DECOMPOSITION OF INTERTIDAL FRESHWATER MARSH PLANTS

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Abstract This paper summarizes the existing information concerning decomposition of marsh plants which grow in the regularly flooded portions of freshwater tidal marshes. The 6 species investigated *(Peltandra virginica, Nuphar luteum, Pontederia cordata, Bidens laevis, Zizania aquatica, Sagittaria latifolia)* all exhibit rapid rates of decomposition. Typically, 40–50% of the original ash-free dry weight is lost from litterbags within 10 days and 70–80% within 60 days. These marsh plants appear to decay more rapidly and produce larger quantities of dissolved organic matter than the salt-tolerant plants from higher salinity, coastal marshes. There are indications that they contain more N and that the pattern of N change during decomposition differs from that of the higher salinity plants. The leaves of *Peltandra virginica* contain initially between 2–3% N on an ash-free dry weight basis. During decomposition this may increase to 4–5.5% N during the first 20 days and then decline to 3–3.8% after 50 days. The C:N ratio follows a similar, but inverse pattern.

Key words Bidens laevis, *C:N ratio, decomposition, freshwater tidal marsh, marsh plants, N change*, Nuphar advena, Nuphar luteum, Peltandra virginica, Pontederia cordata, Sagittaria latifolia, Zizania aquatica.

INTRODUCTION

Although tidal freshwater marshes cover large tracts of the coastal zone of eastern North America, particularly between southern Virginia and northern New Jersey, only a modest research effort has been directed to these environments. This is in marked contrast to the massive literature which exists for saline tidal marshes. As a result, such basic ecosystem processes as

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primary and secondary production, decomposition, nutrient cycling, and succession are poorly understood for the tidal freshwater marsh ecosystem.

The purpose of this paper is to examine the preliminary data which exist for one of these processes, decomposition of tidal freshwater plants. Our objectives are: (1) to summarize existing research results, (2) attempt to synthesize general principles, (3) to compare these preliminary results and principles with the extensive literature on saline tidal marshes, and (4) suggest directions for future research.

We have chosen to restrict our discussion to those marsh plants which occur primarily in the regularly flooded portion of the marsh. These include arrow arum *(Peltandra virginica)*, spatterdock or yellow pondlily *(Nuphar luteum)*,[1] wild rice *(Zizania aquatica)*, pickerel weed *(Pontederia cordata)*, arrowhead *(Sagittaria latifolia)*, and bur marigold *(Bidens laevis)*. Certainly, these are not all of the species which occur in this zone, but they are apparently the only ones for which published decomposition results exist. Plants which are found in the irregularly flooded sections of the tidal freshwater marsh, such as the common reed *(Phragmites communis)* and the cattail *(Typha latifolia)* have been omitted from this discussion. For further information on these thoroughly studied species, see Mason and Bryant (1975).

METHODS

Original data presented in this paper (Heywood, 1977; W. E. Odum *(personal observations)* are based on the following methodology. Decomposition rates were estimated using nylon bags with 2-mm mesh. Forty grams of air-dried, green plant leaves were placed in each bag. Four replicates were removed at intervals, the plant material washed thoroughly, ovendried at 105°C for 48 hours, weighed, and ground in a Wiley mill to 20-mesh size. Replicate 1-g samples were ashed in a muffle furnace at 550°C for 12 hours. Litterbags were placed in the freshwater headwaters of Ware Creek, a tributary of the York River, Virginia. For more detailed description of methods, see Heywood (1977).

Total N was determined by a modified Kjeldahl technique (Jackson, 1958) and by the indol phenol blue method for ammonia using a Technicon Autoanalyzer® I (Anonymous, 1971). Organic carbon was assumed to be equal to 45% of the ash-free dry weight. This was confirmed by analyses of 12 samples on a Perkin-Elmer CHN™ analyzer which gave values ranging from 43–48% and mean of 45%. Analysis of variance was used to test the data for significance.

Methodological Difficulties Decomposition studies of tidal freshwater marsh plants are hampered by several factors which may not be as bothersome in other environments. Foremost among these is the problem of high sedimentation rates. Typically, these marshes are characterized by a substrate composed of fine, unconsolidated sediments. These sediments shift about constantly in response to wind, tide, and precipitation-generated perturbations. As a result, litterbags quickly become infiltrated and covered with fine, sticky sediments. In addition to covering the litterbags and rapidly creating anaerobic conditions, these fine sediments adhere to every surface and fissure in the litter and are almost impossible to remove completely.

[1] *Nuphar luteum* equivalent to *N. advena*, Beal (1977); eds. note.

To circumvent this problem we have found it necessary: (1) to deploy litterbags whenever possible at sites where they are well flushed by tidal action, (2) to scrub and sonicate litter samples thoroughly, and (3) report decomposition rates on an ash-free basis. Even with these precautions a large error factor may be introduced into the results. This is particularly likely to happen when litterbags are placed on the surface of the high marsh in poorly flushed marsh ponds. The most consistent results are obtained from samples suspended in the water column of well-flushed tidal creeks.

A second problem concerns the growth state at which marsh plant tissues should be harvested for litterbag studies. In higher salinity marshes it is usually possible to harvest standing "dead" material which has not been appreciably decomposed. In the tidal freshwater marsh this is virtually impossible because the initial stages of decomposition proceed so rapidly. For a species such as *Peltandra virginica* there is no way to harvest undecomposed dead leaves. The only apparent solution is to harvest living green leaves which appear to be approaching death. This is, of course, artificial and possibly misleading because these leaves contain compounds which the plant would probably translocate back into the root system. For comparative purposes, therefore, it is important to harvest plant tissues from different species at approximately the same growth stage and as near death as possible as evidenced by a color change from green to yellow green.

A similar problem common to other environments concerns the season when litterbag material is harvested. Most marsh species vary in nutrient content seasonally. Leaves of *Peltandra virginica*, for example, may contain as much as 3% N (ash-free dry weight) early in the summer but only 2% or less in the late summer. Obviously, litterbag material for an experiment should be gathered at one location at one time; each batch of material which is gathered at different times or from different locations should be analyzed separately for elemental composition.

RESULTS AND DISCUSSION

Decomposition Rates

From the standpoint of decomposition, the best studied tidal freshwater marsh plant is arrow arum, *Peltandra virginica*. A typical set of decomposition curves for this species is shown in Fig. 1. There are 2 factors that should be emphasized. First, the initial rate of decomposition of this species is extremely high; this indicates a considerable loss of soluble compounds and a high rate of dissolved organic matter (DOM) production. After the initial 30

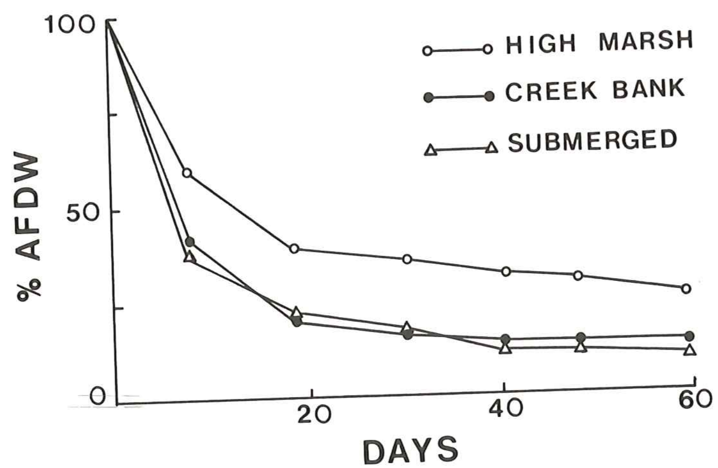

Fig. 1. The percentage of the original ash-free dry weight (AFDW) of leaves of *Peltandra virginica* remaining in litterbags placed on the high marsh (irregularly flooded), creek bank (flooded twice daily) and permanently submerged in the water column. Each data point represents 4 replicates.

to 40 days, the decomposition rate slows dramatically so that it requires from 150–400 days for all of the *Peltandra virginica* tissue to disappear from the litterbags. Second, there are significant differences in decomposition rates depending upon the sites where the litterbags are placed. For example, submerged leaves decompose more rapidly ($P \leq .01$) than those placed upon the marsh surface. There are several factors which may contribute to the higher rates of decomposition of submerged leaves including better access for detritivores, more constant physical conditions for decomposer bacteria and fungi, a greater availability of dissolved nutrients, and a more suitable environment for rapid leaching.

Other investigators have found a similar pattern of rapid decomposition for *Peltandra virginica*. Walker and Good (1976) found 20% remaining after 40 days on a regularly flooded marsh surface. Whigham and Simpson (1976) report high rates of decomposition with <40% of the original material remaining after 90 days.

Because these field results indicated an initial rapid loss of soluble compounds from *Peltandra virginica*, we designed a laboratory experiment to examine soluble losses over very short time intervals. Weighed pieces of air-dried, yellow leaves were placed in flasks of freshwater situated on a shaker table, individual flasks were removed at 1-day intervals, and the detritus filtered out of the water, dried and weighed. The results (Fig. 2) detail the extremely rapid loss of weight during the first 9 days of immersion culminating in a 50% loss of dry weight. For comparison, pieces of green cordgrass, *Spartina alterniflora*, were treated in a similar manner and

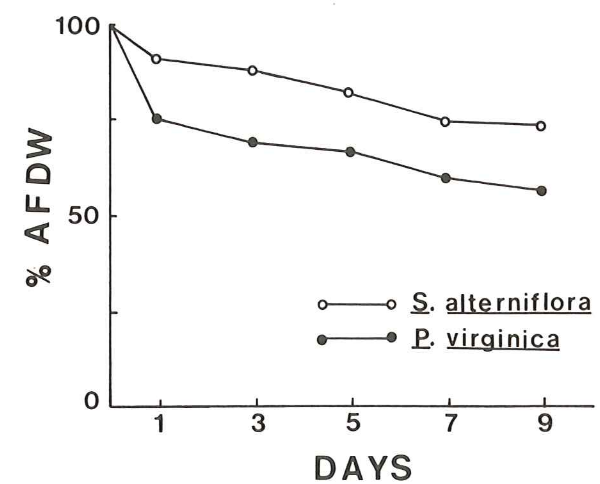

Fig. 2. The percentage of the original ash-free dry weight (AFDW) of green leaves of *Peltandra virginica* and *Spartina alterniflora* retained on filter paper after immersion in freshwater in 250-ml flasks at 20°C. Each data point represents 4 replicates.

showed a significantly ($P \leq .01$) slower loss of weight. This suggests that much of the primary production of tidal freshwater marshes is released rapidly, probably as dissolved organic matter, to surrounding aquatic ecosystems.

Comparison with Saline Species To confirm our initial impression of a more rapid rate of decomposition for tidal freshwater marsh plants when compared to more saline species, we deployed litterbags of *Peltandra virginica* and *Spartina alterniflora* at the same sites in both freshwater and estuarine marshes. The results from the freshwater site (Fig. 3) show a significantly greater decay rate ($P \leq .01$) for *Peltandra virginica*. Almost identical results were obtained from an estuarine marsh (salinity = 25‰).

Other Freshwater Marsh Species Our preliminary data on 4 additional species of tidal freshwater marsh plants (Fig. 4) indicate relatively rapid rates of decomposition. All 4 species exhibit an initial rapid loss of weight (40% or more in the 1st month) followed by a more gradual decline until all material disappears from the litterbags after 150–350 days. In all cases these rates of decay are significantly higher ($P \leq .05$) than for the higher salinity species *Spartina alterniflora* and *Juncus roemerianus* deployed at the same sites.

D. F. Whigham and R. L. Simpson *(personal communication)* have data for *Zizania aquatica* which show a 60% loss in weight after 90 days for litter on the high marsh, but only 35% loss for inundated litter during the same time period. This lack of agreement with our data may be due to either differences in physical and chemical conditions at the sites or may be be-

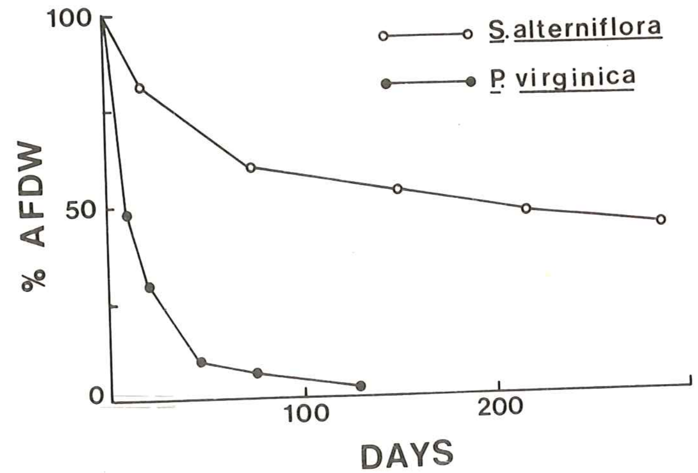

Fig. 3. The percentage of the original ash-free dry weight (AFDW) of green leaves of *Peltandra virginica* and *Spartina alterniflora* remaining in submerged litterbags. Each data point represents 4 replicates.

cause their data are expressed in terms of dry weight while ours are expressed as ash-free dry weight thus excluding adsorbed inorganic sediment particles. D. F. Whigham and R. L. Simpson (*personal communication*) also investigated *Bidens laevis* and found a rapid rate of decomposition similar to that shown in their data for *Peltandra virginica* (75% loss of weight after 90 days at a regularly flooded site).

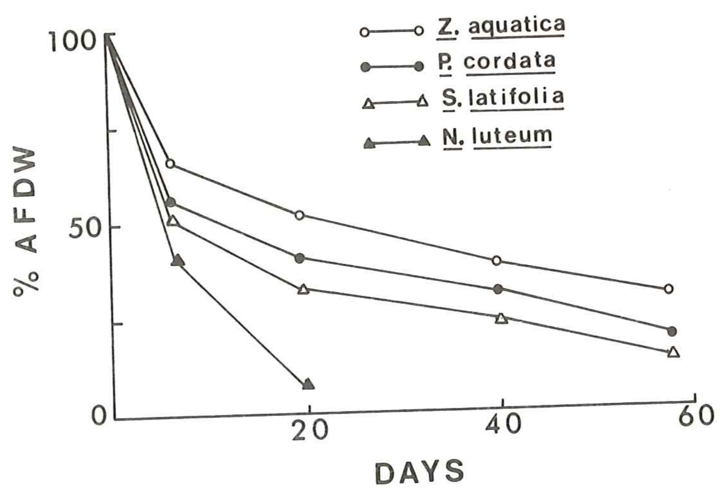

Fig. 4. The percentage of the original ash-free dry weight (AFDW) of leaves of *Zizania aquatica*, *Pontederia cordata*, *Sagittaria latifolia* and *Nuphar luteum* remaining in submerged litterbags. Each data point represents 4 replicates.

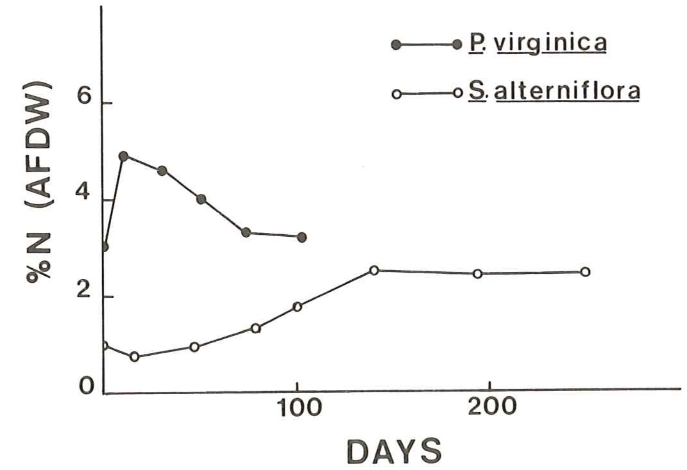

Fig. 5. The relative N content (ash-free dry weight, AFDW) of leaves of *Peltandra virginica* and *Spartina alterniflora* from submerged and intertidal litterbags. Each data point represents 6 replicates.

Nitrogen Changes During Decomposition

The only tidal freshwater marsh species for which we have data concerning N changes during decomposition is *Peltandra virginica* (Fig. 5). Submerged and creek bank litter follows a trend of initial relative N increases followed by subsequent declines. Plant material which was originally 2.9% N (ash-free dry weight) increased to 4.0–5.5% N after 10–20 days and then declined to 3.0–3.8% N after 50 days. The C:N ratio declined initially from 15.5 in fresh *Peltandra virginica* leaves to 7.6–10.6 after 29 days and rose to 12.3–15.2 after 50 days.

In contrast, litter placed on the irregularly flooded high marsh rose steadily in N content from 2.9% to 6.1% after 20 and 6.5% after 50 days. The C:N ratio dropped from 15.5 to 9.2 after 10 days and reached 7.0 after 50 days. We believe that this contrasting pattern can be explained in part by the rapid colonization of the high marsh litter by autotrophic bacteria and nitrogen-fixing blue-green algae, both of which were observed qualitatively on the detrital material.

R. Walker and R. E. Good (*personal communication*) followed N changes in decaying *Peltandra virginica* for 1 month at 3 sites on the Mullica River, New Jersey. Their results showed an increase from initial values of 1.76–2.05% N per gram of ash-free dry weight to values of 3.10–3.80% after 24 days. Two of the sites demonstrated subsequent declines while the litter at the third site rose slightly in N content. At 1 site, the N content dropped from 3.24% to 3.15% between days 24 and 45 while at the other site it dropped from 3.80% to 3.43% between days 24 and 31. Both changes were not statistically significant ($P > .01$).

To summarize, *Peltandra virginica* appears to exhibit an initial increase in relative N content with a drop in the C:N ratio followed by a decline in N and rise in the C:N ratio between days 20 and 40. This pattern does not apply to the high marsh where there is a continual, gradual increase in N. As Heywood (1977) has pointed out, this type of N loss is typical of plants which have a high initial nitrogen content in contrast to species such as *Spartina alterniflora* or *Spartina cynosuroides* which typically contain less than 1.5% N as live or standing dead material, but increase steadily during decomposition and ultimately reach values of 2–3% N after several months of decay.

CONCLUSIONS

Although there are few research data on decomposition of intertidal freshwater marsh plants, certain preliminary conclusions can be drawn. First, these plants appear to decompose more rapidly than species from estuarine and higher salinity marshes. There are also indications (M. Dunn and B. Nash, *personal communication*) that the tissues of freshwater marsh plants are much more readily attacked by detritivores (such as amphipods and isopods) and more easily macerated than tissues from *Spartina* species growing at higher salinities. Both observations can be explained, at least in part, by the chemical composition of the freshwater marsh plants. In addition to their relatively high N content, preliminary analyses suggest that they contain low amounts of lignin and cellulose, a combination which evidently leads to a rapid rate of decomposition. Although this rate may be influenced by physical variables such as salinity and temperature, in all cases it should be more rapid than for the higher salinity marsh plant species with their more refractive tissues.

Second, the production of DOM from tidal freshwater marshes may be higher per unit of primary production than from saline and estuarine marshes. This suggests that the DOM pathway of energy flow (dead plant → DOM → bacteria → consumer) may be important in the tidal river ecosystems where these marshes occur.

Finally the pattern of N change during decomposition of tidal freshwater marsh plants appears to differ from that of saline marsh plants. In either case the C:N ratio of aged detritus is similar (between 12 and 18).

Obviously, there are numerous and varied possibilities for future research on decomposition in tidal freshwater marshes. In addition to more detailed decomposition studies of the 6 species mentioned in this paper, there are 20 to 30 other species which occur in significant quantities to merit some study. Research to date has been limited to stems and leaves. Walker and Good (1976) found that the underground standing crop of a species such as *P. virginica* may be at least 10× higher than that present aboveground. What happens to this material when it dies? Much of the subsequent decomposition must occur under anaerobic conditions. Studies of root decomposition appear to be essential.

Finally, critical questions center on the problem of detritus utilization and secondary production. How important is the DOM pathway? Is freshwater plant material more easily consumed and assimilated by detritivores than material from more saline marshes? Which marshes are dependent upon, or at least utilize, detritus from these marshes? In short, how important are tidal freshwater marshes as the base of a detritus food web?

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