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## RESEARCH NOTE

# Comparison of growth and nitrate uptake by New England *Porphyra* species from different tidal elevations in relation to desiccation

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## SUMMARY

Desiccation stress can determine the upper distribution limits and may enhance the uptake of nitrate and ammonium of eulittoral algal species. Upper shore species may exhibit greater stimulation of nitrate uptake following desiccation and achieve maximum uptake at higher desiccation levels. The objective of this study was to determine whether *Porphyra* species from different vertical elevations respond differently to the desiccation stress, in terms of growth and nitrate uptake. A eulittoral species (*Porphyra umbilicalis*) and a sublittoral species (*P. amplissima*) were compared in the present study. Samples were exposed to air for 0, 30 min ( $40 \pm 10\%$  water loss) and 2 h ( $90 \pm 5\%$  water loss), after an initial 4 h light period every day. Desiccation was more stressful to the sublittoral species, *Porphyra amplissima*, than to the eulittoral species, *P. umbilicalis*. When tissues were exposed for 2 h daily, *P. amplissima* lost weight over a 24 h day, while the growth rate of *P. umbilicalis* dropped by only 30% compared with that of continuously submerged blades. Nitrate uptake rate of sublittoral *P. amplissima* was only 73% ( $40 \pm 10\%$  water loss) and 62% ( $90 \pm 5\%$  water loss) of that of continuously submerged tissue. Nitrate uptake rates of *P. umbilicalis* were not significantly affected by desiccation. These results suggest that species in the eulittoral zone, which have longer exposure times, have a higher time-use efficiency than the sublittoral species in terms of nitrate uptake. This indicates a possible correlation between nitrate uptake and observed vertical distribution patterns.

Key words: desiccation, eulittoral zonation, growth rate, nitrate uptake, *Porphyra*.

*Porphyra* (Bangiales, Rhodophyta) grows rapidly and is an efficient nutrient concentrator. Recently Carmona *et al.* (2006) reported that over 4 day periods the growth rate of *Porphyra* species can exceed  $25\% \text{ day}^{-1}$ . Since this genus consists of one or two cell layers, *Porphyra* has an extremely high surface area to volume ratio. With all cells absorbing nutrients, the *Porphyra* genus must be capable of rapid nutrient assimilation to support the fast growth (Kraemer *et al.* 2004; Neori *et al.* 2004; Carmona *et al.* 2006; Pereira *et al.* 2006; Kim *et al.* 2007).

Along the New England coast, most *Porphyra* species occur seasonally, except for *P. umbilicalis*, which is present as a year-round member of the eulittoral community. As a group, *Porphyra* species show a wide vertical distribution in the eulittoral and sublittoral zones. For example, *Porphyra umbilicalis* is the most abundant species on the New England coast, both spatially and temporally, and occurs throughout the year within the eulittoral zone. *Porphyra amplissima* occurs mostly during spring–summer within coastal areas of northern New England and the Maritime Provinces of Canada. This species is most abundant within the low littoral and sublittoral zones at that time of the year (Villalard-Bohnsack 1995; Chopin *et al.* 1999; West *et al.* 2005).

Eulittoral seaweeds are exposed daily to air because of tidally driven emersion and immersion cycles. During exposure, the eulittoral seaweeds experience various stresses including nutrient limitation, high light, high (or low) salinity, temperature extremes and desiccation (Lobban & Harrison 1994; Davison & Pearson 1996).

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Desiccation stress determines the upper distribution limits of some algal species and affects the extent of recovery of photosynthesis in different species following severe desiccation (Dring & Brown 1982; Davison & Pearson 1996; Beach & Smith 1997; Skene 2004). The recovery of nitrate uptake after periods of desiccation may also be another key factor in determining the zonation of algae on the shore. Desiccation appears to enhance short-term uptake of nitrate, ammonium and phosphate in some eulittoral species (Thomas *et al.* 1987a,b; Hurd & Dring 1991). The degree of desiccation that results in maximal enhancement of nutrient uptake may be related to the species position in the eulittoral zone. Thomas *et al.* (1987b) found that upper shore species, *Pelvetiopsis limitata* and *Fucus distichus* achieved maximum nitrate uptake following severe desiccation that inhibited nitrate uptake in low shore species, *Gracilaria pacifica*. However, the implication to this difference is still not clear. We report here results that compare the growth and nitrate uptake rates of two *Porphyra* species, *P. umbilicalis* from the mid littoral zone and *P. amplissima* from the sublittoral zone to determine whether *Porphyra* species at different vertical habitats respond differently to desiccation stress.

*Porphyra amplissima* (Kjellman) Setchell et Hus (ME-32p) used in this study was obtained from cultures at the Marine Biotechnology Laboratory of the University of Connecticut at Stamford. The strain of *Porphyra amplissima* was originally collected in the sublittoral zone at Gore Point, Cobscook Bay, ME, USA. *Porphyra umbilicalis* Kützinger was collected in the mid to upper littoral zone at Rye, New Hampshire, USA in October 2005. The experiments were conducted using a randomized complete block design of three desiccation treatments (0, 40 ± 10 and 90 ± 5% water loss), and each treatment had three replicates. Experiments were carried out for 2 weeks for *P. umbilicalis* in 50 L tanks at saturating light intensities (100–150 μmol photons m<sup>-2</sup> s<sup>-1</sup>; Kraemer and Yarish 1999; Kim *et al.* 2007). However, *P. amplissima* was cultivated only for 3 days because the biomass decreased under higher desiccation during acclimation. *P. umbilicalis* was cultivated at 10°C and *P. amplissima* was cultivated at 15°C. These culture temperatures were suggested as the optimal temperatures for the growth of each species (Kraemer & Yarish 1999; Carmona *et al.* 2006; Kim *et al.* 2007). Since the temperatures differ, we do not directly compare the rates measured for each species. Light was supplied by 400 watt Ceramalux lamps (Philips, Somerset, NJ, USA). Irradiance was measured by a light meter (LI-185A, Li-Cor Inc.) and adjusted with neutral density filters. Photoperiod was 12:12 h light: dark (LD). The culture medium was filtered (0.45 μm) and UV-irradiated seawater with von Stosch's enrichment (VSE; Ott 1965) was used. The initial stocking density for both species was approximately 0.5 g L<sup>-1</sup>.

Both *Porphyra* species were exposed daily to the air for 0, 30 min, 40 ± 10% (moderate) water loss, and 2 h, 85–95% (severe) water loss, during the light period. Air temperature, humidity and light intensity during emersion were 15–20°C, 37–58%, and 100–150 μmol photons m<sup>-2</sup> s<sup>-1</sup>. Water loss (WL) was estimated as follows:

$$WL(\%) = \frac{FW - TW}{FW - DW} \times 100$$

where FW is the weight obtained after blotting the thalli dry with paper towels. TW is the desiccated weight after a known time interval. DW is the dry weight of the entire sample that was dried at 60°C to constant weight.

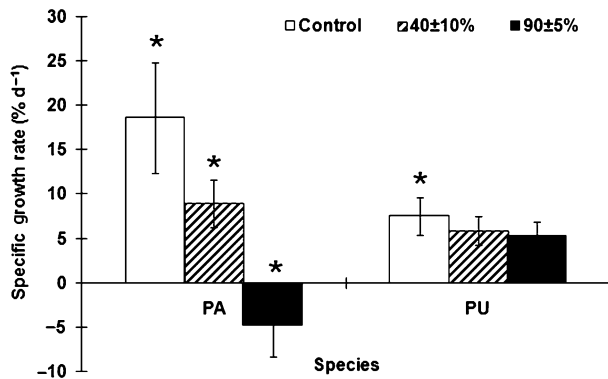
Samples were acclimated under the treatment conditions for one week. During acclimation, filtered seawater with VSE was replaced every 3 or 4 days to prevent nutrient limitation in the algal tissues (Kim *et al.* 2007). All of the biomass in each tank was weighed (FW) and tissue samples were also taken weekly for tissue carbon and nitrogen analyses 5–7 h after re-submergence for *P. umbilicalis* and daily for *P. amplissima*. Water samples were taken for nitrate uptake analysis every time the medium was changed. Specific growth rate (SGR, expressed as percentage increase day<sup>-1</sup>) was calculated as follows:

$$SGR = \frac{\ln S_2 - \ln S_1}{T_2 - T_1} \times 100$$

where S<sub>1</sub> and S<sub>2</sub> are the fresh weight at days T<sub>1</sub> and T<sub>2</sub>, respectively. For the analysis of tissue total nitrogen and carbon content, samples were dried at 60°C before being ground. The powder was analyzed using a Perkin Elmer 2400 series II CHNS/O elemental analyzer. Water samples from the incubated media were analyzed for inorganic nitrate by using a SmartChem Discrete Analyzer (Westco Scientific Instruments, Inc. Brookfield, CT, USA).

One-way split-plot ANOVA (α = 0.05) was used to analyze data. When ANOVA indicated the treatment effect of desiccation, Tukey's Honestly Significant Differences (HSD) analysis (α = 0.05) was used as a post hoc test to determine pairwise comparison probabilities between treatment level means. All statistic analyses were done using SPSS 15.0 (SPSS Inc. Chicago, IL, USA).

Desiccation is a stress for seaweeds because they are essentially marine organisms. We expected that seaweeds inhabiting the eulittoral zone must be better adapted to such environmental stress than are sublittoral species. Not surprisingly, in the present study, desiccation was more stressful to the sublittoral species, *P. amplissima*, than it was to the eulittoral species, *P. umbilicalis*, in terms of growth and nitrate uptake rates. The growth rate of *P. umbilicalis* decreased with desiccation stress. The sublittoral



**Fig. 1.** Specific growth rates of *Porphyra* species at different desiccation treatments (0, 40 ± 10% and 90 ± 5% water loss). PA, *Porphyra amplissima*; PU, *Porphyra umbilicalis*. Error bars represent standard deviation. Bars with an asterisk are significantly different ( $P < 0.05$ ).

species, *P. amplissima*, did not grow after severe desiccation stress but rather shrank (decreased in weight). The daily growth rates of *P. amplissima* and *P. umbilicalis* under a continuous submergence were approximately 18.6% and 7.5%, respectively. When the tissues were exposed for 2 h daily, corresponding with extreme water loss (90 ± 5%), *P. amplissima* lost weight (4.8% day<sup>-1</sup>). When exposed for 30 min, which caused moderate water loss (40 ± 10%), the growth rate of *P. amplissima* decreased significantly to about 50% of the continuously submerged blades ( $P < 0.001$ ). The growth rate of *P. umbilicalis* under a severe water loss condition was 5.4% day<sup>-1</sup>, which is approximately 70% of the continuously submerged blades. The growth rate of *P. umbilicalis* with moderate water loss was about 77% of the continuously submerged blades ( $P < 0.001$ ; Fig. 1).

The acquisition of inorganic nitrogen should be a limiting factor for the eulittoral seaweeds during emersion when seaweeds are isolated from the source of nitrogen. The supply of carbon is also limited. During emersion, CO<sub>2</sub> in the atmosphere was limited for the photosynthesis of eulittoral seaweeds, *Fucus serratus* (Bidwell & McLachlan 1985), *Ascophyllum nodosum* (Johnston & Raven 1986), *Ulva linza*, *Ishige okamurae* and *Gloiopeltis furcata* (Gao *et al.* 1999) and *Porphyra haitanensis* (Zou & Gao 2002). These limitations may be even more severe for the upper shore species if they lack strategies to circumvent the limits. In the present study, carbon and nitrogen contents in tissue were not significantly different in different desiccation treatments ( $P > 0.05$ ; Table 1). The carbon contents in *P. amplissima* were 37.3% (continuously submerged tissues), 37.4% (moderate water loss) and 37.7% DW<sup>-1</sup> (severe water loss), whereas *P. umbilicalis* contained 36.2%, 36.8% and 37.3% DW<sup>-1</sup> of carbon in tissue

**Table 1.** Tissue C and N contents and C : N ratio of *Porphyra amplissima* and *Porphyra umbilicalis* at different desiccation treatment (0, 40 ± 10% and 90 ± 5% water loss)

	C (%)			N (%)			C : N		
	Control	40 ± 10	90 ± 5	Control	40 ± 10	90 ± 5	Control	40 ± 10	90 ± 5
<i>Porphyra amplissima</i>	37.28 (±0.50)	37.44 (±0.41)	37.74 (±0.59)	3.60 (±0.11)	3.64 (±0.09)	3.73 (±0.09)	10.35 (±0.32)	10.28 (±0.14)	10.13 (±0.34)
<i>Porphyra umbilicalis</i>	36.22 (±1.03)	36.82 (±0.79)	37.26 (±1.53)	5.09 (±0.44)	5.33 (±0.21)	5.40 (±0.41)	7.16 (±0.77)	6.92 (±0.22)	6.94 (±0.67)

Mean ± standard deviation (SD).

respectively. The tissue nitrogen contents of *P. amplissima* were 3.60%, 3.64% and 3.73% DW<sup>-1</sup>, respectively, whereas *P. umbilicalis* contained 5.09%, 5.33% and 5.40% DW<sup>-1</sup> of nitrogen in tissue, respectively. C : N ratio decreased as desiccation increased from 10.35 to 10.28 and to 10.13 in *P. amplissima* and from 7.16 to 6.92 and to 6.94 in *P. umbilicalis*, respectively (Table 1). However, the ratio did not significantly differ as a function of treatment in either species. These results suggest that both *Porphyra* species were able to recharge tissue carbon and nitrogen to pre-desiccation levels by 5–7 h after re-submergence.

The effect of desiccation on the photosynthetic performance of eulittoral seaweeds has been studied extensively (Dring & Brown 1982; Thomas *et al.* 1987b; Hurd & Dring 1990; Davison & Pearson 1996; Beach & Smith 1997; Zou & Gao 2002; Skene 2004; Kim & Garbary 2007). These studies found that desiccation stress affects the extent and the rate of recovery of photosynthesis following severe desiccation, and the differential recovery of photosynthesis may contribute to determining the zonation of eulittoral algae. The effect of desiccation on nitrate uptake by eulittoral seaweeds has received less attention than that on photosynthesis. However, the recovery of nitrate uptake after periods of desiccation may also be another factor in regulating the zonation of algae on the shore. In this study, the sublittoral species, *P. amplissima*, did not recover its nitrate uptake function after severe desiccation stresses, while nitrate uptake by *P. umbilicalis* did not differ between desiccated and undesiccated treatments. Under severe water loss, nitrate uptake rate by *P. amplissima* was only 62% of the continuously submerged tissues. At moderate water loss of *P. amplissima*, the nitrate uptake rate was 73% of the continuously submerged tissues. However, in *P. umbilicalis*, the nitrate uptake rates under moderate and severe water loss conditions were approximately 96% and 90% of the continuously submerged tissues but not significantly different in each treatment ( $P > 0.05$ ; Fig. 2).

One gram (FW) of *P. amplissima* under a continuous submergence could take up 151  $\mu\text{mol}$  of nitrate daily. However, when this species was desiccated moderately and severely, the nitrate uptake rates were only 73% and 62% of the control rates, respectively. On the other hand, 1 g (FW) of continuously submerged *P. umbilicalis* took up 141  $\mu\text{mol}$  of nitrate daily, and the uptake rates did not decrease as much as *P. amplissima* when moderately (96% of control) and severely (90% of control) desiccated. These results suggest that enzymes related to photosynthesis and nutrient assimilation were more severely affected by desiccation in the sublittoral species than in the eulittoral species.

Some eulittoral seaweeds photosynthesize during desiccation and even have maximal rates of photosyn-

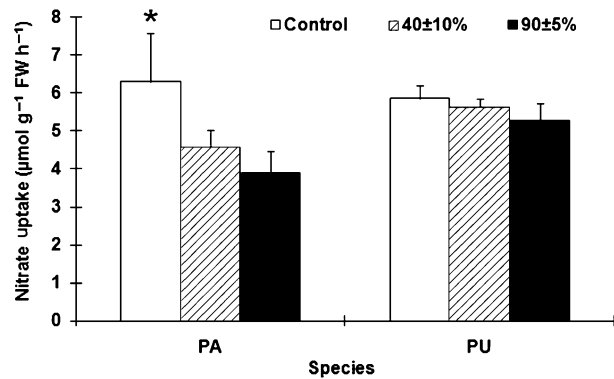


Fig. 2. Nitrate uptake rates of *Porphyra* species at different desiccation treatment (0, 40 ± 10% and 90 ± 5% water loss). PA, *Porphyra amplissima*; PU, *Porphyra umbilicalis*. Error bars represent standard deviation. Bars with an asterisk are significantly different ( $P < 0.05$ ).

thesis when partially dehydrated (Davison & Pearson 1996). For example, maximum rates of photosynthesis by *Fucus vesiculosus* occur when about 70% of tissue water has been lost, by *F. distichus* at about 80%, by *Ascophyllum nodosum* at about 80–85%, and *Porphyra linearis* at about 60% water loss (Quadir *et al.* 1979; Johnston & Raven 1986; Lipkin *et al.* 1993). These seaweeds may use stored nitrogen for growth during periods of emersion. Therefore, an increase in nitrogen uptake rate following emersion may be a mechanism to replenish nitrogen stores that were depleted when seaweeds are exposed by low tide, yet continued to grow. For example, Thomas *et al.* (1987b) reported that inorganic nitrogen uptake by two high littoral species, *Pelvetiopsis limitata* and *F. distichus*, more than doubled upon resubmergence following more than 30% desiccation. The low littoral species, *Gracilaria pacifica*, showed no enhancement of nitrogen uptake following desiccation. We also found that both moderately and severely desiccated tissues of eulittoral *P. umbilicalis* had very similar nitrate uptake rate in comparison with continuously submerged tissues, whereas the uptake rate of sublittoral *P. amplissima* significantly decreased as desiccation increased. Therefore, species in the eulittoral zone that have longer exposure times may have 'higher time-use efficiency' than sublittoral species that have lower nitrate uptake rates per unit time submerged. These results suggest that there may be a correlation between nitrate uptake and observed vertical distribution patterns.

To confirm this hypothesis that the recovery of nitrate uptake following desiccation is another factor in regulating the zonation of algae on the shore, there are questions to be answered: (i) how quickly can nitrate uptake by eulittoral species recover from desiccation stress characteristic of their environment? (ii) do tissue



nitrogen and pigment (as storage of nitrogen) contents change during emersion? and (iii) how does enzyme activity related to nitrogen assimilation change by desiccation stress? The next step to answer these questions will be selecting more species from upper littoral to sublittoral zones and collecting samples more frequently before, during and after desiccation to see the direct effect of desiccation. These measurements will enable us to understand physiological responses of seaweeds under desiccation as well as correlation between nitrate uptake and vertical distribution of seaweeds.

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## REFERENCES

- Beach, K. S. and Smith, C. M. 1997. Ecophysiology of a tropical rhodophyte. 3. Recovery from emersion stresses in *Ahnfeltiopsis concinna* (j Ag) Silva et DeCew. *J. Exp. Mar. Biol. Ecol.* **211**: 151–67.
- Bidwell, R. G. S. and McLachlan, J. 1985. Carbon nutrition of seaweeds: photosynthesis, photorespiration, and respiration. *J. Exp. Mar. Biol. Ecol.* **86**: 15–46.
- Carmona, R., Kraemer, G. P. and Yarish, C. 2006. Exploring Northeast American and Asian species of *Porphyra* for use in an integrated finfish-algal aquaculture system. *Aquaculture* **252**: 54–65.
- Chopin, T., Yarish, C., Wilkes, R., Belyea, E., Lu, S. and Mathieson, A. 1999. Developing *Porphyra*/salmon integrated aquaculture for bioremediation and diversification of the aquaculture industry. *J. Appl. Phycol.* **11**: 463–72.
- Davison, I. R. and Pearson, G. A. 1996. Stress tolerance in intertidal seaweeds. *J. Phycol.* **32**: 197–211.
- Dring, M. J. and Brown, F. A. 1982. Photosynthesis of intertidal brown algae during and after periods of emersion: a renewed search for physiological causes of zonation. *Mar. Ecol. Prog. Ser.* **8**: 301–8.
- Gao, K., Ji, Y. and Aruga, Y. 1999. Relationship of CO<sub>2</sub> concentrations to photosynthesis of intertidal macroalgae during emersion. *Hydrobiologia* **398/399**: 355–9.
- Hurd, C. L. and Dring, M. J. 1990. Phosphate uptake by intertidal algae in relation to zonation and season. *Mar. Biol.* **107**: 281–9.
- Hurd, C. L. and Dring, M. J. 1991. Desiccation and phosphate uptake by intertidal fucoid algae in relation to zonation and season. *Br. Phycol. J.* **26**: 327–33.
- Johnston, A. M. and Raven, J. A. 1986. The analysis of photosynthesis in air and water of *Ascophyllum nodosum* (L.) Le Jol. *Oecologia* **69**: 288–95.
- Kim, J. K., Kraemer, G. P., Neefus, C. D., Chung, I. K. and Yarish, C. 2007. The effects of temperature and ammonium on growth, pigment production and nitrogen uptake in four species of *Porphyra* native to the coast of New England. *J. Appl. Phycol.* **19**: 431–40.
- Kim, K. Y. and Garbary, D. J. 2007. Photosynthesis in *Codium fragile* (Chlorophyta) from a Nova Scotia estuary: responses to desiccation and hyposalinity. *Mar. Biol.* **151**: 99–107.
- Kraemer, G. P. and Yarish, C. 1999. A preliminary comparison of the mariculture potential of *Porphyra purpurea* and *Porphyra umbilicalis*. *J. Appl. Phycol.* **11**: 473–7.
- Kraemer, G. P., Carmona, R., Chopin, T., Neefus, C., Tang, X. R. and Yarish, C. 2004. Evaluation of the bioremediatory potential of several species of the red alga *Porphyra* using short-term measurements of nitrogen uptake as a rapid bioassay. *J. Appl. Phycol.* **16**: 489–97.
- Lipkin, Y., Beer, S. and Eshel, A. 1993. The ability of *Porphyra linearis* (Rhodophyta) to tolerate prolonged periods of desiccation. *Bot. Mar.* **36**: 517–23.
- Lobban, C. S. and Harrison, P. J. 1994. *Seaweed Ecology and Physiology*. Cambridge University Press, New York, 366 pp.
- Neori, A., Chopin, T., Troell, M., Buschmann, A. H., Kraemer, G. P., Halling, C., Shpigel, M. and Yarish, C. 2004. Integrated aquaculture: rationale, evolution and state of the art emphasizing seaweed biofiltration in modern mariculture. *Aquaculture* **231**: 361–91.
- Ott, F. D. 1965. Synthetic media and techniques for the xenic cultivation of marine algae and flagellate. *Va. J. Sci.* **16**: 205–18.
- Pereira, R., Yarish, C. and Sousa-Pinto, I. 2006. The influence of stocking density, light and temperature on the growth, production and nutrient removal capacity of *Porphyra dioica* (Bangiales, Rhodophyta). *Aquaculture* **252**: 66–78.
- Quadir, A., Harrison, P. J. and DeWreede, R. E. 1979. The effects of emergence and submergence on the photosynthesis and respiration of marine macrophytes. *Phycologia* **18**: 83–8.
- Skene, K. R. 2004. Key differences in photosynthetic characteristics of nine species of intertidal macroalgae are related to their position on the shore. *Can. J. Bot.* **82**: 177–84.
- Thomas, T. E., Harrison, P. J. and Taylor, E. B. 1987a. Adaptations of *Gracilaria pacifica* (Rhodophyta) to nitrogen

- procurement at different intertidal locations. *Mar. Biol.* **93**: 569–80.
- Thomas, T. E., Turpin, D. H. and Harrison, P. J. 1987b. Desiccation enhanced nitrogen uptake rates in intertidal seaweeds. *Mar. Biol.* **94**: 293–8.
- Villalard-Bohnsack, M. 1995. *Illustrated Key to the Seaweeds of New England*. The Rhode Island Natural Survey, Kingston, Rhode Island, 144 p.
- West, A. L., Mathieson, A. C., Klein, A. S., Neefus, C. D. and Bray, T. L. 2005. Molecular ecological studies of New England species of *Porphyra* (Rhodophyta, Bangiales). *Nova Hedwigia* **80**: 1–24.
- Zou, D. and Gao, K. 2002. Effects of desiccation and CO<sub>2</sub> concentrations on immersed photosynthesis in *Porphyra hatanensis* (Bangiales, Rhodophyta), a species farmed in China. *Eur. J. Phycol.* **37**: 587–92.