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Ammonium and Phosphate Dynamics in a Virginia Salt Marsh

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ABSTRACT: Experimental chambers were used in a Virginia salt marsh to partition the tidal flux of dissolved nutrients occurring at the marsh surface and in the water column. On five dates from June to October 1989, six replicate chambers in the short *Spartina alterniflora* zone were monitored over complete tidal cycles. When reservoir water, used to simulate tidal flooding in the chambers, was initially low in dissolved nutrients, the marsh surface was a source of both ammonium and phosphate to the water column. Calculations of the physical processes of diffusion and advection could not account for total nutrient release from the marsh surface. We hypothesize the primary source of nutrients was organic matter mineralization in surface sediments, which released nutrients into the flooding water column. Assimilation (uptake) of phosphate measured in water-column incubation experiments was nearly equal to phosphate released from the marsh surface. Surface release of ammonium, however, was somewhat greater than water-column uptake. In this salt marsh, benthic production and release of ammonium and phosphate is comparable in magnitude to pelagic consumption, thereby yielding only a small “net” transfer of these nutrients to the estuary.

Introduction

Exchange of materials between tidal marshes and estuarine waters is studied by monitoring net movements of organic matter and nutrients over tidal or seasonal flooding cycles (Jordan et al. 1983; Chalmers and Wiegert 1985; Whiting et al. 1987; Childers and Day 1988, 1990; Spurrier and Kjerfve 1988; Wolaver and Spurrier 1988). Typically, the intent of such work is to document how processes associated with different components of the intertidal system (e.g., mudflats vs marsh) affect uptake from, or release to, tidal water. It is often difficult, however, to make accurate measurements of the exchange of tidal water volumes, since calculations of the net flux of constituents in that water must incorporate a frequently large error term (Valiela et al. 1978; Boon 1980). Also, since tidal ebb and flow transport large loads of dissolved and particulate material relative to the amount actually exchanged, it is not surprising that the directions for net flux are often difficult to determine statistically (Chrzanowski and Spurrier 1987).

Many of the studies cited above measured materials exchanges over large spatial scales, where wetlands can be viewed as an interface or ecotone between terrestrial and aquatic environments (Chalmers et al. 1985; Odum 1990). This is a sensible approach, since the large surface area of wetlands relative to tidal volume indicates that benthic-pelagic interactions are concentrated in tidal marshes. The integrated exchange studies yield important information on net nutrient movements in natural, unmanipulated systems. Contributions of specific biogeochemical processes to net exchanges, which typically are missed by this method, can be assessed by examining wetlands at a smaller scale (Lee 1979; Keizer et al. 1989; Scudlark and Church 1989). Results from such an experimental approach may be utilized to address the internal mechanisms of nutrient processing and exchange which contribute to the overall net flux of nutrients from a wetland (Whiting et al. 1989).

The present study was designed to observe the dynamics of dissolved ammonium and phosphate exchanges between a salt marsh and flooding tidal waters. The experimental design incorporated small-scale, in situ methods to assess the importance of various mechanisms of dissolved nutrient exchange (diffusion, advection, mineralization, and uptake) as they occur at the marsh surface. With this methodology, we sacrificed the measurement

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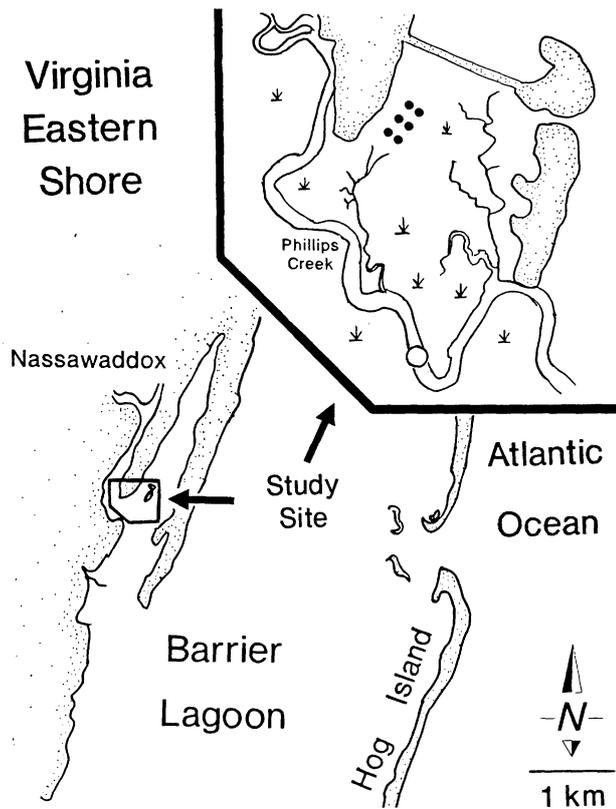


Fig. 1. General study area on the Eastern Shore of Virginia, showing mainland, Hog Island, and associated marsh and mud-flat areas (barrier lagoon). The Phillips Creek study site is located on the mainland fringe opposite Hog Island. Inset: Phillips Creek marsh complex, with location of six experimental chambers (filled circles) and sampling station for creek study (open circle).

of large-scale fluxes to try to separate soil and water column processes which influence dissolved inorganic nutrient exchange. Ammonium and phosphate occur in high concentrations in salt marsh soil porewater, participate in a number of biogeochemical reactions, and are important potential regulators of productivity. Specific exchanges of ammonium and phosphate in various components of the marsh ecosystem, however, have not been adequately quantified.

Using experimental chambers to isolate sections of salt marsh, we assessed soil-water column coupling and identified the seasonal pattern of nutrient exchange between wetland and water. Further, we developed a water budget for the marsh soil to determine the possible contribution of porewater advection to observed nutrient fluxes. Our results showed that over the growing season the salt marsh soil was a source of dissolved ammonium and phosphate to the water column. Much of the nutrient release from marsh soil occurred during the initial stages of the flooding tidal cycle, at rates more rapid than could be accounted for by either ad-

vection or a simple diffusion model. A short-term incubation experiment demonstrated that nutrients released by the marsh could be taken up rapidly by the water column. Measured changes in nutrient concentrations over a tidal cycle in the adjacent creek, however, suggested there was a net export of ammonium from these mainland marshes.

Methods

STUDY SITE

The salt marsh selected was within the Virginia Coast Reserve/Long-Term Ecological Research (LTER) site on the Eastern Shore of Virginia (Fig. 1). The LTER research area encompasses a complex ecosystem of barrier islands, marshes, mud-flats, and oyster reefs. A mainland marsh located along Phillips Creek, in Nassawaddox, Virginia, was chosen for study because of its regular tidal flooding pattern and vegetation typical of salt marshes of the region.

Geomorphologically, the marsh is considered a young high marsh since it is a relict Pleistocene ridge overtopped by rising sea level within the last 200 years (G. Oertel personal communication). The soil is classified as Chincoteague silt loam (Cobb and Smith 1989), with the top 15 cm being higher in organic matter (>10% by weight) than the more clayey soils below 15 cm (<1% by weight) (Chambers unpublished data). There is extensive burrowing activity by fiddler crabs (*Uca* spp.) and wharf crabs (*Sesarma reticulatum*) in these soils.

MATERIALS AND EXPERIMENTAL DESIGN

Six tidally-regulated, experimental chambers were placed in vegetated sections of salt marsh (*Spartina alterniflora*, short form) prior to the onset of the growing season in March 1989. Each chamber isolated a circular area of marsh soil with associated plants (~700 cm²); attached, collapsible reservoirs served as a flooding water source (Chambers 1992). During tidal flooding, increased water pressure outside the reservoirs forced them to collapse, delivering water to chambers in response to changing tidal height. During ebb, decreased water pressure outside the chambers created conditions for water drainage from the chambers back into the reservoirs. In this fashion, water movements onto and off of the marsh were studied in closed systems, hydrologically separate from, but controlled by the flooding regime of the surrounding marsh. Advection of water through the marsh soil was negligible (see below).

For the first two months of the study, synthetic seawater was used as the reservoir water source so that possible transformations of nutrients by planktonic organisms brought in by tidal water were

eliminated. With this control, measured exchanges were limited to nutrient release to or removal from a flooding (physically active), synthetic (biologically inactive) water body inside the enclosed section of marsh. Aerated, deionized water mixed with sea salts was used to make up water of the same salinity as ambient flooding water (approximately 25‰). Average initial concentrations of ammonium and phosphate in synthetic seawater were 2.5 μM and 6.5 μM , respectively.

We examined the effect of initial reservoir concentration of phosphate on net nutrient exchange in the experimental chambers. Ocean water, which had a lower dissolved phosphate concentration than the sea salt mix (0.3 μM vs 6.5 μM), was used in reservoirs during some monitored tides in August and October. Dissolved nutrient concentrations in ocean water were stable; over 2 h there was no measurable change in dissolved phosphate concentration and no significant change in mean ammonium concentration ($\pm\text{SD}$) (1.0 \pm 0.3 μM vs 1.1 \pm 0.7 μM) in four reservoirs. Net exchanges of ammonium and phosphate due to processes in the oceanic water column during a flooding tidal cycle were therefore assumed to be sufficiently small that oceanic water could be utilized in a fashion similar to synthetic seawater.

Chambers on the salt marsh were monitored over complete daytime flooding and ebbing tidal cycles in June, July, August, and October 1989. A complete tidal cycle could not be monitored in September due to unusually high tides which submerged the chambers. Water from reservoirs was collected at half-hour intervals during each monitored tidal cycle. Additionally, water was collected 2 cm, 12 cm, and 22 cm above the marsh surface inside the chambers, depending on height of flooding. No mixing of the flooding water was attempted; information from multiple water collections at different heights was averaged for each sampling time. Water outside the experimental chambers was collected using the same sampling regime to examine changes in nutrient concentrations external to the chambers. Water samples were filtered in the field (0.45- μm pore size), placed on ice in a cooler, and analyzed spectrophotometrically for dissolved ammonium (indophenol technique) and phosphate (molybdate-ascorbic acid technique) in the laboratory within 2 h after collection (Parsons et al. 1984).

DATA ANALYSIS

Observed patterns of nutrient loading onto the flooding marsh surface were compared to expected patterns by calculating masses of ammonium and phosphate in experimental chambers during the tidal cycle. Knowing the height of maximum flood (amplitude, a), the marsh surface area enclosed by

each chamber (A_s), and the length of time between initial and maximum flood (period, P), a simple sine function model was used to calculate the volume of water in the chambers for each sampling interval (t):

$$V_{(t)} = A_s(a \sin(t/P))$$

The "expected" mass of nutrients inside the chambers at each sampling interval, which assumed no changes in dissolved nutrient concentrations, was determined by multiplying the calculated volume of water by the initial nutrient concentration in the reservoir. "Observed" nutrient masses were obtained by multiplying water volume by the average nutrient concentration measured inside the chambers at each sampling time. Nutrient concentrations inside and outside the chambers, and observed and expected masses of ammonium and phosphate inside the chambers were plotted for the entire periods of marsh inundation.

NUTRIENT EXCHANGE IN THE WATER COLUMN

A fixed-level water column experiment was completed to 1) determine the contribution of water column processing to nutrient dynamics on the flooded marsh, and 2) compare marsh responses under conditions of incubation and natural flooding. Changes in nutrient concentrations measured during the previous experiments were compared with changes measured in six chambers in which the water level remained constant over a period of 43 h. On September 7, tidal water was allowed to flood open chambers through 3-cm-diameter holes at the marsh surface, then the openings in the chambers were closed to keep the water inside at a fixed level while water outside the chambers fell and rose with the tide. Water was sampled at five times over 2 d to identify net changes in dissolved ammonium and phosphate concentrations. As with the results from the open chamber experiments, the total turnover of nitrogen and phosphorus was not measured and might be larger than the net rates of exchange actually calculated here.

NUTRIENT EXCHANGE BY DIFFUSION

Molecular diffusive fluxes (J) of nutrients from salt marsh soils were calculated from a Fickian diffusion model:

$$J = -D_s\phi \frac{dC}{dz}$$

On November 14, quadruplicate samples from porewater equilibrators were collected and analyzed for dissolved ammonium and phosphate concentrations at soil depths to 33 cm. Depth profiles of dissolved ammonium and phosphate in soil porewater were used to estimate concentration gradients (dC/dz). Using appropriate diffusion coefficients (D_s) and average soil porosity (ϕ), the

calculated diffusive fluxes were then compared with exchanges measured in both incubation chambers and experimental chambers.

NUTRIENT EXCHANGE BY POREWATER ADVECTION

The contribution of porewater advection to nutrient dynamics in the marsh was determined from a hydrological budget for the soil. A mass balance for soil water is developed for a control volume of soil, which has a square surface of unit area and sides extending vertically downward to a less permeable layer. Fluxes into and out of the control volume include infiltration of surface water (I), upward discharge of groundwater from the underlying aquifer (GW), evapotranspiration from the soil and vegetation (ET), and net horizontal flux (H). For a time-averaged water balance (i.e., no change in water storage in the soil), the sum of the fluxes is zero,

$$q_I + q_{GW} + q_{ET} + q_H = 0 \quad (1)$$

where q is the water flux per unit surface area of marsh, and fluxes into and out of the control volume are assigned as negative and positive, respectively.

Groundwater and evapotranspiration fluxes were calculated as in Harvey and Odum (1990). Net horizontal flux was estimated as the difference between horizontal fluxes entering from upslope (q_{Hin}) and leaving in the downslope direction (q_{Hout}):

$$q_H = q_{Hout} + q_{Hin} \\ = -Kb(1 - \alpha) \left[\left(\frac{dh}{dx} \right)_{Hout} - \left(\frac{dh}{dx} \right)_{Hin} \right]. \quad (2)$$

Hydraulic head (h) is the sum of pressure and elevation potentials which were measured using piezometers. Hydraulic gradients were measured along a horizontal axis (x) pointing in the direction of the steepest topographic slope. Hydraulic conductivity of the marsh soil (K) was estimated by the piezometer method, b was the saturated depth to a less permeable layer, and α was the fraction of time the marsh surface is inundated by the tide.

Infiltration was calculated as the residual in the water balance equation. Only if infiltration is positive is there an advective export of nutrients from the soil.

NUTRIENT EXCHANGE IN THE ADJACENT TIDAL CREEK

To contrast net tidal exchanges of nutrients from experimental chambers with those occurring within the adjacent tidal creek, nutrient concentrations were measured in Phillips Creek on October 24, 1989. Triplicate samples of filtered surface water

were collected hourly over an entire tidal cycle, and analyzed for dissolved ammonium and phosphate. A time-series plot of nutrient concentration and stage of tide was used to determine whether calculations of nutrient exchange on the surface of the marsh were consistent with inferred nutrient exchanges observed in the adjacent tidal creek.

Results

NUTRIENT DYNAMICS IN EXPERIMENTAL CHAMBERS

Although there were monthly differences in the amounts of nutrients released to or removed from the chamber water column, consistent patterns of nutrient exchange within experimental chambers and in flooding marsh waters were present throughout the entire sampling period (June through October). Data from August are used to display typical trends in ammonium and phosphate dynamics over flooding tidal cycles. Note that natural planktonic processes occur only in the tidal water outside the chambers, since inside the chambers this component of nutrient exchange has been removed. Average concentrations and exchanges of nutrients are reported (\pm one standard error of the mean).

On August 3, synthetic seawater was used as the reservoir water for tidal inundation lasting approximately 3 h. The initial and final reservoir phosphate concentrations and the average phosphate concentrations in the six chambers were high ($7 \mu\text{M}$) but similar to concentrations of phosphate in the water which first flooded the marsh surface (Fig. 2). During the early stages of flooding, the concentration was elevated relative to the initial reservoir concentration ($7.3 \pm 0.4 \mu\text{M}$ vs $6.7 \pm 0.2 \mu\text{M}$), but decreased to initial levels before peak flood (100 min). A similar, but amplified pattern was also seen outside the chambers in the flooding marsh water (i.e., high initial phosphate concentration decreasing to peak flood). Phosphate concentrations inside or outside the chambers did not change dramatically on the ebb tide, and final reservoir concentrations of phosphate were not different from initial concentrations ($6.7 \pm 0.2 \mu\text{M}$ vs $6.6 \pm 0.2 \mu\text{M}$), indicating no net input or removal of phosphate from the water column.

The shapes of the expected tidal profile of phosphate mass on the marsh surface and the observed mass calculated from measured nutrient concentrations in the chambers reflect the tidal wave-form (Fig. 2). Under conditions of no nutrient exchange, water volume controls the mass of phosphate loaded onto and drained from the marsh surface in the chamber experiment. The close match of observed and expected curves indicated that at high phos-

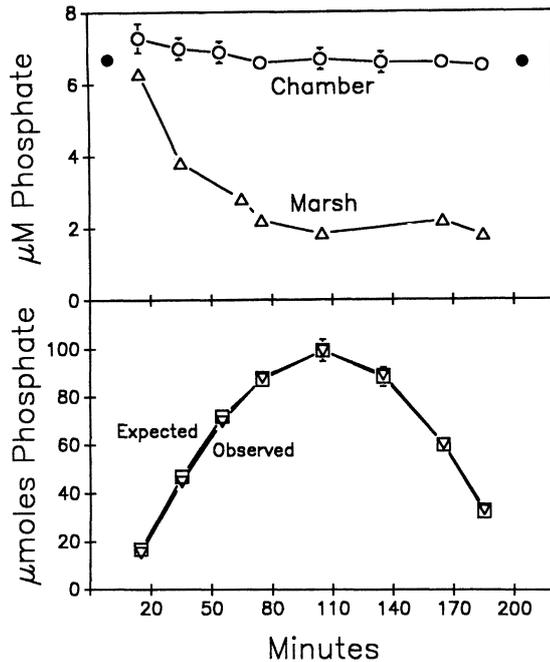


Fig. 2. *Upper.* Phosphate concentrations over the August 3 flooding tidal cycle in marsh water (Δ) and in high-phosphate water inside chambers (\pm SE) (\circ). Initial and final reservoir concentrations are also shown (\bullet). *Lower.* Observed (\pm SE) and expected masses of phosphate in chambers over the tidal cycle.

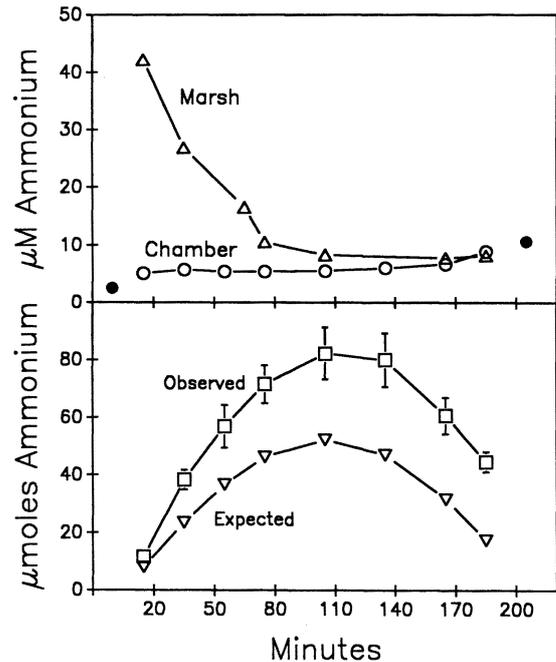


Fig. 3. *Upper.* Ammonium concentrations over the August 3 flooding tidal cycle in marsh water (Δ) and in high-phosphate water inside chambers (\pm SE) (\circ). Initial and final reservoir concentrations are also shown (\bullet). *Lower.* Observed (\pm SE) and expected masses of ammonium in chambers over the tidal cycle.

phosphate concentrations, the net exchange of phosphorus between the marsh and flooding water was small.

Unlike phosphate, ammonium concentrations measured inside the chambers increased at each sampling interval over the August 3 tidal cycle (Fig. 3). Water flooding the chambers at a reservoir concentration of approximately $2 \mu\text{M}$ was enriched quickly with dissolved ammonium, and over the entire tidal cycle the concentration slowly increased in the chambers to almost $10 \mu\text{M}$. The final reservoir concentration of ammonium was even greater than any measured ammonium concentration inside the chambers. In contrast, ammonium concentrations in flooding marsh water were greater than $40 \mu\text{M}$ during initial flood stages, but decreased to roughly $10 \mu\text{M}$ by peak flood tide.

The mass of ammonium observed on the marsh surface ($\geq 75 \mu\text{moles}$ at high tide) was much higher than the expected mass of ammonium calculated from the initial reservoir concentration ($< 55 \mu\text{moles}$) (Fig. 3). Observed nutrient increases measured in flooding chambers and high final reservoir concentrations of ammonium indicated that ammonium was released from the marsh to the tidal water. On an areal basis, the release of ammonium from the marsh was $1,738 \mu\text{moles m}^{-2} \text{ tide}^{-1}$.

On August 5, two days following the preceding experiment, a second tidal cycle was monitored

using clean, unfiltered ocean water as the reservoir source. Ocean water was used to test for a response with a "low phosphate" treatment (Fig. 4). As with synthetic seawater, initial flooding concentrations of phosphate were higher than at any other time during the tidal cycle. Contrary to synthetic seawater experiments, however, these concentrations remained elevated above the concentration of water delivered from the reservoir, as reflected in the higher final reservoir phosphate concentration. Outside the chambers, water flooding the marsh was initially high in phosphate ($6.7 \mu\text{M}$), then decreased to $1.6 \mu\text{M}$ by peak flood tide (Fig. 4).

The large average differences in phosphate concentration measured on the marsh surface relative to the initial reservoir concentration were reflected in differences between observed and expected masses of phosphate flooding the experimental chambers (Fig. 4). The calculated release of phosphate from the vegetated marsh surface was $108 \mu\text{moles m}^{-2} \text{ tide}^{-1}$.

The release of ammonium measured in chambers using synthetic seawater was similar to the response when oceanic seawater was used (Fig. 5). Water flooding the chamber became enriched in ammonium relative to the reservoir source, and remained elevated above this initial concentration throughout the entire tidal cycle. As a consequence, the observed tidal profile of ammonium

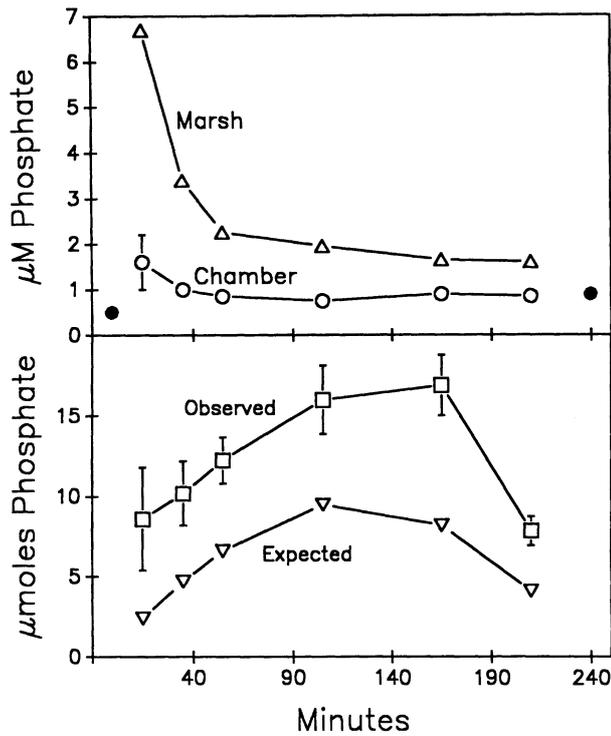


Fig. 4. Upper. Phosphate concentrations over the August 5 flooding tidal cycle in marsh water (Δ) and in low-phosphate water inside chambers (\pm SE) (\circ). Initial and final reservoir concentrations are also shown (\bullet). Lower. Observed (\pm SE) and expected masses of phosphate in chambers over the tidal cycle.

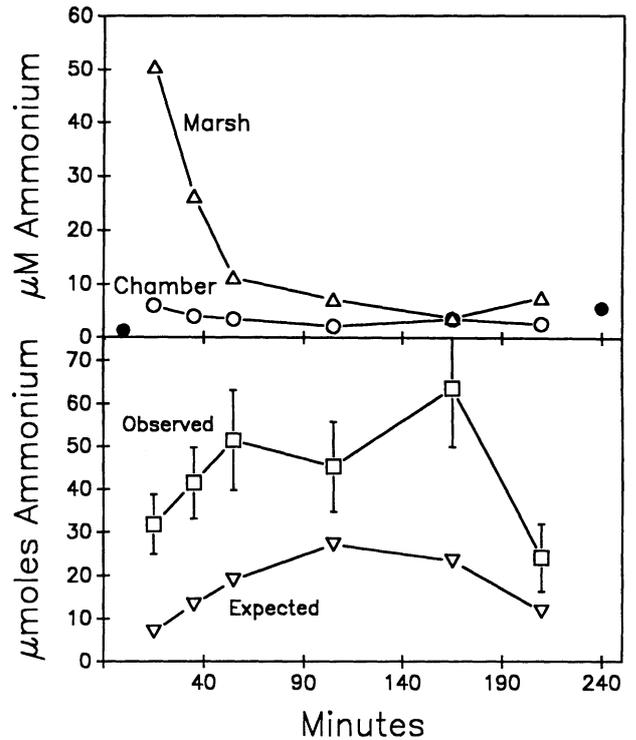


Fig. 5. Upper. Ammonium concentrations over the August 5 flooding tidal cycle in marsh water (Δ) and in low-phosphate water inside chambers (\pm SE) (\circ). Initial and final reservoir concentrations are also shown (\bullet). Lower. Observed (\pm SE) and expected masses of ammonium in chambers over the tidal cycle.

mass in chambers was much greater than the expected profile (Fig. 5), and the net release of ammonium was substantial ($1,188 \mu\text{moles m}^{-2} \text{ tide}^{-1}$).

Net dissolved nutrient flux between salt marsh soils and the water column appeared to depend on initial reservoir concentrations of nutrients (Table 1). With high phosphate loading ($>5 \mu\text{M}$), no phosphate release or removal was observed (June, July, and August); under low loading rates ($<2 \mu\text{M}$), net release of phosphate occurred within chambers (August, September—not shown, and October). Outside the chambers, water flooding the marsh on all dates was initially high in phosphate, then decreased to an average of $2 \mu\text{M}$ at high tide. For ammonium, a net release from the marsh surface to the water column was observed both within chambers and in the flooding waters on marsh surface for every experimental tide; concentrations of ammonium in flooding waters were always higher than initial reservoir concentrations and peak flood concentrations, respectively (see below).

NUTRIENT EXCHANGE IN THE WATER COLUMN

To determine the effect of water-column processes on dissolved nutrient concentrations, water in experimental chambers which had flooded with

surface waters (not attached to reservoirs) was impounded during high tide on September 7 and incubated for 43 h. Highest nutrient concentrations consistently were measured at the lowest positions in the water column at all sampling times (Fig. 6). Further, for both ammonium and phosphate, there was a pattern of decreasing concentration over time, and the greater drop occurred during the first half of the incubation.

TABLE 1. Flux of phosphate and ammonium measured in experimental chambers on five dates at the Phillips Creek marsh. Initial concentrations of phosphate in reservoirs were high for the first 3 dates, but low thereafter; for ammonium they were always low. Fluxes, in $\mu\text{moles m}^{-2} \text{ tide}^{-1}$, are means (SE) of six chambers. Positive (+) flux denotes release from the marsh surface to the water column; negative (-) flux denotes uptake by the marsh surface from the water column.

Date	Phosphate		Ammonium	
	Initial Concentration	Flux	Initial Concentration	Flux
June 6	High	+26 (1.2)	Low	+143 (23)
July 7	High	-64 (2.3)	Low	+656 (38)
August 3	High	-21 (0.6)	Low	+1,738 (121)
August 5	Low	+108 (12)	Low	+1,188 (130)
October 25	Low	+52 (1.3)	Low	+508 (31)

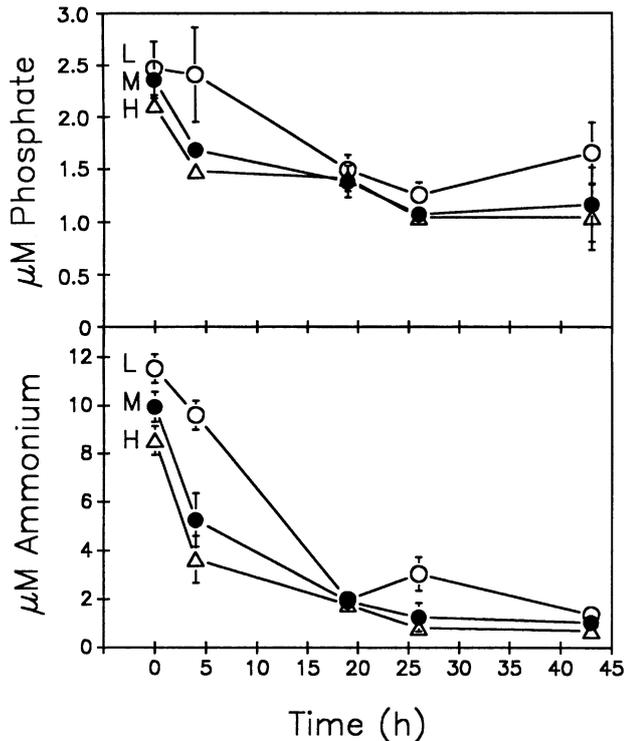


Fig. 6. Results of impounded water column incubations. Plots of phosphate (upper) and ammonium (lower) concentrations (average \pm SE, $n = 6$) from collectors 2 cm, 12 cm, and 22 cm above the soil surface (L, M, H, respectively).

Temporal variations in nutrient concentration were comparable at medium and high positions above the soil surface, with rapid nutrient depletion taking place in the first 4 h, followed by more gradual decreases (Fig. 6). In contrast, the depletion of nutrients at the near-surface sampling position was initially gradual; between some later sampling intervals nutrient concentrations actually increased. The initial drop in nutrient concentration between 0 and 4 h was used to calculate a rate of nutrient uptake by the water column, assuming a 3-h tidal inundation to an average depth of approximately 9 cm. Phosphate removal was estimated as $43 \pm 7.9 \mu\text{moles m}^{-2} \text{ tide}^{-1}$, ammonium removal was $315 \pm 55 \mu\text{moles m}^{-2} \text{ tide}^{-1}$.

NUTRIENT EXCHANGE BY DIFFUSION

Porewater concentrations of nutrients were much higher than surface water, with increasing concentrations measured to depths of 10–20 cm (Fig. 7). Below 20 cm, concentrations decreased to roughly half of the maximum values measured. Surface water concentrations of phosphate and ammonium averaged $2 \mu\text{M}$ and $10 \mu\text{M}$, respectively, whereas porewater concentrations at 10 cm averaged $107 \mu\text{M}$ and $190 \mu\text{M}$. Using the upward concentration gradients between surface waters and porewater

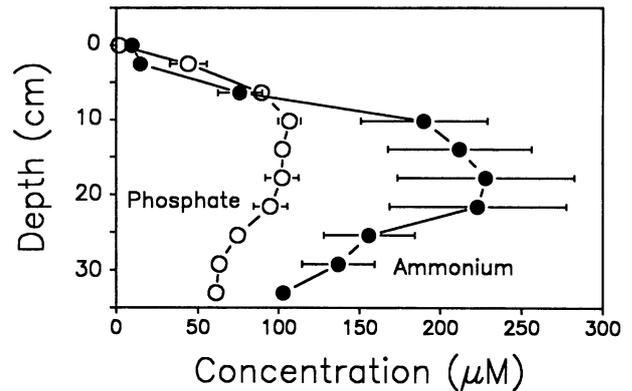


Fig. 7. Porewater profiles of phosphate and ammonium (average \pm SE, $n = 4$) in marsh soils at Phillips Creek, November, 14, 1989.

concentrations at 2.5 cm, an average soil porosity (ϕ) from Phillips Creek marsh soils (0.40) and diffusion coefficients (D_s) appropriate for ion diffusion from soil to water (Krom and Berner 1980, $\text{HPO}_4^{2-} = 3.6 \times 10^{-6} \text{ cm}^2 \text{ s}^{-1}$, $\text{NH}_4^+ = 9.8 \times 10^{-6} \text{ cm}^2 \text{ s}^{-1}$), a steady-state diffusion rate was calculated assuming that concentration profiles accurately represented a time-averaged concentration gradient (Scudlark and Church 1989). The average calculated diffusion rates from the soil to the water column for phosphate and ammonium were 2.2 and $0.85 \mu\text{moles m}^{-2} \text{ h}^{-1}$, respectively.

NUTRIENT EXCHANGE BY POREWATER ADVECTION

During late summer in this marsh, the largest component of the time-averaged water balance is evapotranspiration, which removes $1.92 \text{ l m}^{-2} \text{ tide}^{-1}$ (Table 2). Recharge by groundwater and net horizontal flow are insufficient to match this water export, so that infiltration must be negative to satisfy the water balance. By this calculation, we determine that there is no advective flux of porewater from the soil to the overlying tidal water, and thus no advective export of dissolved nutrients.

TABLE 2. Time-averaged water balance for the Phillips Creek marsh soils. Positive fluxes represent water flow out of the marsh soil; negative flux represents water flow into the soil. Infiltration flux, calculated as the residual to balance groundwater, horizontal, and evapotranspiration fluxes, is negative, indicating that surface water flows into the marsh soil. Advective drainage of porewater to surface water does not occur.

Source	Flux ($\text{l m}^{-2} \text{ tide}^{-1}$)
Horizontal	- 0.003
Groundwater	- 0.006
Evapotranspiration	+ 1.920
Infiltration	(-) 1.911*

* $q_i = -q_{ET} - q_{GW} - q_H$.

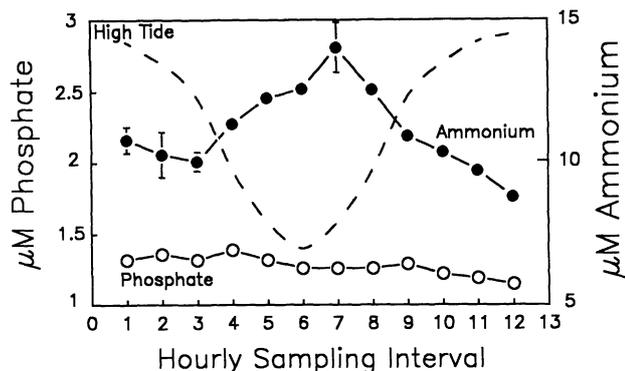


Fig. 8. Hourly concentrations (\pm SE) of ammonium and phosphate in Phillips Creek, October 24, 1989. Tidal trace is simulated based on observed times of high and low tide.

NUTRIENT EXCHANGE IN THE ADJACENT TIDAL CREEK

Over the ebbing and flooding tidal cycle on October 24, there were large differences in dissolved ammonium concentrations in Phillips Creek (Fig. 8). The lowest concentration was recorded near peak flood tide ($8.8 \pm 0.2 \mu\text{M}$), and the highest about an hour after slack tide ($14.1 \pm 0.9 \mu\text{M}$). The tidal pattern in phosphate concentrations was less distinct: over the 12-h sampling period, the mean concentration decreased slightly, albeit significantly, from $1.32 \mu\text{M}$ to $1.15 \mu\text{M}$ (t -test, $p < 0.05$).

Discussion

NUTRIENT DYNAMICS

Relative to ammonium, the net exchanges of phosphate in the salt marsh were small for all sampling dates (Table 1). For tides monitored using high initial concentrations of phosphate, there was little net movement of phosphate between tidal water and marsh soil. Under conditions of low initial phosphate concentration, however, more phosphate was released into the water column (Table 1, Fig. 4). A source of phosphate to the water column could be ion desorption from charged surfaces (Chambers and Odum 1990), that is, the soil surface could function as a buffer to maintain a constant phosphate concentration in the overlying water (Froelich 1988). Since the flooding front of water moving across the marsh was enriched in dissolved phosphate (Figs. 2 and 4), other processes must be responsible for the observed increase in nutrient concentrations.

One possibility is that phosphate concentrations increase because of a diffusive flux from soil porewater into flooding tidal water. For a typical inundation time at the salt marsh site of 3 h, this diffusion rate (calculated from the modeled diffusion rate for October) would be $6.6 \mu\text{moles m}^{-2} \text{ tide}^{-1}$ released to the surface waters. In an exper-

imental chamber volume of 20 l, an initial $2 \mu\text{M}$ solution of phosphate would increase in concentration to $2.02 \mu\text{M}$ after 3 h, a value near the detection limit of the phosphate analytical technique. Diffusion alone cannot account for the observed amounts of phosphate released from these salt marsh soils, although recent work discusses more fully the potential error associated with estimates of the concentration gradient (2.5-cm vertical resolution in this study) (Carignan and Lean 1991) and values of D_s and porosity (Sweerts et al. 1991). Even considering that diffusion can occur during tidal inundation and exposure (Gardner 1975), the rate of phosphorus diffusion over 12 h still does not account for the measured release of phosphate (26 vs $52 \mu\text{moles m}^{-2} \text{ tide}^{-1}$).

Phosphate release to the water column also may occur through bioturbative fluxes and advection of nutrient-rich groundwater to surface water. Bioturbative flux is substantial in some subtidal sediments and salt marshes (Boynton et al. 1980); at the Phillips Creek site its importance to flux is unknown. Large fiddler crab populations probably turnover surface soils extensively (Montague 1982; W. E. Odum personal observation), a process which could expose nutrient-rich subsurface soils to flooding tidal waters and influence soil metabolism. We observed that the filtering action of a single, large, ribbed mussel (*Geukensia*) was sufficient to affect water motion inside one chamber, although measured nutrient exchange in this chamber was no different from chambers without mussels. It is possible that other microscopic organisms contribute to phosphate release into the surface soils (Caponne and Kiene 1988).

Advection of porewater to the surface environment, however, is not predicted when a steady-state water balance (averaged over many tides) is used to calculate water flux (Table 2). If the steady-state assumption is relaxed, advection still will not occur during marsh exposure because evapotranspiration flux greatly exceeds horizontal flux. During marsh inundation, evapotranspiration and horizontal fluxes are zero, so that porewater advection could possibly be driven by the upward groundwater flux. The calculated advection of porewater would be $0.0023 \text{ l m}^{-2} \text{ tide}^{-1}$. Coupled with porewater nutrient concentrations in surface soils, this represents the advection of $0.04 \mu\text{moles m}^{-2} \text{ tide}^{-1}$ and $0.12 \mu\text{moles m}^{-2} \text{ tide}^{-1}$ of ammonium and phosphate, respectively—less than 1% of the observed nutrient release in experimental chambers. Advection cannot contribute substantially to the observed phosphate (or ammonium) flux from marsh soils.

The potential nitrogen sources and sinks which influence the observed pattern of ammonium re-

lease from the marsh surface are manifold. Unlike phosphorus, which has one valence and therefore one oxidative state, the oxidative state of nitrogen ranges from +5 to -3, and the transformations among states are all microbially mediated. Ammonium can be produced by the degradation of organic matter (ammonification), by assimilatory and dissimilatory nitrate reduction, by N_2 fixation, or by desorption from soils. Inputs to the marsh can occur via groundwater flow or tidal subsidy. In turn, available ammonium can be utilized by plant or microbial uptake for biosynthesis, by bacteria for nitrification, and by inorganic soils through physical sorption.

Release of ammonium observed both inside and outside the chambers during the initial stages of flooding (Figs. 3 and 5) suggests there was a high concentration of ammonium built up in the surface soils during low tide which was subsequently mixed into the water column during flooding. Ammonification almost certainly contributes to this flux; mineralization rates measured in wetland soils are typically high (Bowden 1987), and at this salt marsh site, bacterial activities are highest when water begins to flood the marsh (L. Blum unpublished data). Ammonium release by mineralization and ion desorption have both been shown to correlate negatively with overlying water concentrations (Teague et al. 1988), and positively with temperature (Valiela et al. 1978; Scudlark and Church 1989). We measured the largest releases of ammonium in August, the warmest month of the year. Similarly, organic matter mineralization on the marsh surface during slack tide could increase phosphate concentrations in the soils, much of which would be dissolved in advancing tidal water (Nowicki and Nixon 1985).

The N:P ratio of net ammonium and phosphorus release in August and October averaged 10.5 (Table 1). If plants were the organic carbon source for microbial mineralization, then the release of N and P might be expected at the N:P ratio of *Spartina*, which is 15–16 (Chambers unpublished data). The observed smaller ratio of release would suggest either P release was enhanced relative to N (additional P sources), or that N release was occurring as other forms of nitrogen (e.g., dissolved organic nitrogen, nitrate, nitrogen gas). Recent studies of benthic nitrogen recycling in salt marsh sediments indicate mineralized nitrogen release occurs predominantly as ammonium (Gardner et al. 1991), although a significant fraction of ammonium production is still available for nitrification-denitrification reactions (Seitzinger et al. 1991). In either case, with mineralization, net releases of phosphate from the marsh would be expected, but the size of the release would be small relative to nitrogen (Riz-

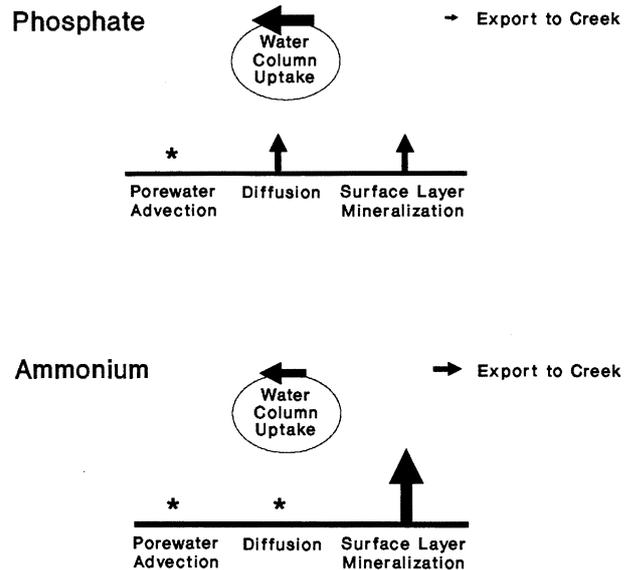


Fig. 9. Summary of nutrient fluxes measured or estimated in the present study. The magnitudes of ammonium and phosphate exchange are depicted by the size of flux arrows, set relative to total observed nutrient release from the marsh surface. In these diagrams, the magnitude of nutrient release from the marsh surface (advection + diffusion + mineralization) is set equal to water column exchange (uptake + export). Fluxes marked with an asterisk (*) contribute less than 2% to observed nutrient release from the marsh surface.

zo 1990). These results also support the observation by Carignan and Lean (1991) that phosphorus flux from sediments is uncoupled from carbon and nitrogen fluxes.

FLUX PARTITIONING

A comparison of nutrient fluxes associated with different exchange processes measured or estimated in September, October, and November summarizes their contributions to net exchange at this time of year (Fig. 9). Release of nutrients from the marsh, measured by the experimental chambers, is larger than the flux estimated by the physical processes of diffusion and advection. We hypothesize that the difference is made up by biologically-mediated organic matter mineralization in the thin surface layer and subsequent nutrient release at the turbid sediment surface. During the period the marsh is actually flooded, water column uptake of phosphate is roughly equal to this release, so that over a tidal cycle there is little net exchange between the marsh and the adjacent tidal creek (Fig. 9). Calculated ammonium uptake by the water column, however, is smaller than the measured surface release, and a larger net release of ammonium from the marsh to the adjacent creek is both predicted (Fig. 9) and observed. Although there appeared to be a 1-h or 2-h lag, increasing ammonium concentrations on the falling tide and

falling concentrations on the rising tide (Fig. 8) supported calculations of ammonium export from the surrounding marshes into the adjacent tidal creek. Other sources of ammonium must contribute to the observed increase in the creek, because the concentrations leaving the marsh are less than the maximum concentration in the creek (see below).

Under natural flooding conditions, the initial flooding front of tidal water appears to pick up dissolved ammonium and phosphate as it moves across the marsh surface. Associated with the flooding front are the terms "swash zone" (Keizer et al. 1989) and "surface film" (Gallagher 1975). The enrichment represents a concentrating of nutrients on the marsh surface during low tide (Gardner 1975) which are diluted by the rising tide. Others have suggested the physical aspects of initial tidal flooding force a turbidity transfer of nutrients off the surface soils, an effect which diminishes with increasing tidal height (Wissmar and Simenstad 1984; Childers and Day 1990). Frontal zone development and tidally-induced areas of chemical and biological concentration have been similarly observed as a larger scale phenomenon of estuarine circulation patterns (LeFevre 1986; Dustan and Pinckney 1989). In this salt marsh it appears that most nutrient release occurs early during the flooding tidal cycle and is associated with soil-water interactions (Keizer et al. 1989).

As the water volume on the flooded marsh increases relative to soil surface area, dissolved nutrient exchanges are more likely to be associated with water-column processing. In the fixed-level water incubation experiment, significant nutrient removal from the water column occurred over just a few hours, presumably due to uptake by organisms suspended in the water column (Fig. 6). At least for the days of measurement, the soil surface appeared to be a dissolved nutrient source to the water column, whereas the water column itself was a dissolved nutrient sink.

The large release of ammonium from the marsh surface to the water column (Table 1) was consistent with observed changes in ammonium concentration measured in the adjacent tidal creek (Fig. 8). Higher ammonium concentrations in creek water during low tide may occur because of the increased relative contribution of flood marsh water, rich in dissolved ammonium, draining into the ebbing creek water. Drainage from the adjacent watershed, where fertilizers are applied to agricultural fields during the growing season, could be an additional nitrogen source. Subsurface seepage of reduced nitrogen in groundwater from fields directly into tidal creeks could also account for the observed higher ammonium concentrations on the ebbing tide (D. Wetzel unpublished data). Esti-

mates of seepage flux of groundwater along creek-banks and more complete investigations of estuarine-watershed interactions, however, have not yet been made at this site.

ASSESSMENT OF EXPERIMENTAL CHAMBER FUNCTION

Naturally-fluctuating water levels were maintained in the experimental chambers used for this study, but some deviations from natural conditions should be noted. The primary drawback of these chambers was the position of the flooding and draining site, which was directly above the soil surface. This position may have promoted enhanced soil-water interaction, since all water entering and leaving the chambers had to pass near the soil surface. Also, the insides of the chambers provided surfaces for potential deposition and attachment of particulate matter and algae. The influence of the epiphytic community on nutrient exchange was not tested, but its potential effect was assumed to be identical in all six chambers. In this regard, the net exchanges of nutrients between tidal water and the interior chamber surfaces (i.e., soil, plant, and chamber wall surfaces) may have been slightly magnified by chamber design.

Summary

The important aspect of this work was demonstration of significant ammonium and phosphate release from this salt marsh during the growing season, a release not caused by water column processing of nutrients, porewater advection, or calculated diffusive exchange. Further, the pattern of nutrient release over the tidal cycle suggested an exchange which occurred via a turbidity transfer of high concentrations of nutrients from the surface soils into the flooding tidal water. We propose that the process of organic matter mineralization concentrates dissolved nutrients in shallow surface soils during tidal exposure, which are then suspended into the flooding water column via bioturbation or physical mixing.

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Ivan Valiela; John M. Teal; Suzanne Volkmann; Deborah Shafer; Edward J. Carpenter

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Nitrogen Exchange Between a Portion of Vegetated Salt Marsh and the Adjoining Creek

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