and wave action (Littler and Littler, 1980), comes at the cost of metabolically-active surface area. The importance of factors other than uptake rate is reflected in the fact that, even in nutrient-poor environments, many numerically abundant seaweed species do not have high SA:V ratios.

The usefulness of the SA:V ratio to predict the nutrient uptake efficiency of a species depends on a number of factors, including the nutrient status of the thallus, the substrate affinity of the nutrient ion pumps, the proportion of metabolically-active to total surface area, and the surrounding water motion (Gavis, 1976). For example, the tightly clumped turf morphology of certain filamentous seaweeds may result in decreased nutrient uptake rates in spite of their high SA:V ratio. This could arise due to decreased water motion and overlapping diffusion gradients within the turf unit (Littler and Arnold, 1980). The kinetics of phytoplankton nutrient uptake have been shown to differ both between similar-sized clones of a single species (Hecky and Kilham, 1974) and within a single clone, as a function of the cellular N quota (Eppley and Renger, 1974). Nevertheless, for seaweed species co-occurring in a particular habitat, the SA:V ratio appears to be a useful comparative index of nutrient uptake capability.

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