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The Nutritional Eco-physiology of *Chaetomorpha linum* and *Ulva rigida* in Peel Inlet, Western Australia

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Abstract

The uptake rates and critical tissue concentrations of nitrogen and phosphorus were determined for *Chaetomorpha linum* and *Ulva rigida*, the dominant algae in Peel Inlet, Western Australia. Both species had rate-saturating mechanisms of phosphate uptake described by Michaelis-Menten type functions; *C. linum* had the faster uptake rate (667 c. f. 272 μg P g dwt^{-1} h^{-1}) although *U. rigida* had a lower half-saturation value. Both species displayed linear relationships between ammonium uptake rates and substrate concentrations with *C. linum* having the greater slope (4.4 c. f. 1.7). *Chaetomorpha linum* also had a linear increase in uptake rate with increasing concentration of nitrate, but *U. rigida* showed rate-saturating kinetics; below 750 μg L^{-1}, *U. rigida* had the higher rate of uptake. *Ulva rigida* had critical tissue nitrogen and phosphorus concentrations of 20 and 0.25 mg g dwt^{-1} respectively. Corresponding concentrations for *C. linum* were 12 and 0.5 mg g dwt^{-1}. *Ulva* is frequently nitrogen limited during spring in Peel Inlet, reflecting the high nitrogen requirements of this plant compared to *Chaetomorpha* as well as the reduced ability of *Ulva* to store nutrients over winter. The growth rate of *Ulva* is negative in winter due to low salinity, temperature and irradience, and this results in negligible biomass at the time of highest inorganic nitrogen concentration. *Chaetomorpha linum* persists over winter allowing it to take advantage of elevated nutrient concentrations at the time; nutrients stored during winter support high growth rates in summer. The maximum tissue nitrogen levels recorded for *Ulva* were only 47% higher than the critical concentration while maximum tissue phosphorus concentration was almost 9 times the critical level. This seasonal limitation by nitrogen supports an earlier hypothesis that production in the system may be nitrogen limited in summer. It was concluded that differences in nutrient requirements and aquisition strategies afforded *C. linum* greater competitive potential for utilizing the seasonal and short-term increases in nutrient concentrations that occur in Peel Inlet.

Introduction

This is the second of two papers dealing with macroalgal nutrition in Peel Inlet, Western Australia. In the first (Lavery and McComb 1990), seasonal changes in tissue nutrient concentrations and the sources of macroalgal nutrition were examined. In this paper physiological aspects of the nutritional biology of *Chaetomorpha linum* Kütz. and *Ulva rigida* C. Agardh are compared, and the rates of nitrogen and phosphorus uptake and the critical tissue concentrations for nitrogen and phosphorus are reported.

The effects of eutrophication in promoting macroalgal growth have been well documented (Sawyer 1965, Waite and Mitchell 1972. Harlin and Thorne-Miller 1981, Kemp *et al.* 1983, Rosenberg 1985, Sfriso *et al.* 1987) and nutrient limitation has been proposed as a factor controlling macroalgal growth in Peel Inlet (Lukatelich and McComb 1986). In estuaries such as Peel Inlet, where nutrient input is highly seasonal, it is possible that species with the fastest rates of uptake have an advantage in utilizing periodic nutrient pulses. It has been speculated that this may account,

in part, for the dominance of *Chaetomorpha linum* in that system (Lavery 1989, Lavery *et al.* 1991). Alternatively, uptake rates may be of little importance in determining the success of different species which have different nutrient requirements or strategies of nutrient utilization, such as luxury consumption or preferences for different ionic forms of the same nutrient. The physiological attributes of *U. rigida* and *C. linum* are examined in this paper, to determine the nutritional characteristics of these species and to assess any competitive advantages these may confer.

Material and Methods

Nutrient uptake rates

Uptake rates of phosphate, ammonium and nitrate + nitrite ('nitrate') were determined from nutrient depletion rates during short-term, 'batch culture' experiments. Due to logistical constraints it was not possible to conduct continuous flow experiments. Probyn and Chapman (1982), Gilbert and McCarthy (1984) and Harrison *et al.* (1989) point out that short-term, batch experiments tend to exaggerate normal uptake rates, particularly of ammonium. Alternatively, it can be argued that short-term experiments do not exaggerate uptake rates, but rather they disclose initial uptake rates which are often higher than rates determined over extended periods. Wallentinus (1984) suggests that short-term uptake rates should not be regarded as over-estimation but rather as an expression of the potential for an alga to utilize available nutrients. Since one of the primary aims of this work was to establish the potential rates of nutrient uptake for both species, the experimental design used was considered appropriate.

Collection

Algae were collected four to six weeks before use in experiments. Small, whole thalli of *Ulva rigida* and strands of *Chaetomorpha linum*, generally free of sediment, diatoms and other epiphytes, were collected from Boodalan Island in Peel Inlet (Fig. 1). Material was stored in estuary water and returned to the laboratory for preconditioning.

Preconditioning

Plants were preconditioned for four to six weeks at 25 °C and 250 μmol m^{-2} s^{-1} PAR (Daylight incandescent, 60 W bulbs and Cool White fluorescent 60 W tubes; 12/12-L/D cycle). Enriched seawater medium (Table I) was used, omitting soil extract, since preliminary work showed that *C. linum* grew poorly in a number of artificial media. The medium was changed daily during preconditioning. A weight to volume ratio of approximately 1.0 g L^{-1} (fresh weight) was maintained throughout the experiment to reduce factors such as nutrient limitation and self-shading (Littler 1979). Plants used to determine phosphorus uptake rates were preconditioned with non-limiting concentrations of NH_4Cl (2 mg N L^{-1}) but no phosphorus, while those used in nitrogen uptake experiments were grown in non-limiting KH_2PO_4 (0.5 mg P L^{-1}) but no nitrogen.

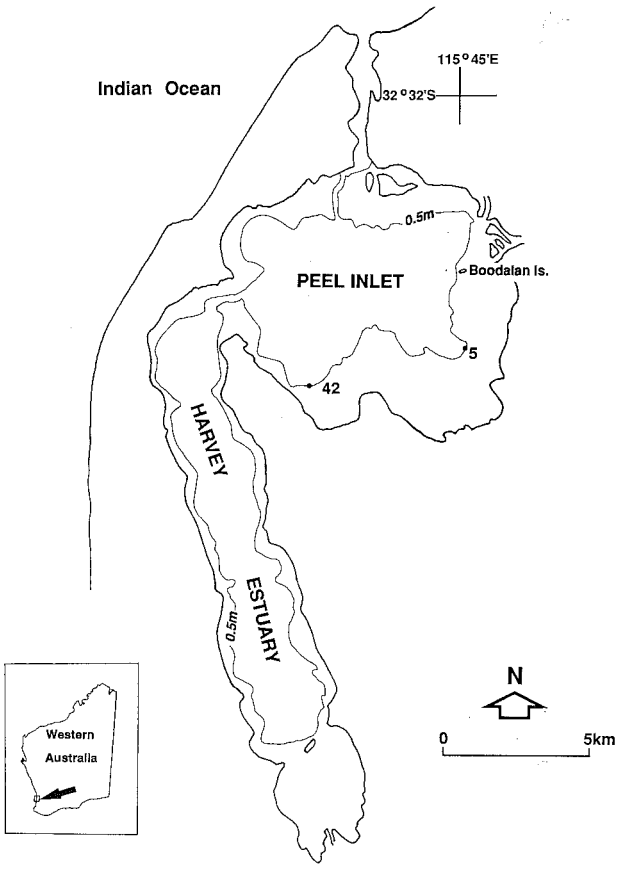

Fig. 1. The Peel-Harvey Estuarine System, showing its location in Western Australia and the sampling sites used in the study.

Table I. Enriched seawater medium used in salinity experiments. The recipe is a modification of SWM medium (McLachlan 1973).

Supplement	Concentration (L^{-1} filt. seawater)
$NaNO_3$	2 mg
KH_2PO_4	1 mg
Na_2SiO_3	24.4 mg
Fe. EDTA	0.692 mg
Trace metal solution*	TMS-1
Thiamine. HCl	100 μg
Biotin	0.5 μg
Cyanocobalamin	0.5 μg

* TMS-1 contains: 2.28 mMol Zn; 0.55 mMol Mn; 0.48 mMol Mo; 17,7 μMol Co; 19 μMol Cu; 4.32 mMol B; Chelate: Metal 2:1.

Experimental design

Rates of nitrogen and phosphorus uptake were determined over five treatment concentrations with non-limiting concentrations of all other nutrients in the medium. Phosphate-P treatment concentrations were in the range of approximately 0.05 – 1.20 mg L^{-1} as KH_2PO_4, with 2.0 mg N L^{-1} as NH_4NO_3. Nitrate and ammonium treatment concentrations were approximately 0.07 – 1.5 mg N L^{-1} as $NaNO_3$ and NH_4Cl respectively with 0.5 mg L^{-1} phosphate-P. Three replicate samples were used for each treatment.

Experiments were conducted in 2 L Ehrlenmeyer flasks, under the conditions described above, with a small pump (EKTA, Italy) circulating water through the flasks (2 L min^{-1}) to reduce boundary layer effects. Water was drawn from the bottom of the flask through a plastic tube (2 cm diameter) connected to the pump and returned by tube to the top of the flask. Inlet and outlet pipes were capped with perforated tubing to prevent damage to the algae. Dye tests revealed that the contents of each flask were completely mixed within 5 s. The medium was gently aerated with compressed, oil-free air. Plastic tubing was secured inside the flask and connected to an external syringe to withdraw water samples. All equipment was thoroughly washed and rinsed in de-ionized water.

Water samples were collected every 15 min for 4 h following the addition of algae to the treatment flasks. Samples were collected by syringe, filtered (GFC, Whatman No. 1), stored in polyethylene bags (Whirlpac, NASCO, USA) and frozen until analysed. Controls were established as described above, but lacking macroalgal material, to estimate nutrient depletion due to microbial or other activity. Algal dry weights were determined after drying to constant weight at 70 °C.

Water samples were analysed for phosphate, ammonium or nitrate using standard methods (Lukatelich and McComb 1986), and the rates of depletion used to calculate rates of nutrient uptake. Regressions were performed on the first linear portion of the depletion curves and the negative of the slope taken as rate of uptake. Regressions were only accepted if statistically singificant ($\alpha = 0.05$) with a minimum of 4 data points.

The data were fitted to either linear or Michaelis-Menten type functions describing nutrient uptake. For the latter, the three linear transforms described by Dowd and Riggs (1965) were used to estimate V_{max} (maximum rate of uptake) and K_s (half saturation constant). The transformation which most accurately fitted the data was used.

In situ *nutrient uptake rates*

On a single occasion (November 1988), *in situ* rates of nutrient uptake were determined for plant material at Stations 5 and 42 in Peel Inlet (Fig. 1). The problems associated with measurement and interpretation of *in situ* nutrient uptake rates have been discussed by McCarthy (1981), and include inability to accurately define the physical and chemical environment and the resident population. For these reasons the assessment of *in situ* uptake rates in this study was intended only as a crude estimation. Phytoplankton and faunal contamination were reduced and controls established to account for these factors. Nitrogen and phosphorus concentrations were raised to easily detectable, but ecologically relevant concentrations.

Plastic bags were used as experimental vessels, allowing high light penetration and mixing of the internal water, through the action of water movement on the bags. Each was filled with 2 – 3 litres of treatment medium (0.48 µm filtered estuary water supplemented with phosphate and ammonium). Three treatment concentrations of each nutrient were used: 98, 170 and 240 µg L^{-1} phosphate-P (as KH_2PO_4) and 20, 180 and 220 µg L^{-1} ammonium-N (as NH_4Cl) with four replicates of each treatment. Whole thalli of *U. rigida* and clumps of *C. linum*, both of known fresh weight, were added to each treatment. Controls were established as described above but lacking algal material.

An initial sample of medium was collected from each bag for nutrient analysis, and the bags sealed, weighted and placed in the water column. They were retrieved and re-sampled after one hour.

Water samples were removed by syringe, and processed as described above. Algal material was returned to the laboratory for dry weight determination at 70 °C, material being dried to constant weight. Rates of uptake were calculated from the change in total nutrient content of each bag less the mean of any nutrient depletion in the control bags.

Critical tissue nutrient concentrations

Collection and medium

Plant material was collected from Peel Inlet and grown in filtered (0.45 µm) seawater medium. The medium was as described above, with either nitrogen or phosphorus additions. To ensure minimal nitrogen and phosphorus content of the base seawater, a single collection was made in mid-summer, when ambient nutrient levels were lowest (7 µg L^{-1} phosphate-P, 3 µg L^{-1} nitrate-N and 8 µg L^{-1} ammonium-N), stored in a dark cold-room, and used for all critical nutrient experiments.

Preconditioning

Preliminary experiments revealed that high nutrient concentrations (> 100 μg L^{-1} P and > 500 μg L^{-1} N) encouraged epiphytic contamination of *C. linum* by a small filamentous chlorophyte. Attempts at inducing sporulation to gain uni-algal cultures of *C. linum* were unsuccessful, as is often the case for free-floating algae (Norton and Mathieson 1983). Other options such as using selective culture media were of limited potential as host and epiphyte were chlorophytes and tended to respond in the same way to treatments. Surface sterilization was the most successful method for reducing epiphytic contamination, using a modification of the technique of Lawler *et al.* (1989). Material was dipped into 70% ethanol for 5 s, and held in de-ionized water for 5 min. It was returned to aquaria and dead or unhealthy strands removed after 7 days. The technique was effective in removing epiphytic contamination in about 30% of cases (Lavery 1989). Small strands of *C. linum* and disks of *U. rigida* (cut from the sub-marginal areas of large thalli) were preconditioned in seawater medium (Table I) at 25 °C and 250 μmol m^{-2} s^{-1} PAR (12/$\overline{12}$ h-L/D) for 7 days prior to experimentation.

Experimental design

Determinations of critical tissue concentrations were conducted in two stages. In the initial stage 1 g samples of *C. linum* or single disks of *U. rigida* (approx. 0.1 g) were grown in 1 litre Ehrlenmeyer flasks at one of five nitrogen or phosphorus concentrations. All flasks were placed in growth cabinets, at the temperature and light levels described above, and gently mixed and aerated with oil-free compressed air. The flasks were randomly re-assorted in the cabinets each day to provide each with an average of any variation in the climate. Nitrogen treatments were in the range 0.0 – 1.5 mg L^{-1} added NH_4-N with 0.5 mg L^{-1} P as PO_4. Phosphorus treatments were in the range 0.0 – 0.25 mg L^{-1} added PO_4-P and 2.0 mg L^{-1} N as NH_4. Three replicates were established for each treatment. The medium was changed daily, and fresh weights of blotted material determined at the beginning and end of each 7 day period.

After 14 days the material was harvested back to the original weight (*U. rigida* material was re-cut into disks) and the three replicates returned to the treatment conditions. After a further 7 days the algae were weighed and the relative growth rates calculated from changes in biomass (Hunt 1978). Algal tissue was dried and analysed for total nitrogen or phosphorus, as described by Lukatelich and McComb (1986).

This two-stage approach had a number of advantages. Firstly, a period of less than three weeks was insufficient to establish detectable differences in growth rates between treatments. However, simply establishing replicates and allowing them to grow for more than three weeks resulted in nutrient limitation and self shading as the biomass increased. This problem was overcome by returning the treatments to a lower biomass for the final week and recording the growth rates over this period. Secondly, the high biomass of the first phase ensured that the tissue was not continuously bathed in high nutrient concentrations since even moderate nutrient uptake rates would rapidly lower the nutrient concentration in the medium; a range of tissue nutrient concentrations was still generated through the differences in nutrient loading to the treatments. This prevented the germination and rapid growth of epiphytic material in much the same way that Ryther *et al.* (1981) recommended pulse nutrient additions to suppress epiphytic growth on cultured seaweeds.

Observed growth rates were plotted against tissue nutrient concentrations, and the critical nutrient concentration estimated as that below which maximum growth rates were not maintained. An exponential function was used to describe the data.

Results

Nutrient uptake rates

The depletion of nutrients from the medium was linear over the period 15 – 75 minutes, and this part of the curve was used to estimate uptake rates (Fig. 2).

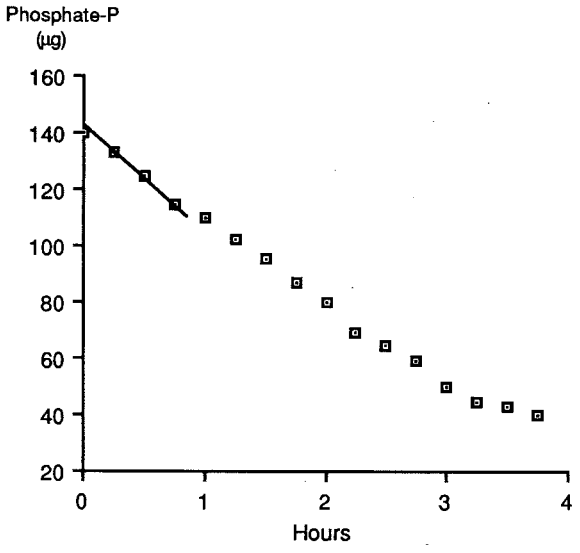

Fig. 2. A typical nutrient depletion curve; depletion of phosphate-P from the medium by *Chaetomorpha linum*. The rate of uptake was estimated from the linear regression of the first four points.

Chaetomorpha linum demonstrated greater phosphate and ammonium uptake rates than *Ulva rigida*, while the latter had higher nitrate uptake rates at low concentrations (Table II; Fig. 3).

Both species had rate-saturating mechanisms of phosphate uptake (Fig. 3) with the V_{max} for *C. linum* more than twice that of *U. rigida*. The half-saturation constant (K_s) of *C. linum* was almost three times that of *U. rigida*. The data were best estimated by the Michaelis-Menton-type functions described in Table II.

Both species displayed linear relationships between the rate of ammonium uptake and substrate concentration (Fig. 3). The slope was greater for *C. linum* (4.4) than *U. rigida* (1.73). Data conformed to the linear functions described in Table II.

The rate of uptake of nitrate by *U. rigida* was saturated as substrate concentrations increased and was described by Michaelis-Menten-type kinetics (Table II). This contrasted with the linear response of *C. linum* (Fig. 3; Table II). *Ulva rigida* exhibited greater rates of uptake up to a concentration of 750 µg N L^{-1}, while at higher concentrations *C. linum* showed a faster rate.

Considerable differences were found between the estimations of the Michaelis-Menten constants K_s and V_{max} using the three linear transforms outlined by Dowd and Riggs (1965). In all cases the S against S/V transformation yielded the greatest coefficient of regression, and most closely modelled the data.

The *in situ* rates of uptake of both nutrients varied almost linearly with substrate concentration and approximated the laboratory uptake rates described above (Fig. 4). For example, at 223 µg L^{-1} phosphate-P the expected uptake rates by *C. linum* and *U. rigida* were 235 and 160 µg g dwt^{-1} h^{-1} respectively, while the observed rates were 200 ± 12 and 227 ± 21 µg g dwt^{-1} h^{-1} respectively. The *in situ* uptake rate of ammonium-N at 203 µg L^{-1} by *U. rigida* (356 µg g dwt^{-1} h^{-1}) was similar to that recorded during laboratory estimations (440 µg g dwt^{-1} h^{-1}), however the *in situ* rate exhibited by *C. linum* (500 ± 66 µg g dwt^{-1} h^{-1}) was only about half of that expected from laboratory determinations (1048 µg g dwt^{-1} h^{-1}). There was no significant difference between the uptake rates of the two species for either ammonium or phosphate ($p = 0.152$ and 0.254 respectively), while substrate concentration had a significant influence ($p = 0.0001$ in both cases).

Critial tissue nutrient concentrations

The growth rate of *U. rigida* was saturated at tissue nitrogen and phosphorus concentrations (critical con-

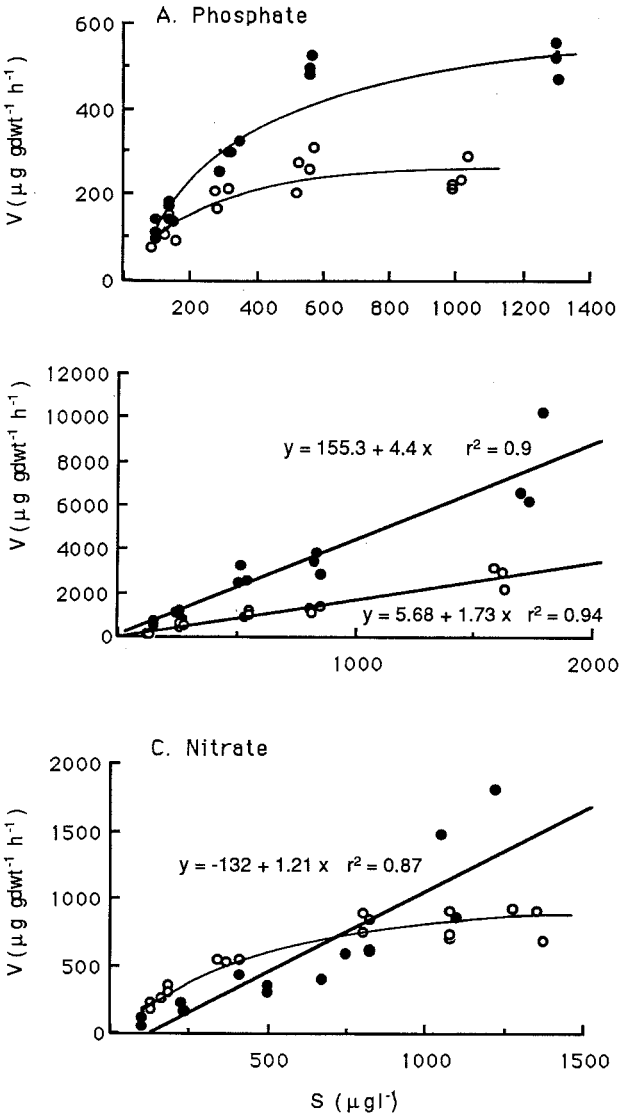

Fig. 3. Rate of (a) phosphate-P, (b) ammonium-N and (c) nitrate-N uptake by *U. rigida* (○) and *C. linum* (●) as a function of substrate concentration.

Table II. Uptake kinetics parameters of *C. linum* and *U. rigida* for phosphate, nitrate and ammonium from Michaelis-Menten (S against S/V) tranforms of raw data. Linear estimates are all significant ($p < .0005$ in all cases).

	C. linum		*U. rigida*	
	K_s (µg L^{-1})	V_{max} (µg g dwt^{-1} h^{-1})	K_s (µg L^{-1})	V_{max} (µg g dwt^{-1} h^{-1})
PO_4-P	321	667	113	272
NO_3-N	V = −132 + 1.21 S*		250 469	820 1193
NH_4-N	V = 155 + 4.40 S*		V = 5.68 + 1.73 S*	

* V = rate of nutrient uptake, and S = substrate concentration, from the linear regression of the data since no saturation kinetics were obtained.

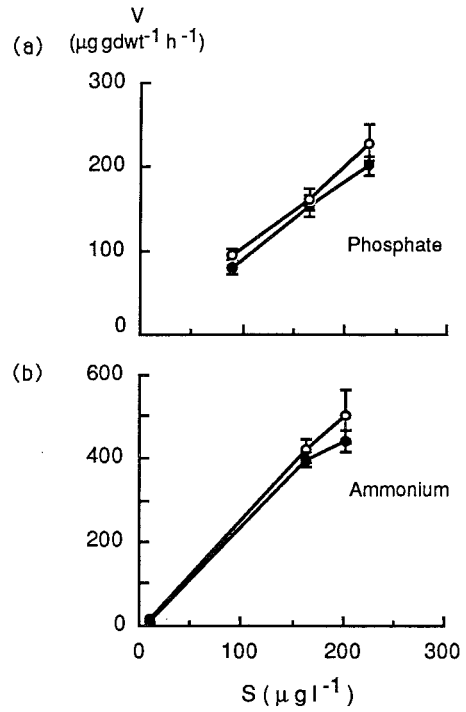

Fig. 4. Mean *in situ* uptake rates of (a) phosphate-P and (b) ammonium-N by *C. linum* (•) and *U. rigida* (○) at various substrate concentrations. n = 4 with bars representing the std error.

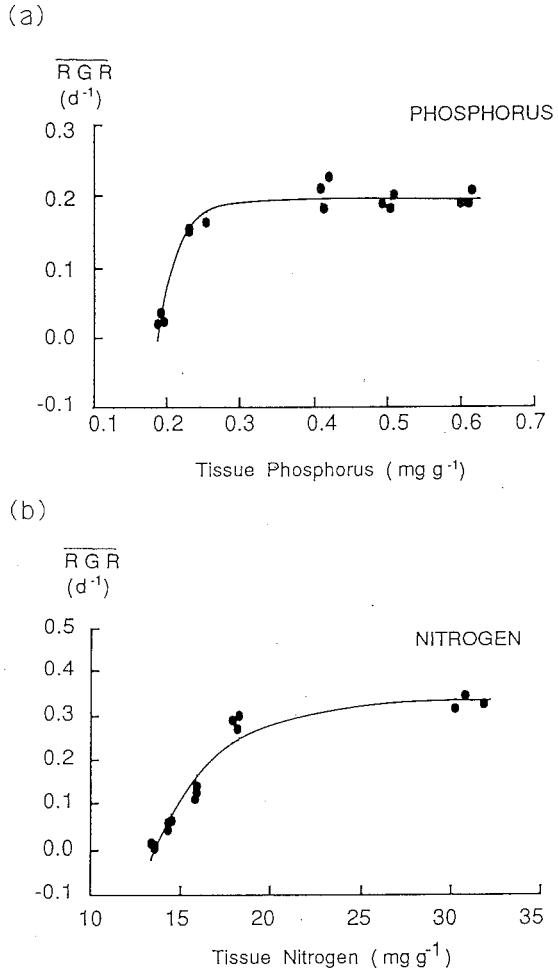

Fig. 5. Mean relative growth rates *U. rigida* as a function of (a) tissue phosphorus and (b) tissue nitrogen concentrations. Fitted curves are exponential approximations ($R^2 = 0.95$ in both cases).

centrations) of 20 and 0.25 mg g^{-1} respectively (Fig. 5). Growth was most severely reduced by nitrogen deprivation; the zero nitrogen and phosphorus treatments had mean relative growth rates over the first week of 0.125 ± 0.004 and 0.207 ± 0.007 d^{-1} respectively. By the end of week three the zero phosphorus treatment had a relative growth rate 2.7 times that of the minus nitrogen treatment (0.024 compared to 0.009 d^{-1}).

Chaetomorpha linum had a lower nitrogen requirement than *Ulva rigida* but a higher phosphorus requirement. The growth rate of *C. linum* was saturated at tissue nitrogen and phosphorus concentrations (critical concentrations) of 12 and 0.5 mg g^{-1} respectively (Fig. 6). As for *U. rigida*, growth was most severely reduced by nitrogen deprivation; over week three the zero phosphorus treatment had a relative growth rate 2.27 times that of the minus nitrogen treatment (0.073 compared to 0.032 d^{-1}).

Discussion

Uptake rates

The observed nutrient uptake rates display a number of interesting features. Firstly, the differences in uptake rates were surprisingly large, given that the species are both simple, green algae; *Chaetomorpha linum* incorporated phosphate and ammonium at twice the rates of *Ulva rigida*. In the case of phosphate however, *U. rigida* had a lower K_s value indicating a greater affinity for phosphate at lower concentrations. The relative advantages of high V_{max} or low K_s will differ under various circumstances, with *C. linum* favoured during periods of short-term nutrient enrichment, such as discrete run-off events or high nutrient concentrations generated by sediment nutrient release. Interestingly, dense accumulations of *C. linum* have a demonstrated ability to induce sediment phosphorus flux through their effect of reducing oxygen levels in the overlying water, resulting in high P concentrations in the inter-algal water (Lavery and McComb 1991).

Species differences in uptake rates may be related to differences in morphology. Wallentinus (1984) observed that filamentous, delicately branched and monostromatic forms of algae generally exhibit the highest nutrient uptake rates as a result of their higher surface area to volume ratios and lack of internal and supportive tissue which cannot contribute to nutrient uptake. *Chaetomorpha linum*, an unbranched filamen-

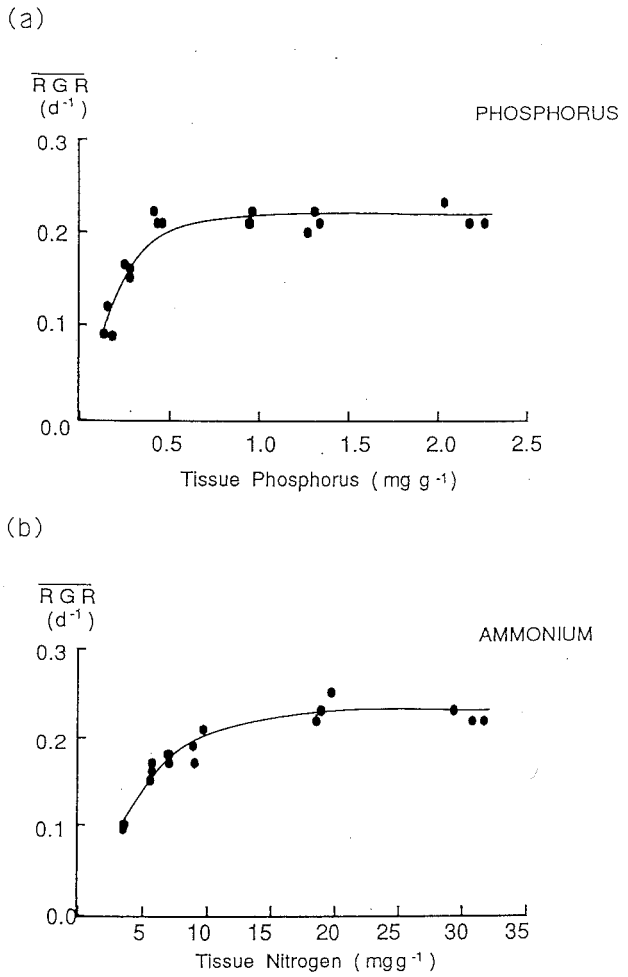

Fig. 6. Mean relative growth rates of *C. linum* as a function of (a) tissue phosphorus and (b) tissue nitrogen concentrations. Fitted curves are exponential approximations ($R^2 = 0.95$ in both cases).

tous-type alga, has a surface area : dry weight ratio 1.5 to 6 times that of the distromatic, membranous *U. rigida*, depending on which region of the *Ulva* thallus is measured (unpublished data). The area of thallus available for nutrient uptake is correspondingly higher for *C. linum* and this, apart from any physiological or biochemical considerations, could significantly enhance its rates of nutrient uptake.

Wallentinus (1984) lists a large range of published uptake rates of ammonium, nitrate and phosphate by macroalgae. Since that date nutrient uptake rates have been published by Probyn and McQuade (1985), Thomas and Harrison (1985), Thomas *et al.* (1987), Williams and Fisher (1985) and Duke *et al.* (1989). These literature values are generally lower than those reported here for *U. rigida* and *C. linum*, supporting the suggestion of Wallentinus (1984) that these simpler functional-form groups should have relatively high uptake rates. The K_s values for phosphate-P in this study are higher than many literature values, suggesting relatively poor efficiencies in incorporating nutrients at low concentrations. This may reflect localized adaptation to the relatively nutrient-rich estuarine environment, since most of the literature values relate to marine species.

Another interesting feature of the uptake experiments was the difference in nitrogen uptake mechanisms. Nitrate uptake by *U. rigida* conformed to a rate-saturating mechanism but for *C. linum* increased linearly with substrate concentration. A linear relationship was observed for ammonium uptake in both species. Linear relationships between S and V have been reported as components of di- or multi-phasic uptake mechanisms (D'Elia and DeBoer 1978, Haines and Wheeler 1978, MacFarlane and Smith 1982, Friedlander and Dawes 1985, Harrison *et al.* 1986, Thomas *et al.* 1987, Druehl *et al.* 1989). These multiphasic models of uptake generally consist of a high affinity, saturable uptake rate a low concentrations and a low affinity, non-saturable uptake mechanism, such as diffusion, at high concentrations. It is probable that the linear relationships between S and V observed in this study reflect similar di- or multiphasic uptake mechanisms. The high Y-intercept values for some of the regression suggest that the data conform to a multiphasic uptake mechanism rather than to simple linear functions which should theoretically approach the origin. Most examples of such mechanisms are for ammonium uptake and the evidence presented here represents one of only a few reported cases of a linear uptake phase for nitrate (Probyn and McQuade 1985, Harrison *et al.* 1986, Thomas *et al.* 1987, Druehl *et al.* 1989).

In all cases of saturable uptake rates, the S vs S/V linear transformation most accurately predicted V_{max} and K_s. This supports Dowd and Riggs' (1965) criticism of common use of Lineweaver-Burk transformations to estimate these constants. Nonetheless, the estimated values were usually higher than the raw data, or untransformed, uptake rates that were observed for a nutrient at a particular concentration. Thus, while the fitted curves accurately predict V over the experimental range of nutrient concentrations, extrapolation to higher substrate concentrations will reduce the accuracy; this should be considered when incorporating such data into models of nutrient uptake. On the other hand, the experimental nutrient levels used here cover the range of concentrations likely to be encountered *in situ*. Functions describing the algal responses at laboratory concentrations may reasonably reflect the response of algae in the field. Certainly the phosphate uptake rates observed *in situ* were reasonably similar to those expected from laboratory results. Differences between *in situ* and laboratory estimates may be expected because of differ-

ences in nutritional histories of the plants, and environmental factors which may limit growth or metabolic processes (*e. g.* Harlin and Craigie 1978, D'Elia and DeBoer 1978, Hanisak and Harlin 1978, Topinka 1978, Thomas and Turpin 1980, Lapointe and Tenore 1981, Thomas *et al.* 1987).

The ability of *C. linum* and *U. rigida* to utilize both nitrate and ammonium would be particularly advantageous in Peel Inlet. High ammonium concentrations persist inside algal banks throughout the year, while there is a strong winter influx of nitrate into the system (Lavery and McComb 1991). Up to concentrations of about 750 μg N L^{-1} *U. rigida* would have uptake rates for nitrate greater than those of *C. linum*. However, the biomass of *U. rigida* is lowest during winter, the period of maximum nitrate concentrations, due to light, salinity and temperature limitation (Lavery 1989) and so the capacity for luxury uptake may be limited. *Chaetomorpha*, on the other hand, demonstrates a higher rate of ammonium uptake at all concentrations tested and maintains high biomass over winter, the time of maximum ammonium concentrations. Thus, depending on the source available, either species would be able to take advantage of sudden high nitrogen concentrations although the persistence of *Chaetomorpha* biomass over winter would offer it an advantage in storing excess nutrient reserves.

Kautsky (1982) suggested that differences in the nutrient uptake parameters of species could determine the outcome of inter-specific competition between macroalgae at different nutrient concentrations. The potential of *Chaetomorpha* and *Ulva* to incorporate nitrogen was compared by assuming that the uptake rates and nitrate or ammonium were not affected by either the concentration of the other N-source or the nutritional history of the plants. With these assumptions the potential for nitrogen uptake could be calculated as the instantaneous rate of ammonium-plus-nitrate uptake at the ambient concentrations. In this case the high Y-intercept values in the linear regressions were omitted as they are considered spurious and would have over-estimated the rate of ammonium uptake by *Chaetomorpha* at low concentrations. Ambient concentrations for 1988 were available through the regular monitoring programme of the Centre for Water Research. As expected, *Chaetomorpha* had greater uptake rates of total inorganic nitrogen throughout the year despite the higher nitrate uptake rates of *Ulva* at lower concentrations (Fig. 7).

Cladophora montagneana Kütz., the previously dominant alga in Peel Inlet, is reported to have lower uptake rates but higher affinties for phosphate, ammonium and nitrate than the species in this study

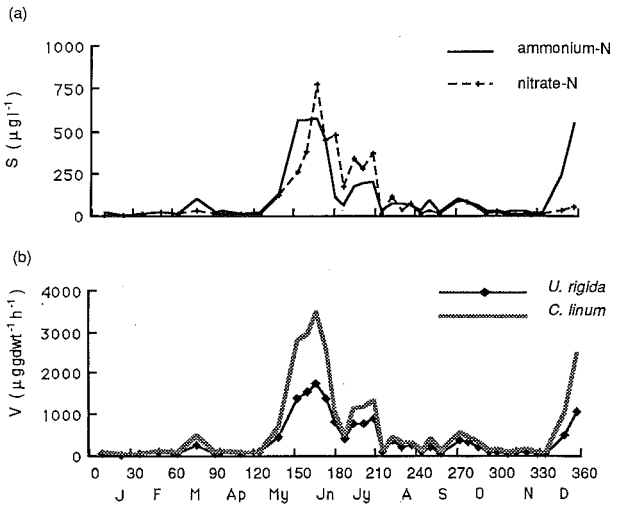

Fig. 7. The observed concentrations of ammonium-N and nitrate-N in at Station 7 in the centre of Peel Inlet (a), with (b) the calculated, uptake rates of these nutrients (NO_3 and NH_4) by *Ulva rigida* and *Chaetomorpha linum* based on rates determined in the laboratory.

(Gordon *et al.* 1981). The implications of the lower uptake rates for this species have been considered elsewhere (Lavery 1989, Lavery *et al.* 1991), and it suffices to say here that, at most nutrient concentrations, *Chaetomorpha* had faster rates of nutrient uptake than *Cladophora*. This supports the hypothesis that the nutrient uptake abilities of *Chaetomorpha* afforded it a competitive advantage over *Cladophora* and contributed to its replacement by *Chaetomorpha* as the dominant alga in the system.

It has been reported elsewhere (Lavery 1989, Lavery *et al.* 1991) that *Chaetomorpha* is seldom nutrient limited and that *Ulva* is frequently nitrogen limited during spring in Peel Inlet. The critical nutrient levels reported here, help to explain these differences. *Ulva* requires about half the tissue phosphorus of *Chaetomorpha*, while *Chaetomorpha* requires about half the tissue nitrogen of *Ulva*. The nitrogen limitation of *Ulva* over spring-summer reflects the high nitrogen requirements of this plant compared to *Chaetomorpha* as well as the reduced ability to store nutrients over winter. The maximum tissue nitrogen levels recorded for *Ulva* (29.4 mg g^{-1}) were only 47% higher than the critical concentration. This compares with a maximum tissue phosphorus concentration (2.22 mg g^{-1}) which was almost 9 times the critical level. This seasonal limitation by nitrogen supports the hypothesis of McComb *et al.* (1981) that production in the system may be nitrogen limited in summer, a conclusion based on tissue nutrient concentrations of *Cladophora* (Gordon *et al.* 1981).

The low phosphorus requirements reported here and the high inorganic phosphorus inputs to the system

in winter may account for the lack of phosphorus limitation for both of these species. The relatively mild affect of phosphorus starvation on the plants compared to nitrogen in the critical concentration experiments also indicates a more effective phosphorus storage and recycling mechanism. In contrast, the phosphorus requirement of *Cladophora* (3.3 mg g^{-1}; Gordon *et al.* 1981) is considerably higher than either *Chaetomorpha* or *Ulva*, and *Cladophora* was often phosphorus limited, as indicated by tissue concentrations (McComb *et al.* 1981, Lavery *et al.* 1991).

The maintenance of *C. linum* biomass over winter would permit this plant to take full advantage of the elevated nutrient concentrations. This is reflected in the luxury consumption of both nitrogen and phosphorus in winter with concentrations about twice the critical concentration of nitrogen, and five times in the case of phosphorus. This appears to prevent nutrient limitation over summer. The occasions on which *Chaetomorpha* appeared to be phosphorus- and nitrogen-limited, were towards the end of summer, and followed winters of low nutrient loading. Nutrient limitation seems unlikely for the remainder of the year.

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