Fig. 7 Percentage of P remaining in Typha shoot litter --- distilled water, — artificial water, 10 °C, 18 °C.

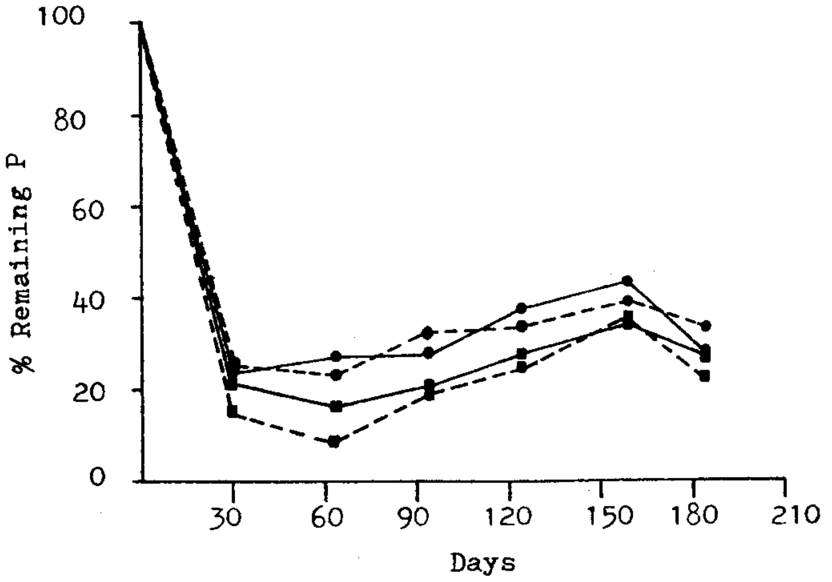
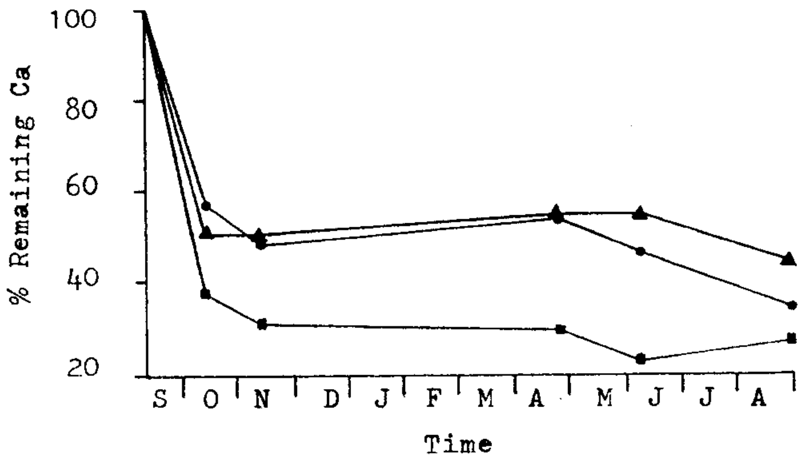
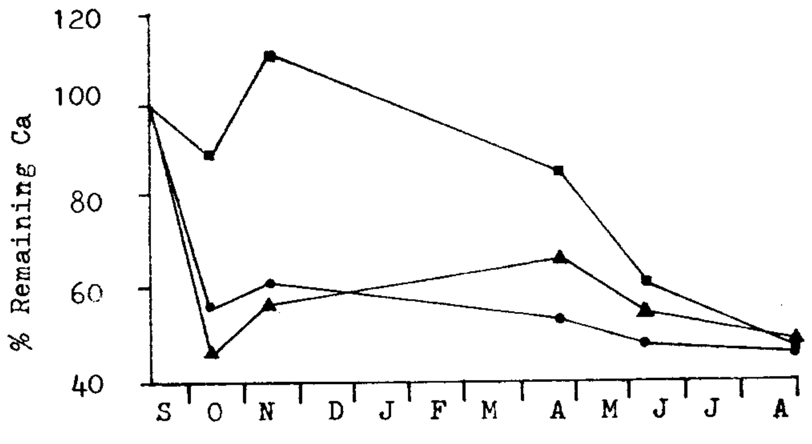


Fig. 8 Percentage of remaining calcium of shoot (a), and root - rhizome (b), September 18 , 1997 - August 31,1978 ● Typha , ■ Sparganium , ▲ Scirpus.



(a)



(b)

ctively. Typha root—rhizomes showed a decrease in Ca of about 45% of original content at 26 days,then Ca rose to 61% of the original content in November. Calcium values showed little change during April-August. Sparganium root-rhizomes showed temporary Ca accumulation in November. At 348 days the % remaining was 46.2%. Calcium in Scirpus root-rhizomes dropped rapidly in the first month ,then increased in November. The Ca values of June and August were relatively stable.

Under controlled conditions the losses of Ca in all treatments were neither influenced by the types of water nor by temperature. Very rapid leaching of Ca occurred in the first month; the amount lost at 50 days ranging from 69.7% of original content in artificial water 10C to 65.1% in distilled water 18 °C . At 184 days the remaining Ca in the plant residue of all treatments was less than 1% of the original value.

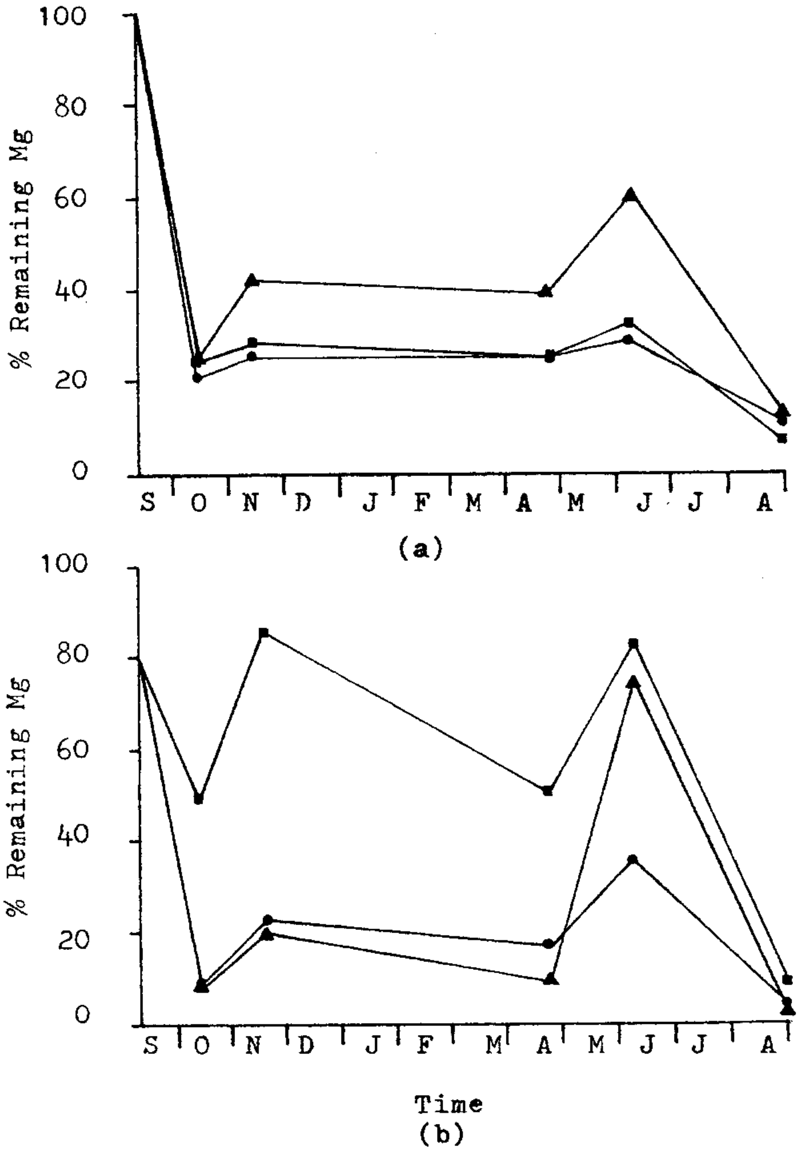
Magnesium

Most Mg in all shoot and root-rhizome samples was released within the first montb(Fig.9). Like other elements, Mg showed increases in all groups in June. The increases were relatively high for root— rhizome litter. In the laboratory,Mg was also leached out rapidly in the first month,then the remaining Mg stayed in the range of 4 -30% for all treatments. Analysis of variance showed no significant effect of water or temperature factors nor interaction of time,water,and temperature factors on Mg contents of all treatments.

Carbon

The rapid loss of carbon in the treatment and control of both sterilization and antibiotic experiments in the first 15 days supports

Fig. 9 Percentage of remaining Mg of shoot (a), and root—rhizome (b), September 18,1977-August 51,1978. ● Typha , ■ Sparganium , ▲ Scirpus.



solubilization of carbon compounds as the cause of loss(Fig.5). After 15 days C content in the sterilization control was between 58.85 -47.94% dry weight and 40.80 -48.17% dry weight in the antibiotic control. Significant difference in C contents between treatment and control was found only in antibiotic experiment.

Water nutrients

The fluctuations of NH_4-N, soluble reactive P,Ca , and Mg in the marsh water are shown in Table 2. NH_4-N corresponded with the pattem of decomposition better than other nutrient groups; the concentration increased to 0.51 mg/l in October suggesting a net gain from decomposition of dissolved organic matter that was released by leaching and autolysis of dead macrophytes. NH_4-Ndecreased slightly in November and reached a minimum level for the year(0.29 mg/i) in April. As decomposition processes increased in summer, NH_4-N increased to 0.61 and 0.68 mg/l in June and August.

Soluble reactive P fluctuated between 0.12 mg/l in April and 0.52 mg/l in September, Calcium concentration was high(90.55mg/l) in September,then decreased to about 28 mg/l in October and November. The range during spring and summer was 45.15—55.79 zng/l. Magnesium concentrations were relatively stable(9.96-14.80 mg/l),except for a low reading in August(4.05 mg/l). There were significant interrelationships between nutrients in the litter(N,P,Ca,Mg) and marsh water nutrients(NH_4-N,soluble reactive P, Ca, Mg).

Table 2 NH_4-N, soluble reactive P, Ca, and Mg of water (mg l^{-1}) ± one standard deviation, Theresa Marsh.

Date	NH_4-N	Soluble reactive P	Ca	Mg
9-18-77	.44 ± .15	.52 ± .16	90.33 ± 3.80	14.80 ± 2.41
10-14-77	.51 ± .07	.31 ± .14	27.11 ± 6.15	9.96 ± 1.50
11-11-77	.46 ± .06	.34 ± .18	27.62 ± 12.65	14.17 ± 1.55
4-22-78	.29 ± .05	.12 ± .04	55.79 ± 5.88	10.90 ± 2.45
6-7 -78	.61 ± .06	.32 ± .12	45.13 ± 11.20	10.62 ± 2.25
8-31-78	.68 ± .08	.25 ± .09	54.48 ± 6.44	4.05 ± 2.10

DISCUSSION

Weight loss

The results of laboratory and field experiments suggested two major components of emergent macrophyte litter degradation. First, a rapid leaching of soluble organic compounds which accounts for the sharp drop in dry weight and nutrient elements producing dissoloved organic matter available to microorganisms. Second, physical and biological breakdown of plant litter occurs mainly in the spring and summer.

The weight loss of Typha shoot litter in Theresa Marsh in the first month was about the same as those found in both water types at 10C and in the controls of antibiotic and sterilization experiments,indicating that water types and field conditions have little influence on leaching of soluble compounds. Although Kauskiik and Hynes(1971) found temperature also showed little effect on early leaching rate in the first two or three days,in my study leaching loss at 18C was considerably higher than at 10C. The leaching rates were found to be greater in root - rhizome than in shoot. Loss of dissolved organic matter in the early stage of decomposition have been reported for Typha latifolia(Boyd,1970), T.angustifolia and Phragmites communis(Mason and Bryant,1975), and Scirpus subterminalis(Otzuki and Wetzel,1974).

After the first month, the rates of decomposition under laboratory conditions and in the marsh slowed down dramatically, indicating the refractory nature of emergent macrophyte litter. The combination of low temperature, high fiber content and low nutrient content,especially N and P, limited growth of decomposers, revealed in the laboratory by the slower rates of decomposition at 10 ^{O}C and in Theresa Marsh during the winter months. At both temperature levels, Typha leaves served as the sole source of microbial nutrients, whereas in artificial water the microorganisms were supplied with soluble nutrients in addition to plant nutrients. The added nutrients in water can be easily taken up and presumably are utilized first. The exoenzyme digestion and competition for the new food source probably began after the initial nutrients in water became scarce, resulting in slower rate of degradation. The rate of dry weight loss increases correspondingly with increasing temperature as shown in the results of Typha litter at 18 ^{o}C and the acceleration of decomposition rates of all three species in the marsh during summer.

The sharp drop in dry weight of both shoot and root - rhizome litter in June and August results from fragmentation losses.Several agents are responsible for fragmentation of the litter. Colonization of senescing and dead herbaceous tissues by microorganisms follows the sequence of weak parasite, primary saprophytic flora, secondary saprophytic flora (Bell, 1974). The weak parasites associate with senescing tissues, primary and secondary saprophytic flora utilize simple carbohydrates and eventually cellulose and lignin of dead plant materials. Suppression of microbial growth and activities by antibiotics and sterilization resulted in inhibition of decomposition. The presence of arthropods,annelids and epiphytes in the litter bags during summer confirms the belief that the breakdown of plant litter in later stages is mainly biological.

Site differences have pronounced effects on the rate of weight loss in the marsh. l3esides the difference in biotic factors between sites, differences in physical factors and chemistry of water should also be considered. Typha litter at site 2 and Sparganium at site 4 were influenced by the continuous water flow into the outflow during the warm months, resulting in faster weight loss. Scirpus shoots which senesced earlier than Typha and Sparganium probably had already lost some soluble matter through leaching, possibly explaining why Scirpus litter exhibited the lowest weight loss at 26 days. In addition, the triangular culms and hard tuberous rhizomes of Scirpus are resistant to biological and physical degrad - ation,resulting in the lowest decomposition rate.

The root-rhizome litter probably would have decomposed more slowly if the sample3 had *been placed* in their underground habitats. Though the study was conducted for only 548 days, the results indicate that the shoot and root - rhizome litter of and Sparganium in Theresa Marsh would undergo complete decomposition in about two years,and somewhat longer in the case of Scirpus.

Nitrogen and protein

In all experiments, the % N increased with time. The increase in N was found to be associate with microbial biomass as shown in sterilization experiment. The absence of living organisms on Typha leaves and in marsh water after sterilization resulted in no net weight loss after the early leaching period and also in nosignificant increase in nitrogen. Decrease in N in the first 15 days resulted from leaching loss of soluble substances including dissolved organic nitrogen. Variation of N content in the apex, middle and base of the leaves may explain the minor variations in N contents in the sterilization experinent. Some plant proteins may be denatured during sterilization and became insoluble resulting in a smaller leaching loss of nitrogen.

A combination of low temperature, high fiber content, and low nitrogen remaining after leaching loss may limit the growth of microorganisms resulting in a low N value at 50 days. This is evident in Typha shoot litter at 10 °C n This combination may explain the decrease in litter nitrogen in the field during October-November. In Theresa Marsh, maximum nitrogen content of the litter occurred in summer when environmental factors were favorable for growth and development of decomposers. Nitrogen increases in June and August indicate that partially decomposed litter made an excellent substrate for microorganisms. Nitrogen peaks of Typha and Sparganium shoot litter occurred in August,and for shoots in June. High N content of root-rhizome litter for all species also falls between April and August. Analyses of litter nutrients at any one time may show either increased or decreased nutrients, when general growth pattern and competition of microorganisms are considered.

Epiphytes colonizing the macrophyte litter may also be partially responsible for N increase. During spring and summer months epiphytes, algae in particular, were found in abundance on the litter and litter bags. Though they were not uniformly distributed on the substrate, they were difficult to separate from the substrate. These epiphytes not only account for increased N but also are a potential cause of increases of other elements.

The antibiotic experiment indicatel an unexpected. increase of N. This could have been caused by colonization of microorganisms resistant to the antibiotic used or by adsorbtion of antibiotics by Typha leaves. Microbial growth as the cause of N increase does not seem probable since dry weight after leaching loss remained relatively stable throughout the experiment. The adsorbtion of antibiotics is possible and degradation of these antibiotics produces compounds which can be N and C sources, e.g., amines and ketones.

Sparganium shoots which are relatively rich in N have the fastest weight loss, Scirpus shoots with low N content decompose very slowly. Coulson and Butterfield (1978) proposed that the rate ef microbial decomposition of plant substrates is highly correlate with substrate N and P concentration. This does not hold true for all species in the case of root-rhizome decomposition; the structural components of the plants have to be considered together with their nutrient content.

Phosphorus

The shoots of the three species studied. in the marsh have low initial P, their root-rhizoines have P coucentration 2 to 5 times higher than the shoots. Leaching loss of P in the first month and faster in root-rhizome than in shoot. In the early stage of decay this leaching loss appears related tn dry weight loss. There is little difference in P content of Typha leaves in arti- ficial and distilled water at 10 °C or 18 °C suggesting little effect of these factors on early leaching. Several workers(Cowen and Lee,1973; Triska et. al.,1975)attribute a substantial loss of P from leaves of various species to leaching during the first few days or hours after wetting. Cutting up the leaves resulted in a three fold increase in leached soluble P(Cowen and Lee, 1973).

During the November to April period, Phosphorus release from litter in the marsh was negligilbe. P accumulation in spring and summer and between day 94 to 184 in the laboratory, indicating elemental enrichment of partially decayed litter. Increase in microflora inhabiting the plant litter tends to be a major cause of P increase. The P increment observed by Cruz and Gabriel(1974) during decomposition of Juncus roemerianus they presumed was due to microbial biomass and absorbtion.

Calcium and magnesium

Most of the Ca and Mg were lost in the first month, indicating that they are mainly held as components of soluble organic compounds. After leaching, the reamaining Ca and Mg are mainly in the cell walls and more resistant to decomposition. The increases of Ca and Mg in the litter in the marsh may be explained by contamination by the soil(Thomas,1970), precipitation of $CaCO_5$(Mason and Bryant,1975), or accumulation by epiphytes. Accumulation by epiphytes apprears plausible especially in the case of calcium. The removal of CO_2 from water by photosynthesis causes the reaction $CaCO_3 \rightleftharpoons Ca(HCO_3)_2$ to shift to the left.

Carbon

Carbon concentration was examined in this study because C may account for the apparent or relative increase of N in the plant litter. Since the C in most plant materials accounts for 45—47% at the dry weight(Allen et al., 1974), rapid carbon loss can lead to an increased N percentage in the remaining litter.

Laboratory experiments demonstrated that N increase as a % dry weight in Typha leaves during the first two weeks of decomposition results from the loss of soluble compounds. The increased N in later months is undoubtedly from microbial biomass.

Typha leaves (C=42.85%) have a high C:N ratio,56.5, far lower in N than the diet required by most animals at any trophic level. A generalized diet for most animals has C:N ratio of 17 (IRussel-Hunter, 1970). Similarly, the C:P ratio(226.6) is very high in Typha leaves, compared with microalgae(" ~70) and bacteria (" ~27) (Spector,1956). These characteristics minimize herbivore exploitation.

During the 120 days at 10C, C content is lost chiefly through leaching. The small fluctuation after 15 days probably resulted from microbial colonization. 1'he decrease in C:N ratio results from N accumulation. A low C:N ratio in submersed, floating, and emergent species as a consequence of N accumulation was reported recently by Godshalk and Wetzel(1978). The decrease in C:N ratio in the antibiotic treated Typha leaves is attributable to adsorbtion of antibiotics.

Water nutrients

Change in NH_4-N in Theresa Marsh appeared correlated with macrophyte decomposition. As autolysis and leaching of the macrophytes occurred in the fall, dissolved organic matter increased and consequently NH_4-N , generated as the primary end product of decomposition by heterotrophic bacteria, increased. Ammonification ceases during winter and increases as water temperature rises in summer. The sources of NH_4-N in the marsh include plant litter, detritus of previous growing seasons, input from three inlets, invertebrate excretion,and release from the bottom sediment. NH_4-N does not increase tremendously in summer, though decomposition rates increase. This may be explained by faster nitrification during summer, increased utilization of NH_4-N by autotrophs and microorganisms, and increased adsorbtion of NH_4-N on to the mud partcles in the sediment (Kamiy- 4 ama et al., 1977).

Orthophosphate is the form of P immediately useful for autotrophic plants and microorganisms. Its turnover time in lake water is very rapid and may be less than an hour (Rigler, 1964). Some authors (Johannes,1965; Pomery,1970) have suggeste that in the absence of bacterial grazers, nutrients(in partcular P) would become tied up in the bacterial populations. Barsdate et al.(1974) showed that PO_4^3 is indeed cycled more rapidly in grazed than ungrazed system. Fluctuation of orthophosphate during the 548 days in the marsh was largely governed by microorganisms that are more competitive in utilizing orthophosphate than algae and macrophytes. The low orthophosphate and NH_4-N concentrations in April indicate low microbial activity, low rate of release from macrophytes, probably increased turnover time,and probably affected by dilution as stream flow reaches its annual maximum at this season while decomposition is still low. In addition to biotic factors,orthophosphate concentration is affected by chemical properties of water and may be chelated and precipitated, resorbed or desorbed from clay minerals (Stumm and Morgan, 1970).

Calcium concentrations in the marsh water undergo marked seasonal dynamics. Marked decreases in October and November are probably due to precipitation of CaCO5 and dilution by rain. Calcium and magnesium values do not drop in April are probably the result of high levels in inflow from dolomitic parent material of soils in the watershed. Calcium decrease in June is prbably due to increased photosynthesis in summer.

In general, magnesium compunds are more soluble than calcium compounds and are rarely pre precipitated. Magnesium carbonates and hydroxides precipitate significantly only at very high pH (>10) under most natural conditions(Wetzel, 1975). As a result of these properties, the concentration of Mg fluctuates little. This was evident in the relatively stable Mg concentrations in the marsh. Dcreased Mg in August may result from greater amounts becoming tied up in living biomass , inc~'eased loss through outflow or decreased input from inflows.

SUMMARY

Decomposition of *Typha latifolia*, *Sparganium* and *Scirpus fluviatilis* shoot and root-rhizome litter was examined at Theresa Marsh during September 18,1977 to August 31,1978. The effects of temperature and water types on the decomposition of *Typha* shoot were studied in the laboratory for 6 months. To study N & C changes in *Typha* shoot litter, antibiotics(cycloheximide, nystatin, penicillin, streptomycin) and sterilization techniques were employed to suppress the growth of microorganisms in the second laboratory experiment.

In all experiments dry weight, N, C, P, Ca, and Mg content of the litter declined abruptly in the first month. These losses are attributed to leaching of soluble compounds in the litter. The leaching rates were greater in root—rhizome than in shoot litter. The fallen emergents released large amounts of DON into the marsh water in September and October. Microorganisms and microscopic algae tend to have a major role in immobilizing nutrients, but large amounts of nutrients tend to enter open water and are lost through the outflow.

Temperature had a significant effect on the rate of dry weight loss. At 10 °C the dry weight losses in both artficial and distilled water were slower than those at 18 °C . At both temperatures, dry weght losses in distilled water were greater than those in artificial water.

Dry weight losses from shoot and root-rhizome litter were negligible during the winter(November-April). Decay rates increased in spring and summer. At 348 days the remaining dry weights of *Sparganium*, *Typha*, and *Scirpus* shoot litter were 26.9, 47.6, 51.1% respectively, and those of root—rhizome were 27.8, 42.1, 59.1 (*Typha* <*Sparganium* <*Scirpus*).

Antibiotics and sterilization effectively inhibited decomposition; the remaining dry weights of both treatments were relatively stable throughout the last 105 days after initial leaching loss.

The nitrogen content of litter as percentage by dry weight increased overtime both in the marsh and in the laboratory. The increases in and Sparganium shoot litter in August reached about three times the initial percentages, N increases in root - rhizome material were less dramatic. In the laboratory, N accumulation apparently resulted from microorganisms inhabiting the Typha leaves. N increases in antibiotic trested Typha leaves probably resulted from adsorbtion of antibiotics or of compounds derived from antibiotic degradation.

Fluctuation of C content of Typha leaves in the controls of both antibiotic and sterilization experiments was small after the early leaching loss. The C:N ratio decreased over time, mainly a result of N accumulation.

Increases in protein content in decomposed litter in spring and summer indicated increasing nutritive value of litter for detrittivores.

P accumulation in the later stages of decomposition in both laboratory and field experiments is probably from microbial biomass. Increases of Ca and Mg levels of litter in the marsh were probably the results of $CaCO_3$ precipitation and epiphyte biomass.

NH_4-N , soluble reactive P, Ca, and Mg in the marsh water showed significant intercorrelation with N, P, Ca, and Mg in the plant litter. The values of NH_4-N and soluble reactive P place Theresa Marsh in the eutrophic lake category.

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