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Scaling of ammonium uptake by seaweeds to surface area:volume ratio: geographical variation and the role of uptake by passive diffusion

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ABSTRACT: Rates of ammonium uptake per g dry weight for seaweeds from the Mokohinau Islands, northeastern New Zealand were much lower than published values for northern hemisphere (east coast of North America and Baltic Sea) seaweeds. For the New Zealand seaweeds, the rate of ammonium uptake expressed per cm^2 surface area was relatively constant (23.9 ± 3.4 nmol cm^{-2} h^{-1}), irrespective of seaweed surface area:volume (SA:V) ratio. Moreover, there was a linear relationship between rates of ammonium uptake per g dry weight and ammonium concentration for 2 of the species used, *Xiphophora chondrophylla* and *Ulva* sp., which had low and high SA:V ratios, respectively. These results are consistent with most or all of ammonium uptake being due to passive diffusion of NH_3. In addition, of 3 other species investigated, *Pterocladia capillacea*, *Porphyra* sp. and *Enteromorpha* sp., only *P. capillacea* exhibited saturation kinetics.

KEY WORDS: Seaweed · Nutrient uptake · Ammonium · Diffusion · New Zealand

INTRODUCTION

Seaweed-based ecosystems are amongst the most productive on Earth (Mann et al. 1980, Leigh et al. 1987). This high productivity is particularly surprising given that some of the major nutrients (e.g. nitrogen and phosphorus) required for growth are often present at low concentrations in coastal waters (Sharp 1983, Lobban & Harrison 1994). Seaweeds acquire these nutrients through uptake across the entire surface area of the thallus. Consequently, the rate of uptake of a given nutrient should be a function of the surface area presented by the seaweed per unit of its biomass, in other words, its surface area:volume (SA:V) ratio. In general, this relationship has been observed (Rosenberg & Ramus 1984, Hein et al. 1995), with rates of uptake per unit biomass being positively correlated with SA:V ratio. However, most of this data has been compiled for the east coast of North America and the Baltic Sea, giving little impression of any geographical variation. Furthermore, the mechanistic basis (e.g. whether uptake is active and/or passive) of this compelling relationship has not been explored in any detail.

Ammonium can be taken up by an alga in 2 forms, i.e. active uptake of NH_4^+ and/or passive diffusion of NH_3 (Raven 1984, Rees 1995). For seaweeds, the dominant line of evidence for the former is saturable uptake kinetics, though a combination of saturable and linear kinetics indicates the involvement of both mechanisms (Harrison & Druehl 1982). A major reason for the apparent importance of an active uptake mechanism is the typically low concentration of ammonium in seawater (Sharp 1983). However, it should be noted that uptake of ammonium measures an ill-defined combination of active and/or passive transport at the plasma membrane and assimilation within the cell or tissue (Rees et al. 1998).

In this paper, we compare the relationship between the rate of ammonium uptake per unit biomass and SA:V ratio of seaweeds from northeastern New Zealand with that for seaweeds from the northern

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hemisphere (east coast of North America and the Baltic Sea). We then investigate the hypothesis that low observed rates of ammonium uptake in New Zealand seaweeds are due to the absence of an active uptake system for ammonium in these plants.

METHODS

Glossophora kunthii (C. Agardh) J. Agardh, *Zonaria turneriana* J Agardh (Phaeophyceae, Dictyotales), *Xiphophora chondrophylla* (Turner) Montagne ex Harvey (Phaeophyceae, Fucales), *Lessonia variegata* J. Agardh (Phaeophyceae, Laminariales), and *Ulva* sp. (Chlorophyceae, Ulvales) were collected from 1 to 5 m depth at the Mokohinau Islands, in temperate northeastern New Zealand (35° 55' S, 175° 7' E) on 9 occasions (4 to 11 wk apart) between November 1994 and December 1995. The annual range of surface seawater temperature is 14 to 21°C. Plants were transported to the laboratory submerged in a shaded fish bin and rates of ammonium uptake were determined within 6 to 8 h of collection. Water samples for nutrient analysis were taken from just below the surface adjacent to the seaweed collection site and transported on ice to the laboratory, where they were filtered (GF/F) and analysed immediately (ammonium) or after freezing (nitrate and nitrite). Nutrient concentrations were determined by established procedures for ammonium (Koroleff 1983) and nitrate and nitrite (Parsons et al. 1984). Total inorganic nitrogen (ammonium, nitrate and nitrite) ranged from 0.45 µM (January 1995) to 4.73 µM (November 1994). Ammonium ranged from 0.03 µM (December 1994) to 1.93 µM (November 1994).

Entire individual plants were incubated in perspex chambers containing 0.2 to 2 l seawater at 17.5°C and 40 µmol photons m^{-2} s^{-1} (photosynthetically active radiation), with approximately 10 (*Glossophora kunthii*), 60 (*Lessonia variegata*), 15 (*Ulva* sp.), 50 (*Xiphophora chondrophylla*) or 12 (*Zonaria turneriana*) g wet weight plant per litre seawater. The photon flux density used was sufficient to give maximum rates of ammonium uptake in the presence of 10 µM ammonium (R. B. Taylor & T. A. V Rees unpubl.). With the exception of experiments determining the effect of ammonium concentration on the rate of uptake, all rates were determined in the presence of 10 µM ammonium chloride (2 replicates per seaweed species for each determination). Water samples were taken following stirring by hand and immediately prior to addition of the plant, and at 2.5, 5, 7.5, 10, 15 and 20 min. Water was not stirred mechanically; aeration or continuous stirring had a negligible effect on rates of ammonium uptake (R. B. Taylor & T. A. V. Rees unpubl.). Dry weights (DW) of plant tissue used in the experiments were determined by drying at 80°C to constant weight. The rate of ammonium uptake for each replicate plant was calculated by taking the slope at time zero of an exponential rise curve fitted to a plot of cumulative ammonium in the plant (= disappearance from medium) versus time, as described by Taylor & Rees (in press). Seaweed surface area was determined from the weight of photocopies of subsamples; seaweed volume was determined by displacement in water, using a graduated cylinder.

We chose to measure rates of uptake in the presence of 10 µM ammonium because this was the concentration used by Rosenberg & Ramus (1984), thereby allowing direct comparison with their data. For other data from the literature, uptake rates at 10 µM were calculated from published values for K_m and V_{max} (compiled by Hein et al. 1995), using the Michaelis-Menten equation, with K_m expressed as µM and V_{max} as µmol g DW^{-1} h^{-1}. For the data from the Baltic Sea (Wallentinus 1984) only rates determined at 10°C or higher were used. Only data for seaweeds with a SA:V ratio less than 250 cm^2:1 cm^3 were used.

Rates of ammonium uptake were measured at ammonium concentrations ranging from 5 to 100 µM for *Ulva* sp. from the Mokohinau Islands (July 1995), and for *Xiphophora chondrophylla* (September 1995), *Pterocladia capillacea* (Gmelin) Bornet et Thuret (Rhodophyceae, Gelidiales) (September 1995), *Porphyra* sp. (Rhodophyceae, Bangiales) (July 1995) and *Enteromorpha* sp. (Chlorophyceae, Ulvales) (September 1995) from Goat Island, mainland northeastern New Zealand (36° 16' S, 174° 48' E), as described above, with 3 replicates per ammonium concentration.

Reduced major axis (RMA) regression (Sokal & Rohlf 1995) was used to describe relationships between SA:V ratio and uptake rate. Analysis of covariance was used to test for differences in uptake rates among regions (with SA:V ratio as the covariate). Where relationships between uptake rate and ammonium concentration were linear they were described using ordinary least squares regression, with the line constrained to pass through the origin. A Michaelis-Menten curve was fitted to non-linear relationships between uptake rate and ammonium concentration, using an iterative least squares method (SigmaPlot®).

RESULTS

There was a strong positive correlation between log SA:V ratio and log rate of ammonium uptake per g DW for the 5 New Zealand seaweeds (Fig. 1). Data from the 9 sampling periods were pooled as there were no significant differences (α = 0.05) in slopes or elevations amongst regression lines for the individual sampling

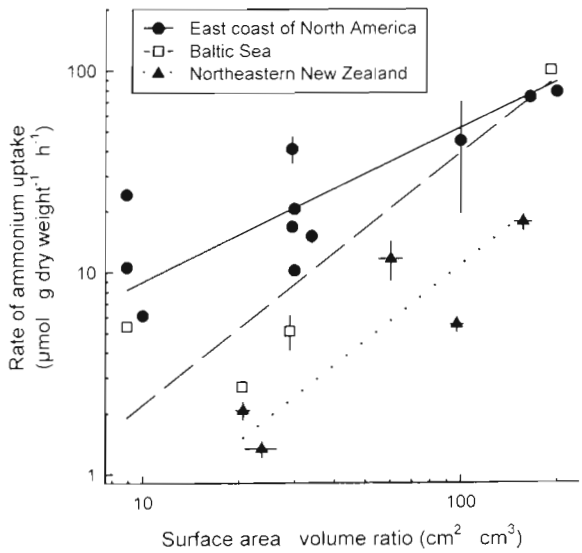

Fig. 1. Biomass-specific rate of ammonium uptake versus SA:V ratio for seaweeds from northeastern New Zealand, the east coast of North America and the Baltic Sea. Each data point corresponds to a single species. Error bars represent 1 SE. Reduced major axis regression equations and coefficients of determination are as follows. North America: $y = 1.542x^{0.765}$, $r^2 = 0.66$, $p < 0.01$; Baltic Sea: $y = 0.124x^{1.250}$, $r^2 = 0.78$, $p > 0.1$; New Zealand: $y = 0.034x^{1.253}$, $r^2 = 0.79$, $p < 0.05$

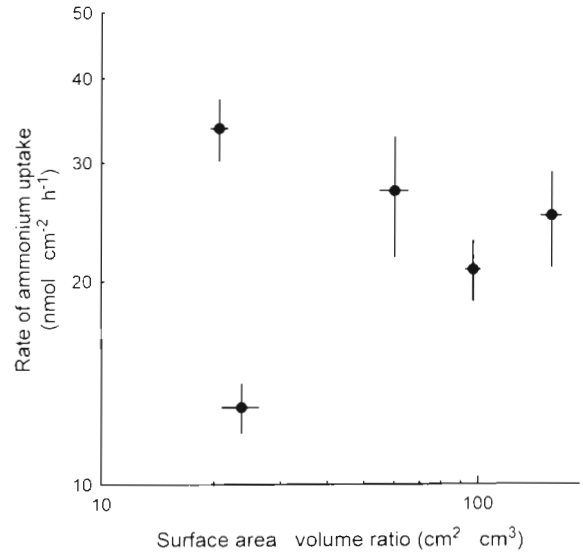

Fig. 2. Area-specific rate of ammonium uptake versus SA:V ratio for seaweeds from the Mokohinau Islands, northeastern New Zealand. Error bars represent 1 SE

periods (tests run on log-log data following Zar 1984), and plots of ammonium uptake rate versus time for each seaweed species showed no apparent seasonal trends (data not shown).

Seaweeds from the Baltic Sea and the east coast of North America also exhibited strong positive correlations between log rate of ammonium uptake per g DW and log SA:V ratio (Fig. 1). However, there were substantial differences in uptake rates among the 3 regions (Fig. 1; ANCOVA: $F = 15.53$, $p < 0.001$). Rates were highest in North America, intermediate in the Baltic, and lowest in New Zealand. Uptake rates of the New Zealand and North American seaweeds were significantly different (ANCOVA: $p = 0.0001$), but rates of the Baltic seaweeds did not differ significantly from the New Zealand or the North American seaweeds ($p > 0.05$). Uptake rates of North American seaweeds were 10.5 times higher than those for New Zealand plants at a SA:V ratio of 20 cm^2:1 cm^3, and 3.4 times higher at a SA:V ratio of 200 cm^2:1 cm^3. Uptake rates of Baltic seaweeds were 3.6 times higher than the New Zealand plants across all SA:V ratios.

Rates of ammonium uptake per cm^2 of seaweed surface showed no clear relationship to SA:V ratio for the 5 New Zealand seaweed species ($r^2 = 0.015$, $p = 0.85$) (Fig. 2). The range of variation in uptake rates per unit surface area (2.6-fold) was far lower than for the mass-specific uptake rates (13.6-fold) (Table 1). The mean rate of uptake for the 5 species was 23.9 (SE = 3.4) nmol cm^{-2} h^{-1}. One interpretation of this constancy, and the low rates of ammonium uptake (Fig. 1, Table 1), is that uptake of ammonium was due predominantly to passive diffusion of the uncharged base, NH_3. If so, for these seaweeds, the rate of ammonium uptake should be a linear function of ammonium concentration. For both *Xiphophora chondrophylla* (Fig. 3A) and *Ulva* sp. (Fig. 3B), which were the seaweeds with the lowest and highest SA:V ratios respectively (Table 1), rates of ammonium uptake were a linear function of ammonium concentration. Of the other species, *Porphyra* sp. (Fig. 3C), *Enteromorpha* sp. (Fig. 3D), and *Pterocladia capillacea* (Fig. 3E), only *P. capillacea* exhibited saturation kinetics.

Table 1. Surface area:volume ratios and rates of ammonium uptake at 10 µM for 5 seaweed species from northeastern New Zealand. Values are mean ± 1 SE. n: total number of plants sampled, usually 2 individuals per sampling period

Species	n	SA:V ratio (cm^2:cm^3)	Uptake rate (µmol g DW^{-1} h^{-1})	Uptake rate (nmol cm^{-2} h^{-1})
Glossophora kunthii	7	60.3 ± 5.3	11.6 ± 2.6	27.2 ± 5.5
Lessonia variegata	18	23.7 ± 2.6	1.3 ± 0.1	13.0 ± 1.1
Ulva sp.	18	156.8 ± 9.9	17.7 ± 1.6	25.0 ± 4.0
Xiphophora chondrophylla	18	20.7 ± 1.0	2.1 ± 0.2	33.7 ± 3.5
Zonaria turneriana	16	97.3 ± 4.4	5.5 ± 0.5	20.8 ± 2.1

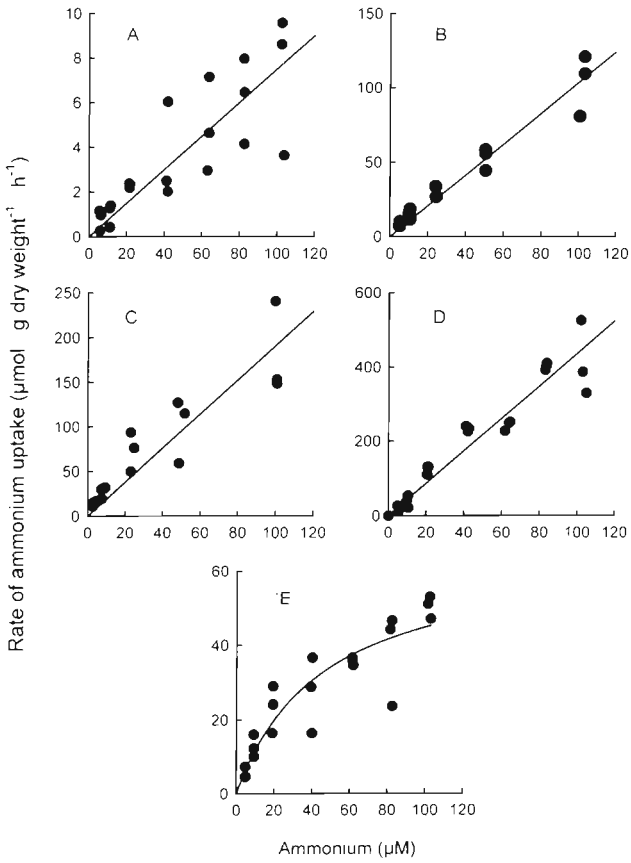

Fig. 3. Effect of ammonium concentration on rate of ammonium uptake by the northeastern New Zealand seaweeds (A) *Xiphophora chondrophylla*, (B) *Ulva* sp., (C) *Porphyra* sp., (D) *Enteromorpha* sp. and (E) *Pterocladia capillacea*. For (A) to (D), the regression line is constrained to pass through the origin. A Michaelis-Menten curve is fitted for (E), with K_m = 45 µM and V_{max} = 65 µmol g DW^{-1} h^{-1}

DISCUSSION

The low rates of ammonium uptake per g dry weight compared with seaweeds from the northern hemisphere (Fig. 1), the relatively constant rate of uptake per cm^2 of seaweed surface (Fig. 2), and the linear relationship between rate of ammonium uptake and ammonium concentration for 5 out of 6 seaweeds from northeastern New Zealand (Fig. 3) (Taylor & Rees in press) suggest that uptake was due largely to passive diffusion of NH_3. From the rate of uptake per unit surface area (6.64×10^{-8} mol m^{-2} s^{-1}) (Fig. 2), we calculate (as described in Ritchie & Gibson 1987) an apparent permeability for NH_3 of 155 µm s^{-1} (assuming pH = 8.3; pK = 9.65). This value is high compared with values for freshwater algae and cyanobacteria of about 6 µm s^{-1} (Barr et al. 1974, Ritchie 1987, Ritchie & Gibson 1987). However, values for animal membranes range from 5 to 2100 µm s^{-1} (Labotka et al. 1995, Yip & Kurtz 1995). Furthermore, any underestimate of seaweed surface area would result in an overestimate of both the rate of uptake per unit surface area and the apparent permeability. The functional surface area of our seaweeds could be greater because of the presence of hyaline hairs (see below) and/or the ratio of plasma membrane surface area:tissue surface area. The value for the latter is 8.35 in *Ulva rigida* (MacFarlane & Smith 1982); this would decrease our apparent permeability to 19 µm s^{-1}.

For some seaweeds, the relationship between uptake rate and concentration is a combination of a hyperbolic component due to active uptake and a linear diffusive component (Harrison & Druehl 1982). Examples from multiple-flask experiments include *Fucus distichus* (Thomas et al. 1985), *F. spiralis* (Topinka 1978), and *Ulva lactuca* (Pedersen 1994). These algae have SA:V ratios of 30, 34 and 400 cm^2:1 cm^3 (Hein et al. 1995), respectively. We have calculated the rate of uptake at 10 µM for the apparent diffusive component in these algae as 2.8, 2.0 and 6.8 µmol g DW^{-1} h^{-1}, respectively. These values are close to the rates of uptake for seaweeds of comparable SA:V ratios from the Mokohinau Islands (Fig. 1). From Topinka (1978), we calculate a value of 23 nmol cm^{-2} h^{-1} for the apparent diffusive component in *F. spiralis* at 15°C, which is very close to the rate of uptake (measured at 17.5°C) for the 5 seaweed species from the Mokohinau Islands (Fig. 2). The apparent diffusive component in *F. spiralis* decreases with decreasing temperature (Topinka 1978). This observation could be accounted for by a decreased membrane permeability for NH_3 with decreased temperature (Bindslev & Wright 1976, Labotka et al. 1995).

Other southern hemisphere seaweeds also have low rates of ammonium uptake. *Ecklonia radiata* from western Australia has a SA:V ratio of 27 cm^2·1 cm^3 and an uptake rate of 2.6 µmol g DW^{-1} h^{-1} with 10 µM ammonium, and the rate of uptake is a linear function of increasing ammonium concentration (Paling 1991). In addition, *E. maxima* from South Africa has an uptake rate of 2.1 µmol g DW^{-1} h^{-1} with 10 µM ammonium (Probyn & McQuaid 1985). Fucoid algae from Scotland also exhibit low rates of ammonium uptake compared with their North American counterparts (Brenchley et al. 1997). In both *Xiphophora chondrophylla* and *Ulva* sp. the rate of ammonium uptake was a linear function of ammonium concentration (Fig. 3). In contrast, most northern hemisphere seaweeds exhibit saturable or biphasic kinetics. However, there are a few exceptions, including *Gracilaria tikvahiae* (Friedlander & Dawes 1985), low-intertidal *Gracilaria pacifica* (Thomas et al. 1987), and *Laminaria groenlandica* (Harrison et al. 1986). For the 2 Pacific

seaweeds, we calculate that the rates of uptake at 10 µM ammonium are 10 µmol g DW^{-1} h^{-1} for *G. pacifica* and 0.8 to 3.2 µmol g DW^{-1} h^{-1} for *L. groenlandica*. Assuming that the SA:V ratio for *G. tikvahiae* (Hein et al. 1995) is similar to that for *G. pacifica*, the rate for *G. pacifica* is close to that for other North American seaweeds (Fig. 1). However, the rates for *L. groenlandica* are close to those we obtained for another member of the Laminariales, *Lessonia variegata* (Table 1), assuming a similar SA:V ratio.

One possible reason for the difference in rates of uptake between seaweeds with the same apparent SA:V ratios is the presence or absence of hyaline hairs (Whitton 1988). The method that we, and others, have used to measure the surface area of seaweeds is relatively coarse and would lead to an underestimate if hairs were present. For example, hairs increase the thallus surface area by 180% in *Gracilaria pacifica* and by 50% in *Gelidium vagum* (Oates & Cole 1994). Though seaweeds with hairs have been shown to possess increased rates of nutrient uptake (DeBoer & Whoriskey 1983, Hurd et al. 1993), it is unlikely that this alone would account for the discrepancy between uptake rates of plants from the Mokohinau Islands and the east coast of North America (Fig. 1). Rates of ammonium uptake by *Ceramium rubrum* are up to 2.7 times greater in plants with hairs (DeBoer & Whoriskey 1983) and rates of phosphate uptake in *Fucus spiralis* are up to 3.5 times greater in plants with hairs than those without (Hurd et al. 1993). These increases are not sufficient to account for the discrepancy in uptake rates at low SA:V ratios (Fig. 1). Moreover, local *C. rubrum* possesses hairs (our observations), as does another New Zealand seaweed, *Gelidium caulacantheum* (Dromgoole & Booth 1985).

Nitrogen-replete algae should exhibit low rates of ammonium uptake, with most or all of this uptake being due to passive diffusion of NH_3 (Rees 1995). In contrast, nitrogen-deficient algae should possess high ammonium uptake rates due, in part, to the possession of an NH_4^+ transport system (D'Elia & DeBoer 1978, Rosenberg et al. 1984, Fujita 1985, Pedersen 1994, Rees 1995, McGlathery et al. 1996). These characteristics would suggest that seaweeds from the Mokohinau Islands are nitrogen-replete, whereas those from the east coast of North America are relatively nitrogen-deficient. However, concentrations of inorganic nitrogen (ammonium, nitrate and nitrite) during the austral summer at the Mokohinau Islands were low (0.5 µM), suggesting that seaweeds collected during this period should have possessed higher rates of ammonium uptake. We found no pattern of increased rates of ammonium uptake for seaweeds collected during the austral summer (data not shown). An alternative explanation is that growth of seaweeds at the Mokohinau Islands was limited by the availability of a nutrient other than nitrogen, e.g. phosphorus (Lapointe 1987, Lobban & Harrison 1994) or iron (Matsunaga et al. 1994, Suzuki et al. 1995).

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