Alternative criteria for assessing nutrient limitation of a wetland macrophyte (*Peltandra virginica* (L.) Kunth)

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ABSTRACT

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Various nutrient incorporation and plant production parameters were measured to assess their relative usefulness in determining possible nutrient limitation of the wetland plant *Peltandra virginica* (L.) Kunth. From four stations located along a transect in a tidal freshwater marsh, we documented spatial differences in peak standing biomass of plants. Plant biomass was positively correlated with porewater concentrations of both ammonium and phosphate, but not with sediment concentrations of total nitrogen and phosphorus. Tissue nitrogen and phosphorus concentrations decreased significantly over the growing season, but there were no differences among plants from the four stations, and correlations between plant biomass and ratios of carbon to nitrogen and carbon to phosphorus were weak. Because in situ fertilization of plants had no effect on either peak biomass or tissue concentrations of nitrogen and phosphorus, growth of *Peltandra* was probably not nutrient limited. Other criteria did predict nitrogen or nitrogen and phosphorus limitation, however, demonstrating that application of parameters used by ecologists to support contentions of nutrient limitation can yield conflicting results. Assessment of nutrient limitation of primary producers may be an ambiguous and unnecessary task in some environments where these criteria are utilized.

INTRODUCTION

In recent reviews, Howartt (1988) and Smith (1984) discuss the ambiguities associated with defining and identifying nutrient limitation in aquatic ecosystems. They point out that research approaches to questions of nutrient limitation are often system-specific, e.g. techniques for documenting limitation in phytoplankton and vascular plants are quite different. Partly because of Redfield's (1958) pioneering work with marine phytoplankton, however, many of the techniques for estimating nutrient limitation have been devel-

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oped for systems in which microalgae are the dominant primary producers (Ryther and Dunstan, 1971; Boynton et al., 1982). Additional methodologies have arisen from research in aquatic systems dominated by macroalgae (Hanisak, 1979; Fageneli et al., 1986; Lapointe and O'Connell, 1989), seagrasses (Atkinson and Smith, 1983; Short et al., 1990), and wetland vegetation (Shaver and Melillo, 1984; DeLaune et al., 1986; Reddy et al., 1989).

In many aquatic environments, the logistics and expenses involved in completing the appropriate experiments have precluded direct assessment of nitrogen or phosphorus limitation. Whether working with individual plants or entire ecosystems, nutrient limitation often is difficult to measure because effects due solely to the addition or removal of nitrogen or phosphorus cannot always be segregated in the field. Laboratory fertilization experiments document how additions of nutrients stimulate carbon fixation or growth of primary producers (for review see Howarth, 1988), but incomplete experimental designs or laboratory assays make interpretations of nutrient limitation in the field difficult. As a consequence, alternative criteria have been used to infer nutrient limitation, as in theory the ramifications of nutrient limitation should be expressed in the biomass accumulation, growth morphology and/ or nutrient status of producers. Generally, relative concentrations of nitrogen and phosphorus either in the environment (Boyd and Hess, 1970; Smart and Barko, 1978; DeLaune and Pezeshki, 1988), taken up by plants (Gerloff and Krombholz, 1966; Shaver and Melillo, 1984), or incorporated into tissues (Goldman et al., 1979; Atkinson and Smith, 1983) may correspond with observed differences in the standing stocks or growth rates of primary producers. Where this occurs, the plants are considered nutrient limited, and by inference the measured parameters are assumed to be valid criteria for assessing nutrient availability. Because of the overlap amongst criteria and occasional tautological interpretation of these assessments, however, there is some confusion regarding the validity of any of these alternative criteria for nutrient limitation. The absence of a specific method for measuring nutrient limitation has made it sometimes difficult to compare systems for which nutrient limitation has been assessed differently.

Potentially more significant than difficulties arising from comparisons of nutrient limitation among ecosystems are comparisons within a particular environment, where the applicability of nutrient limitation criteria established by other researchers to assess limitation in different ecosystems is unknown. Our a priori notion was that we would be able to identify nitrogen or phosphorus limitation of the growth of the wetland plant *Peltandra virginica* (L.) Kunth in a tidal freshwater marsh by applying some of the methodology and reasoning from previous nutrient limitation studies developed in other environments. Specifically, we thought we would be able to identify variability in the incorporation of nutrients and growth of natural stands of *Peltandra* which would indicate whether nitrogen or phosphorus, if either, was limiting. From

four stations located along a transect in a tidal freshwater marsh, we documented differences in above-ground standing stocks of *Peltandra* early in the growing season and at the time of peak biomass. A group of published parameters used as proxies for nutrient availability was measured, and the validity of each parameter as a criterion for nutrient limitation of *Peltandra* was assessed. We found that these proxies yielded conflicting interpretations of the nutrient limitation status of plant growth.

METHODS

Study site

The study was conducted in Eagle Bottom marsh, a fringing tidal freshwater marsh on the Chickahominy River in southeastern Virginia (Fig. 1). The Chickahominy is a tributary of the James River sub-estuary of Chesapeake Bay. Tidal amplitude is 0.8 m, and tides are diurnal. Dominant vegetation is the perennial *Peltandra virginica. Peltandra* grows in hummocks, with vegetated sections of marsh higher than surrounding unvegetated soils (Harvey, 1990). Leaves emerge from a below ground corm in spring, and peak aboveground biomass is in late June (Odum et al., 1984). Other annual species, including *Zizania aquatica* L. and *Hibiscus moscheutos* L., grow in the higher, interior marsh areas.

Nutrient concentrations in porewater

Four stations in the marsh were established at roughly 30 m intervals along a single transect starting from a small creekbank near the river and sloping gradually upward to a forested hillslope adjacent to the marsh (Fig. 1, inset). Station 1, nearest the hillslope, was flooded less frequently than Station 4. At each station, replicate porewater samplers (sippers: see Chambers and Odum, 1990) were placed in the root zone of the soil to sample water at depths of 10, 20, 30, 40, and 50 cm. At peak growth during June 1988, porewater from each of the four stations was collected and filtered (0.45 μm pore size) into acidified vials in the field, then brought back on ice to the laboratory for nutrient analysis. All water samples were analyzed colorimetrically for ammonium and phosphate (Parsons et al., 1984), the dominant dissolved inorganic species of nitrogen and phosphorus in reduced marsh soils (Buresh et al., 1981; DeLaune et al., 1981).

Nutrient concentrations in sediments

Replicate cores from unvegetated soils surrounding *Peltandra* hummocks were collected during June 1988 using a thin-walled aluminum corer, 10 cm
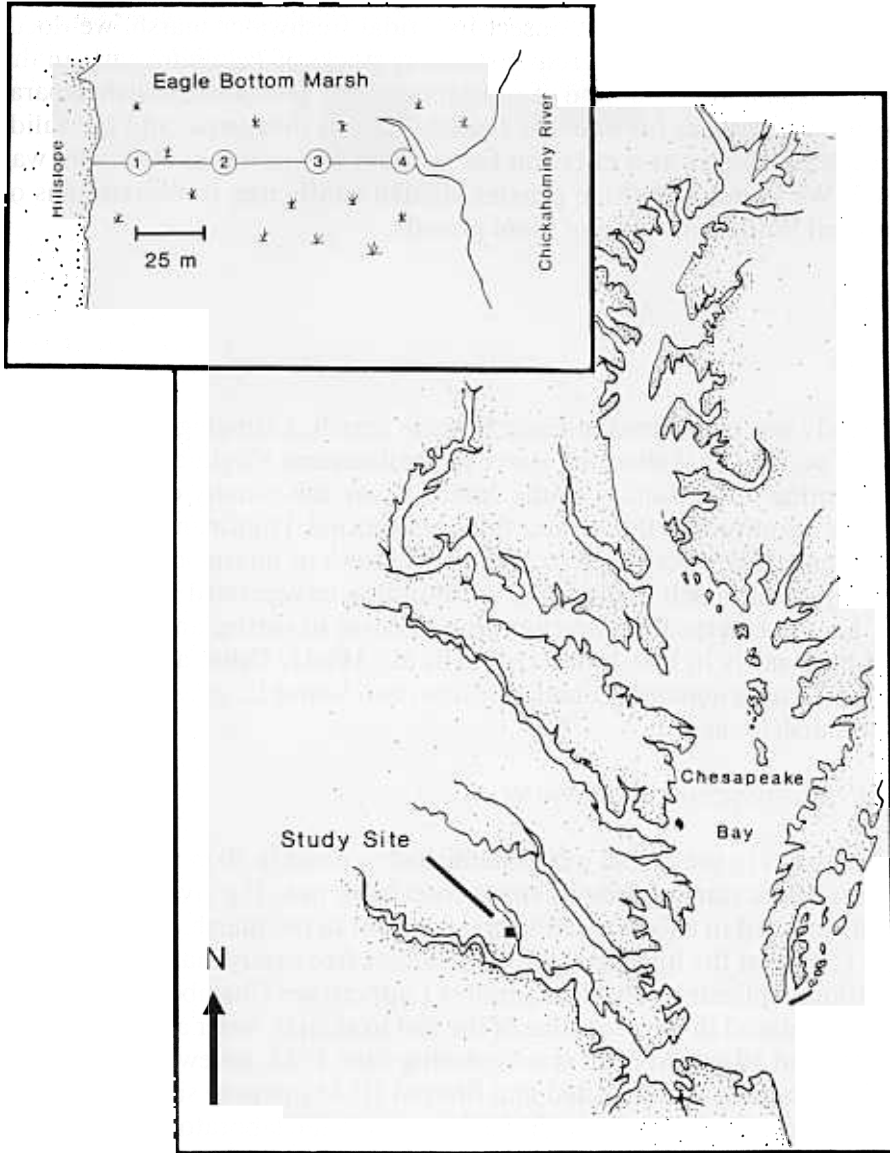
Fig. 1. Location of the tidal freshwater marsh on the Chickahominy River, a tributary of the James River sub-estuary of Chesapeake Bay. Inset: transect across Eagle Bottom marsh, showing position of the four sampling stations relative to the river and adjacent hillslope.

in diameter. The cores were sliced horizontally to yield vertical 2.5 cm sections. Every other section from 0 to 30 cm (the depth of the root zone in adjacent hummocks) was retained for analysis. Macro-organic matter was not separated from sediments, although small plant roots were a very minor frac-

tion of the total core volume. The soils were lyophilized and milled to pass a No. 40 mesh screen. Total nitrogen and phosphorus concentrations in duplicate subsamples of the soils were determined using procedures described for plant analyses.

Plant biomass and carbon, nitrogen and phosphorus determinations

Plants from each station were harvested twice during the 1989 growing season. Early in the season (21 April), all above-ground vegetation from replicate 0.25 m^2 quadrats was harvested at each of the four stations by clipping the plants to within 2 cm of the soil surface. Sampling was repeated at the approximate time of peak biomass (26 June). On each date, plants were clipped, rinsed, placed in plastic bags and taken back to the laboratory and frozen. Plants from 21 April were lyophilized to a constant weight to determine standing biomass. For the peak biomass collection, subsamples were weighed, lyophilized and re-weighed to calculate standing biomass.

Dried plant samples were homogenized by milling through a No. 40 mesh screen. Carbon and nitrogen contents of duplicate subsamples of each sample were determined with a Carlo Erba model 1500 CN analyzer. Phosphorus content was measured using a modification of the method presented in Solorzano and Sharp (1980) for particulate total phosphorus determination. Duplicate subsamples of each sample were weighed (5–20 mg) into tared glass scintillation vials; 0.5 ml of 0.17 M Na_2SO_4 and 2.0 ml of 0.017 M $MgSO_4$ were added to each vial, and the vials were dried in an oven at 90°C. Standards were treated identically. Dry vials containing samples and standards then were ashed at 500°C for 3 h. After cooling, 5.0 ml of 0.2 N aqueous HCl were added to each vial, the vials were capped, and then they were placed in an oven at 80°C for 30 min. Each vial was diluted with 10.0 ml of deionized water, shaken, and allowed to stand overnight to allow the ash to settle. Phosphate concentrations of the vial solutions were determined colorimetrically using the molybdate blue method (Parsons et al., 1984). We found this method to yield 95–103% of the reported phosphorus content of NBS standard orchard leaves.

Effects of fertilization

During the 1990 growing season, the response of *Peltandra* growth to fertilization was examined. Triplicate experimental plots at each of the four stations (Fig. 1) received a single application of 1400 g m^{-2} of a timed-release fertilizer (Osmocote®, nitrogen:phosphorus = 14:14), which was worked into the surface soils on 18 April. Untreated plots served as controls. In the middle of June, plants from 0.25 m^{-2} experimental and control plots were harvested, and biomass and nutrient concentrations in tissues were measured using methods described previously.

Data analysis

Our a priori hypothesis was that differences in peak standing crop of *Peltandra virginica* would be correlated with relative nutrient concentrations in the environment or in above-ground plant tissues, which would in turn reflect nutrient availability. We therefore documented general between-station differences in average plant biomass using ANOVA, and plotted peak biomass as a function of average porewater concentrations of ammonium and phosphate. The depth profiles of total nutrient concentrations in sediments from different stations were also compared. Seasonal differences in nutrient concentrations of the plant tissues (April vs. June) were assessed using t-tests. Carbon, nitrogen and phosphorus concentrations in plants from each of the harvested quadrats, as well as the respective carbon to nitrogen, carbon to phosphorus and nitrogen to phosphorus ratios of the tissues, were correlated with biomass in April and June 1989 using regression analysis. Finally, the effects of fertilization at the four stations in 1990 were assessed using a two-way ANOVA, testing treatment and location in the marsh as main effects.

RESULTS

Large differences in biomass of *Peltandra virginica* were found between April and peak standing crop at the end of June (Fig. 2(A)). Also, there were large differences among stations at the time of peak standing crop (ANOVA, $P < 0.05$); the greatest average biomass was found nearest the creekbank (1552 g m^{-2}, Station 4), and the least from the interior of the marsh (769 g m^{-2}, Station 2). Plants adjacent to the creekbank appeared more robust, with much thicker petioles and broader leaves, than plants from the interior of the marsh.

Depth-averaged ammonium and phosphate concentrations in porewater were different by station in the marsh, and exhibited the same marsh-wide pattern as peak biomass (Fig. 2(B)). In general, ammonium and phosphate concentrations were lowest at Station 2 (2.5 μM and 3.3 μM, respectively, $N = 10$) and highest at Station 4 (48 and 72 μM, $N = 10$). There was also a substantial amount of variation in nutrient concentrations among water samples at each station (note size of error bars), suggesting significant microscale differences in the porewater environment. Correlations of average peak biomass vs. average ammonium and phosphate concentrations from the four stations were highly significant (Fig. 3). Sections of marsh with high peak aboveground biomass were positively associated with high porewater concentrations of dissolved ammonium and phosphate. The molar ratios of DIN:DIP (μmol ammonium:μmol phosphate) were low at all four stations, averaging less than 1:1 (Fig. 2(B)).

In contrast, elemental analysis of soils from the stations exhibiting the largest differences in peak biomass and dissolved nutrient concentrations in soil
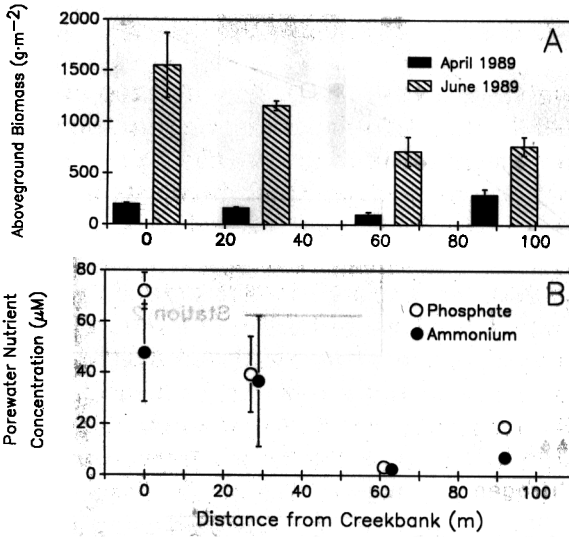
Fig. 2. Distance from creekbank and measurements of: (A) average above-ground biomass early in the growing season (April) and at the time of peak standing crop (June); (B) average porewater concentrations of dissolved phosphate and ammonium at the time of peak standing crop. Means and standard deviations are based on sample sizes of two and ten for biomass and porewater concentrations, respectively.
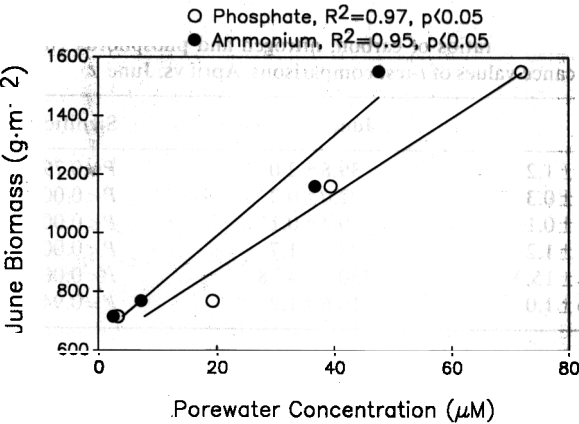

Fig. 3. The association of June above-ground biomass with porewater concentrations of dissolved phosphate and ammonium ($N=4$).

porewater (Stations 2 and 4) revealed no differences in total soil nitrogen and phosphorus (Fig. 4). For both nutrients at Stations 2 and 4, there was a trend of decreasing concentration (expressed as weight percent) with soil depth. One phosphorus profile from Station 2 was higher than the three from the other cores, and nitrogen concentrations in surface sediments were higher
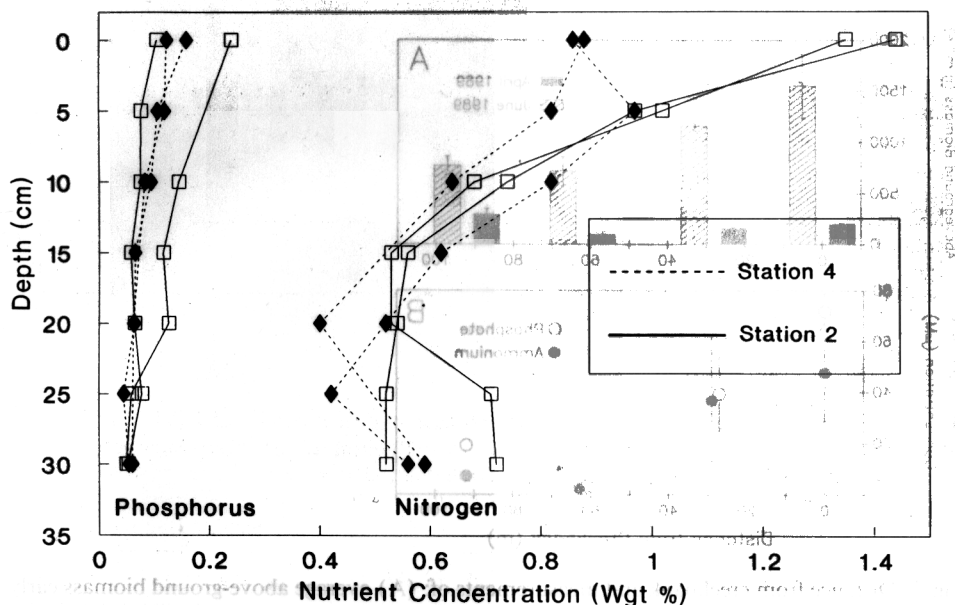
Fig. 4. Total phosphorus and nitrogen profiles in soils from creekbank (Station 4) and interior (Station 2) marsh. Each point represents a single value, with two cores analyzed per station.

TABLE 1

Nutrient content by weight percent and atomic ratios of carbon, nitrogen and phosphorus (mean ±SD) of *Peltandra virginica*, plus significance values of *t*-test comparisons, April vs. June

	April	June	Significance
Carbon (% wt.)	40.0±1.2	39.8±2.0	P=0.791
Nitrogen (% wt.)	3.2±0.3	2.0±0.2	P<0.001
Phosphorus (% wt.)	0.7±0.1	0.4±0.1	P<0.001
C:N ratio	14.5±1.2	23.6±1.7	P<0.001
C:P ratio	153.6±15.2	250.5±41.8	P<0.001
N:P ratio	10.6±1.0	10.6±1.2	P=0.948

at Station 2 than at Station 4 (1.40% vs. 0.87%). It is interesting to note that soils at Station 2, with lower biomass and dissolved nutrient concentrations, exhibited roughly equal, and at some depths higher, total nitrogen and phosphorus contents than soils at Station 4.

On average, the carbon content of above-ground plant tissue was 40% by weight for plants collected from all four stations, and this concentration did not change between April and June, 1989 (Table 1). With the accumulation of biomass during the growing season, however, the concentrations of both nitrogen and phosphorus in plant tissues decreased significantly (*t*-tests, P<0.001). A concomitant increase in the atomic ratios of carbon to nitrogen

TABLE 2

Correlation coefficients of plant biomass vs. nutrient content of above-ground leaf tissue

Month of biomass measurement	%C	%N	%P	C:N	C:P	N:P
April	0.13	0.65*	0.48	−0.57	−0.36	0.17
June	−0.80**	−0.10	0.04	−0.47	−0.14	−0.21

*$P<0.05$; **$P<0.01$

TABLE 3

Results of fertilization experiment, 1990 growing season. Nutrient contents by weight percent and atomic ratios of C, N and P (mean ±SD) for control and fertilized treatments. Significance values are for two-way ANOVA, testing treatment and station main effects

	Treatment		Significance of effect	
	Control	Fertilized	Treatment	Station
Carbon (% wt.)	43.9±1.2	43.4±1.2	$P=0.50$	$P=0.48$
Nitrogen (% wt.)	1.9±0.1	1.9±0.2	$P=0.66$	$P=0.33$
Phosphorus (% wt.)	0.4±0.02	0.4±0.04	$P=0.75$	$P=0.09$
C:N ratio	27.2±1.0	27.8±3.0	$P=0.69$	$P=0.18$
C:P ratio	307.0±18.5	310.0±35.3	$P=0.88$	$P=0.07$
N:P ratio	11.3±0.5	11.3±1.3	$P=0.97$	$P=0.23$

and carbon to phosphorus occurred because of the stable carbon concentrations and decreasing nitrogen and phosphorus concentrations. Although the nitrogen and phosphorus contents of *Peltandra* tissues decreased between April and June, the average atomic ratio of nitrogen to phosphorus remained constant at 10.6.

Above-ground *Peltandra* biomass in April was significantly correlated with nitrogen content of the tissues, but correlations of biomass with phosphorus and atomic ratios of nutrients were not significant (Table 2). In June, carbon content was negatively correlated with biomass, a trend reflecting increased mineral accumulation in larger plants near the creekbank. Larger plants did not accumulate larger percentages of nitrogen and phosphorus, however, as correlations between biomass and nutrient content were weak.

General growth patterns across the marsh in 1990 were similar to those observed 1989 (Fig. 2(A)), with vegetation near creekbanks larger than plants from the interior marsh (ANOVA, $F_{3,16}=17.2, P<0.001$). Across the marsh, however, plants from fertilized plots were no larger than from control plots (ANOVA, $F_{1,16}=1.4, P>0.25$). Further, fertilized plants did not contain higher percentages of nitrogen and phosphorus than unfertilized plants, nor

were there significant differences in the nutrient content of plants from different stations (two-way ANOVA Table 3).

DISCUSSION

An inherent assumption of all limitation studies is that differences in nutrient availability are demonstrable in measures of nutrient uptake, growth and/or biomass accumulation of primary producers. As there is no universally applicable methodology for determining limitation, however, a number of nutrient incorporation and plant production parameters are used by aquatic and terrestrial ecologists to identify nutrient limitation. We applied some of these established methods to assess their relative usefulness in determining possible nutrient limitation of *Peltandra virginica* in a tidal freshwater marsh. Our results indicated that such an approach may be too simplistic, as application of different methodologies led to different and sometimes contradictory conclusions about nitrogen or phosphorus limitation.

We found significant differences in peak biomass of *Peltandra virginica* across a transect in Eagle Bottom, a tidal freshwater marsh (Fig. 2(A)). These biomass differences corresponded closely with concentrations of dissolved inorganic nitrogen and phosphorus (DIN, DIP) in the soil porewater (Fig. 3). If porewater concentrations of nutrients were a valid proxy for nutrient availability (Gerloff and Krombholz, 1966; Bayly et al., 1985), then it could be argued that *Peltandra* is either nitrogen or phosphorus limited, as increased availability was associated with increased biomass accumulation. There are many reasons, however, why DIN and DIP concentrations may not be adequate indicators of nutrient availability to primary producers (Smith, 1984; Howarth, 1988). The use of DIN and DIP concentrations may lead to an underestimation of the availability of nutrients, as nitrogen and phosphorus sorbed to clays and organic/mineral complexes, and in labile organic matter were not measured. Uptake rates and turnover times of dissolved nutrient pools are unknown, yet clearly these are the crucial parameters necessary to relate nutrient availability to uptake and growth (Howarth, 1988). Observed differences in porewater nutrient concentrations could be a cause, a consequence, or a coincidence of the amount of accumulated plant biomass, a feature which cannot be determined from simple regression analysis.

In the absence of turnover estimates of nutrient pools, however, DIN and DIP standing stocks have been used to assess nutrient availability by comparing the ratio of total nitrogen to total phosphorus in plant tissue with that of DIN:DIP in the surrounding water (e.g. Boynton et al., 1982). Nitrogen or phosphorus limitation is inferred if plants incorporate nutrients into biomass at a ratio that differs from source waters. In this study, atomic DIN:DIP ratios were less than 3 from all stations (Fig. 2(B)), yet the atomic ratio of nitrogen to phosphorus in *Peltandra* was 10.6 (Table 1). Using this criterion,

the growth of *Peltandra* is apparently nitrogen limited, because the source of nutrients (porewater) is depleted in nitrogen relative to the plants. Plants must incorporate more nitrogen than phosphorus relative to apparent availability.

We found no differences in total nutrient concentrations in soils from stations supporting the largest and smallest peak standing crops of *Peltandra* (Fig. 4), even though there were large differences in DIN and DIP in the porewater. Strong correlation between total nutrient concentrations in the sediments and nutrient concentrations in the plants have been used as a potential measure of nutrient availability for production. Under some circumstances, total soil nutrients is probably a valid criterion for nutrient limitation to growth, as the amounts of nutrient incorporation may be different for plants of different size (DeLaune and Pezeshki, 1988). As no such relationship was found in this study, this criterion indicates that total nitrogen and phosphorus concentrations in soils do not limit *Peltandra* growth. Environmental factors besides total in situ concentrations of nutrients must affect the availability of nutrients as evidenced by the porewater concentration data (Fig. 2(A)), and the abilities of plants to assimilate them (Boyd and Hess, 1970).

In addition to the preceding assays of nutrient availability measured in soils and solutions external to the plants, other researchers have focused in more detail on measurable nutrient responses in the actual plant tissues. One of the first studies of nutrient limitation in aquatic macrophytes was by Gerloff and Krombholz (1966), who based their notion of nutrient limitation on the relative amounts of nitrogen and phosphorus incorporated into plant tissue. If a nutrient was limiting, then additions of nutrients would lead to greater biomass accumulation, plus higher percentages of nitrogen or phosphorus in plant tissue. Similarly, Shaver and Melillo (1984) used the inverse of nitrogen and phosphorus concentrations in plant tissues as estimates of nutrient use efficiency. Plants with more available nutrients would decrease their nutrient use efficiency (and increase the amount of nutrient relative to total biomass), thus documenting nutrient limitation. Our data did not detect this effect: higher *Peltandra* biomass was not associated with higher concentrations of nitrogen and phosphorus in the plant tissue. Applying this criterion, we conclude that neither nitrogen nor phosphorus is limiting in the tidal freshwater marsh.

Tissue concentrations of nitrogen and phosphorus in *Peltandra* decreased between April and June (Table 1), but whether these decreases were a reflection of nutrient limitation is not clear. An interpretation of temporal changes in nutrient concentrations in plant tissues was given by Lukatelich et al. (1987), who suggested that non-limiting nutrients would be incorporated into biomass at the same percentages over a growing season, and that concentrations of limiting nutrients would gradually decrease. Alternately, Broome et al. (1975) assumed that physiological constraints were the cause of observed

constant nitrogen concentrations in tissues of different-sized plants of *Spartina alterniflora* Loisel. They inferred nitrogen limitation based on greater biomass accumulation which was associated with a constant percentage of nutrient incorporation. Our data do not meet the criterion for nutrient limitation established by Broome et al. (1975); instead, application of the method suggested by Lukatelich et al. (1987) indicates that both nitrogen and phosphorus are limiting to *Peltandra* between the onset and peak of the growing season. Of course, the decreases in nutrient concentrations may simply reflect the accumulation of structural carbohydrate relative to nitrogen and phosphorus assimilation.

We documented seasonal differences in nutrient concentrations of *Peltandra* tissues. Within sampling dates, however, biomass from harvested quadrats in Eagle Bottom marsh was not consistently correlated with the percentage of phosphorus or nitrogen in the plant tissue (Table 2). Biomass in April was significantly correlated with nitrogen, not phosphorus, content; at the time of peak above-ground biomass in June, neither nutrient was an adequate predictor of standing crop. These results suggest nutrient limitation may be transient over the growing season. In contrast, the standing stocks of nutrients (peak biomass×%N or %P) were different among stations, but this was a consequence of greater biomass and not greater nutrient concentration per unit weight of plant.

Some plants are reported to take up more nitrogen and phosphorus when available (luxury nutrient uptake, sensu Gerloff and Kromholtz, 1966), yet greater uptake is not always associated with greater growth rates or biomass accumulation. Whigham and Simpson (1978) found that sewage effluent applied to a community of tidal freshwater marsh plants (including *Peltandra*) increased the nitrogen and phosphorus concentrations of tissues, but that above-ground biomass was not significantly different between enriched and control plots. Walker (1981) also found that fertilization did not always increase biomass accumulation in a *Peltandra* marsh, and our results indicate that neither above-ground biomass nor nutrient contents of plant tissues were affected by fertilization (Table 3). One possible explanation of our data is that the method of fertilization was inappropriate, but using an identical method in experimental salt marsh plots, we have increased above-ground biomass and leaf nitrogen concentrations in *Spartina alterniflora* (R.M. Chambers and W.E. Odum, unpublished data, 1989). Also, the freshwater marsh plant *Panicum hemitomon* Schult. did grow more in a nitrogen enrichment study by DeLaune et al. (1986), but the nitrogen content of plants was only slightly greater in fertilized plots (0.70% vs. 0.67%). DeLaune et al. (1986) point out that significant amounts of organic nitrogen in wetland soils are mineralized in situ and, compared with tidal or even fertilization subsidies, can be the major source of reduced nitrogen for uptake by and growth of wetland plants. The absence of a fertilization response by *Peltandra* in the

present study suggests that nutrient demands are met by in situ nutrient concentrations, or that some other environmental factor limits nitrogen and phosphorus availability to the plant. Also, *Peltandra* is a perennial plant with a large storage rhizome, or corm, from which nutrient mobilization to developing above-ground tissues occurs; supplemental nutrients from the porewater environment may not even be important during the growing season. The lack of a significant growth response to fertilization in the present study therefore may not be that unusual, although the amounts of nutrients in storage are not usually sufficient to sustain growth over an entire season (DeLaune et al., 1986).

Owing to different nutrient sources, and different requirements for nutrients (especially carbon) in tissue structure, comparisons of the Redfield ratio of carbon, nitrogen and phosphorus incorporation into oceanic phytoplankton with those of macrophytes probably are not instructive for assessments of nutrient limitation of emergent macrophytes. Nonetheless, the Redfield ratio of 106:16:1 is still used as a benchmark for comparing relative amounts of carbon, nitrogen and phosphorus, and extreme departures from it may be taken as evidence of nutrient limitation (Faganeli et al., 1986). Other researchers are more cautious in comparing nutrients contents in macrophytes with deep-water phytoplankton, and have proposed more specific scales for comparison. Atkinson and Smith (1983) developed the notion of optimal growth ratios in submerged macrophytes from an original idea by Gerloff and Kromholtz (1966) and subsequently expanded by Shaver and Melillo (1984). They reasoned that plant species under optimal growth conditions exhibit specific ratios of carbon, nitrogen and phosphorus incorporation. Knowing this 'local' Redfield ratio (Smith and Hollibaugh, 1989), observed departures from it could be used as evidence for nutrient limitation. From our data, the carbon: nitrogen: phosphorus ratio in April was 137:11:1, and in June it was 250:11:1 (Table 2). Over the growing season, the ratio of nitrogen to phosphorus was constant, and the changes in organic matter as a result of carbohydrate production led to an increase in the relative amounts of carbon. An observed constant nitrogen to phosphorus ratio suggests that neither nitrogen or phosphorus is limiting to *Peltandra* growth in this marsh, and that relative to nitrogen and phosphorus, carbon appears most responsive to physiological constraints imposed by environmental factors other than nutrient availability (Goldman et al., 1979). On the other hand, Booth (1989) found that nitrogen to phosphorus ratios in *Peltandra* increased over the growing season from 11.9 to 16.2, which suggests phosphorus limitation in his study. Even with seasonal differences in nitrogen to phosphorus ratios, however, the establishment of an optimum ratio, above and below which phosphorus or nitrogen is limiting, is somewhat arbitrary.

Results of this study support conclusions drawn by others, that factors besides nutrient concentration may limit nutrient availability to plants or trans-

lation of these nutrients into biomass (Gallagher, 1975; Chalmers, 1979; Morris, 1980; Craft et al., 1989; Bradley and Morris, 1990). Walker (1981) found that nitrogen and phosphorus concentrations were higher in 'stressed' (water-logged) plants, a pattern he attributed to decreased photosynthate production and increased carbohydrate utilization below ground for anaerobic respiration. Contrary to the implied direct effect of nutrient limitation on plant growth, physiological constraints under genetic and environmental control may indirectly limit nutrient availability for primary production.

To summarize we applied various proxies from the literature to determine whether growth of the wetland plant *Peltandra virginica* was nutrient limited. Although a majority of these proxies indicated neither nitrogen nor phosphorus were in limiting supply to *Peltandra*, the results were conflicting. The non-unanimous conclusion reached by these assessments points out the hazard associated with reliance on any one criterion for demonstration of nutrient limitation. Conceptually, nutrient limitation is an important ecological term describing the relationship between primary producers and their environment. Without the appropriate experiments, however, identification of nutrient limitation may not be a straightforward task, as edaphic features of aquatic ecosystems may preclude the applicability of nutrient limitation criteria.

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REFERENCES

Atkinson, M.J. and Smith, S.V., 1983. C:N:P ratios of benthic marine plants. Limnol. Oceanogr., 28: 568–574.

Bayly, S.E., Zoltek, J., Hermann, A.J., Dolan, T.J. and Tortora, L., 1985. Experimental manipulation of nutrients and water in a freshwater marsh: Effects on biomass, decomposition, and nutrient accumulation. Limnol. Oceanogr., 30: 500–512.

Booth, P.M., 1989. Nitrogen and phosphorus cycling strategies in two tidal freshwater macrophytes, *Peltandra virginica* and *Spartina cynosuroides*. Ph.D. Dissertation, VIMS, College of William and Mary, Williamsburg, VA, 250 pp.

Boyd, C.E. and Hess, L.W., 1970. Factors influencing shoot production and mineral nutrient levels in *Typha latifolia*. Ecology, 51: 296–300.

Boynton, W.R., Kemp, W.M. and Keefe, C.W., 1982. A comparative analysis of nutrients and other factors influencing estuarine phytoplankton production. In: V.S. Kennedy (Editor), Estuarine Comparisons. Academic Press, New York, pp. 69–90.

Bradley, P.M. and Morris, J.T., 1990. Influence of oxygen and sulfide concentration on nitrogen uptake kinetics in *Spartina alterniflora*. Ecology, 71: 282–287.

Broome, S.W., Woodhouse, W.W. and Seneca, E.D., 1975. The relationship of mineral nutrients to growth of *Spartina alterniflora* in North Carolina: I. Nutrient status of plants and soils in natural stands. II. The effects of N, P, and Fe fertilizers. Soil Sci. Soc. Am. Proc., 39: 295–307.

Buresh, R.J., DeLaune, R.D. and Patrick, W.H., 1981. Influence of *Spartina alterniflora* on nitrogen loss from marsh soils. Soil Sci. Soc. Am. Proc., 45: 660–661.

Chalmers, A.G., 1979. The effects of fertilization on nitrogen distribution in a *Spartina alterniflora* salt marsh. Estuarine Coastal Mar. Sci., 8: 327–337.

Chambers, R.M. and Odum, W.E., 1990. Porewater oxidation dissolved phosphate and the iron curtain: Iron–phosphorus relations in tidal freshwater marshes. Biogeochemistry, 10: 35–52.

Craft, C.B., Broome, S.W. and Seneca, E.D., 1989. Nitrogen, phosphorus and organic carbon pools in natural and transplanted marsh soils. Estuaries, 11: 272–280.

DeLaune, R.D. and Pezeshki, S.R., 1988. Relationship of mineral nutrients to growth of *Spartina alterniflora* in Louisiana salt marshes. Northeast Gulf Sci., 10: 55–60.

DeLaune, R.D., Reddy, C.N. and Patrick, W.H., 1981. Accumulation of plant nutrients and heavy metals through sedimentation processes and accretion in a Louisiana salt marsh. Estuaries, 4: 328–334.

DeLaune, R.D., Smith, C.J. and Sarafyan, M.N., 1986. Nitrogen cycling in a freshwater marsh of *Panicum hemitomon* on the deltaic plain of the Mississippi River. J. Ecol., 74: 249–256.

Faganeli, J., Vukovic, A., Saleh, F.I. and Pezdic, J., 1986. C:N:P ratios and stable carbon and hydrogen isotopes in the benthic marine algae, *Ulva rigida* C. Ag. and *Fucus virsoides* J. Ag. J. Exp. Mar. Biol. Ecol., 102: 153–166.

Gallagher, J.L., 1975. Effect of ammonium nitrate pulse on the growth and elemental composition of natural stands of *Spartina alterniflora* and *Juncus roemerianus*. Am. J. Bot., 62: 644–648.

Gerloff, G.C. and Krombholz, P.H., 1966. Tissue analysis as a measure of nutrient availability for the growth of angiosperm aquatic plants. Limnol. Oceanogr., 11: 529–537.

Goldman, J.C., McCarthy, J.J. and Peavey, D.G., 1979. Growth rate influence on the chemical composition of phytoplankton in oceanic waters. Nature, 279: 210–215.

Hanisak, M.D., 1979. Nitrogen limitation of *Codium fragile* ssp. *tomentosoides* as determined by tissue analysis. Mar. Biol., 50: 333–337.

Harvey, J.W., 1990. Hydrological transport in tidal marsh soils. Ph.D. dissertation, University of Virginia, Charlottesville, 248 pp.

Howarth, R.W., 1989. Nutrient limitations of net primary production in marine ecosystems. Ann. Rev. Ecol. Syst., 19: 89–110.

Lapointe, B.E. and O'Connell, J., 1989. Nutrient-enhanced growth of *Cladophora prolifera* in Harrington Sound, Bermuda: eutrophication of a confined, phosphorus-limited marine ecosystem. Estuarine Coastal Shelf Sci., 28: 347–360.

Lukatelich, R.J., Schofield, N.J. and McComb, A.J., 1987. Nutrient loading and macrophyte growth in Wilson Inlet, a bar-built southwestern Australian estuary. Estuarine Coastal Shelf Sci., 24: 141–165.

Morris, J.T., 1980. The nitrogen uptake kinetics of *Spartina alterniflora* in culture. Ecology, 61: 1114–1121.

Odum, W.E., Smith, T.J., Hoover, J.K. and McIvor, C.C., 1984. The ecology of tidal freshwater marshes of the United States east coast: A community profile. FWS/OBS-83/17, 177 pp.

Parsons, T.R., Maita, Y. and Lalli, C.M., 1984. A Manual of Chemical and Biological Methods for Seawater Analysis. Pergamon Press, New York, 173 pp.

Reddy, K.R., Agami, M. and Tucker, J.C., 1989. Influence of nitrogen supply rates on growth and nutrient storage by water hyacinth (*Eichhornia crassipes*) plants. Aquat. Bot., 36: 33–43.

Redfield, A.C., 1958. The biological control of chemical factors in the environment. Am. Sci., 46: 205–222.

Ryther, J.H. and Dunstan, W.M., 1971. Nitrogen, phosphorus, and eutrophication in the coastal marine environment. Science, 171: 1008–1013.

Shaver, G.R. and Melillo, J.M., 1984. Nutrient budgets of marsh plants: efficiency concepts and relation to availability. Ecology, 65: 1491–1510.

Short, F.T., Dennison, W.C. and Capone, D.G., 1990. Phosphorus-limited growth of the tropical seagrass *Syringodium filiforme* in carbonate sediments. Mar. Ecol. Prog. Ser., 62: 169–174.

Solorzano, L. and Sharp, J.H., 1980. Determination of total dissolved phosphorus and particulate phosphorus in natural waters. Limnol. Oceanogr., 25: 754–758.

Smart, R.M. and Barko, J.W., 1978. Influence of sediment salinity and nutrients on the physiological ecology of selected salt marsh plants. Estuarine Coastal Shelf Sci., 7: 487–495.

Smith, S.V., 1984. Phosphorus versus nitrogen limitation in the marine environment. Limnol. Oceanogr., 29: 1149–1160.

Smith, S.V. and Hollibaugh, J.T., 1989. Carbon-controlled nitrogen cycling in a marine 'macrocosm': an ecosystem-scale model for managing cultural eutrophication. Mar. Ecol. Prog. Ser., 52: 103–109.

Walker, R., 1981. Nitrogen, phosphorus and production dynamics for *Peltandra virginica* (L.) Kunth in a southern New Jersey freshwater tidal marsh. Ph.D. Dissertation, Rutgers University, 166 pp.

Whigham, D.F. and Simpson, R.L., 1978. Nitrogen and phosphorus movement in a freshwater tidal wetland receiving sewage effluent. Proceedings of a Symposium on Technological, Environmental, Socioeconomic, and Regulatory Aspects of Coastal Zone Management. ASCE, San Francisco, pp. 2189–2203.