

## Effects of Flooding on Leaf Litter Decomposition in Microcosms

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**Summary.** The effects of hydroperiod on decomposition rates of senescent *Acer rubrum* leaves were tested in microcosms in a controlled laboratory environment. Microcosm treatments included continuously flooded, continuously unflooded, and fluctuating hydroperiods. All flooding treatments promoted decomposition but variations in hydroperiod had no significant effects. A leaching experiment indicated the higher decay rates under flooded conditions were primarily due to high leaching losses from soaking. Unlike nutrient dynamics in the field, where net accumulation occurs, nitrogen and phosphorus in the litter in the microcosms exhibited net losses. The major external inputs which provide a source of nitrogen and phosphorus for immobilization in the field were lacking in the microcosms. Calcium, magnesium, and potassium exhibited net losses except for calcium in the unflooded microcosms. The microcosm results demonstrated the importance of external inputs to litter nutrient relations.

### Introduction

The mechanisms and controlling factors of decomposition processes in terrestrial and aquatic habitats have been well described (Dickinson and Pugh 1974; Anderson and Macfadyen 1976; Singh and Gupta 1977; Swift et al. 1979). However, information is still lacking on critical aspects of decay in wetland ecosystems, which are quite varied and complex (Brinson et al. 1981). Several studies have shown litter decomposition to be faster in flooded habitats than in adjacent drier sites (Brinson 1977; Bell et al. 1978; Ewel and Odum 1978; Merritt and Lawson 1979; Shure et al. 1980 and 1981; Day 1982), but the exact causes of these site differences have not been definitely established. In reviewing the literature, Brinson et al. (1981) could not conclude that increased flooding leads to increased decay rates. I have previously reported that litter quality (phosphorus concentration, C:N ratio, lignin and tannic acid content) is primarily responsible for variation in decomposition rates among sites experiencing different hydroperiods in the Great Dismal Swamp (Day 1982). Tree species (e.g. *Nyssa aquatica*) found on the more extensively flooded sites were more susceptible to rapid decay. Davis (1981) also found litter quality to be more important than environmental conditions (including water logging) in affecting decay rates of mosses in the Antarctic. The Dismal Swamp study gave some indications of at least indirect effects of hydroperiod

on decomposition, but the results from the field did not establish a direct relationship between flooding and decay rates (Day 1982). Recognizing that other factors, especially oxygen availability, affect decay in wetlands (Brinson et al. 1981), I conducted a study to evaluate the effects of flooding under controlled conditions.

The present study, a follow-up to the field research, tested the direct effects of hydroperiod on decomposition rates by using a single litter type in microcosms in a controlled laboratory environment. An experiment was conducted to evaluate the importance of leaching in this test system. Nutrient dynamics in the microcosms were also examined.

### Methods

#### *Microcosm Experiment*

The microcosms consisted of 38 l (10 gal) styrofoam coolers lined with plastic. Blocks of soil (0.02 m<sup>3</sup>; 15 cm deep), including litter, were removed from the maple-gum site described by Dabel and Day (1977) and Day (1982) and placed in each of twenty-five coolers. The maple-gum site is periodically flooded during winter and spring, is dominated by *Nyssa aquatica*, *Acer rubrum*, and *Nyssa sylvatica*, and has a mineral soil high in organics with an average pH of about 4.9. Five treatments representing varied hydroperiods (Table 1) were assigned to the microcosms (five replicates each). Flooding was simulated with deionized water carefully poured to a depth of 6 to 7 cm above the soil surface and drydown was simulated by siphoning until the water level was at least 10 cm below the soil surface. Deionized water was used so nutrient additions would not be a factor in the experiment. In the A treatment (no flooding)

**Table 1.** Hydroperiods of the experimental microcosms. The study period is divided into eight segments (one month intervals) and an F indicates the microcosm was flooded during that time

Treatment	Days 0 to 28	Days 28 to 63	Days 63 to 90	Days 90 to 119	Days 119 to 154	Days 154 to 183	Days 183 to 215
A							
B	F	F	F	F	F	F	F
C	F	F	F	F	F		
D		F	F		F		
E				F	F		

the soil surface was kept moist with dionized water; this was necessary only a couple of times during the study. All microcosms were kept in a darkened room at 22.5° C so that light and temperature conditions were constants. Soil and water pH and redox potential, which were monitored throughout the study, decreased in all microcosms. Water pH ranged from 5.05 to 4.10 and redox potential in the water ranged from 250 mv to 125 mv. Apparently all microcosms remained aerobic in the water column.

Senescent *Acer rubrum* leaves were picked from a single tree on the maple-gum site on November 7, 1979. After air drying and subsampling for oven-dry mass conversions, leaves were weighed individually, labeled with a plastic tag, and placed into the microcosms (24 leaves each). One to two leaves were collected monthly from each microcosm, oven dried and weighed. Toward the latter part of the study it became difficult to recover two leaves from every microcosm because some leaves were separated from their labels. Decay rates were computed on the basis of percent dry mass remaining using an exponential decay model (Olson 1963).

The oven-dried leaves were pooled by treatment and date for nutrient analysis, ground in a Wiley Mill using a 40 mesh screen, and digested in a Technicon block digester by the sulfuric acid-hydrogen peroxide technique. Total Kjeldahl nitrogen concentrations and phosphorus concentrations detected by the molybdate blue method were determined on a Scientific Instruments autoanalyzer (Technicon Industrial Method 329-74 W/B). Calcium, potassium, and magnesium concentrations were determined on a Perkin-Elmer 603 atomic absorption spectrophotometer. National Bureau of Standards orchard leaves were processed with each group of samples digested and analyzed.

#### Leaching Experiment

The significance of leaching losses of mass and nutrients from litter in flooded conditions was tested by soaking senescent *Acer rubrum* leaves using two different treatments (five replicates and two controls each). The leaves came from the same group collected for the microcosm experiment. One treatment, patterned after Brinson (1977), consisted of soaking approximately 5 g of air dry senescent *Acer rubrum* leaves in five successive changes of 1 l deionized water in 2,000 ml polyethylene beakers in the dark at 22.5° C. Intervals of soaking, in hours, were 0-2, 2-5.5, 5.5-21, 21-45.5, and 45.5-93. The other treatment simulated periods of alternate soaking and drying, which might occur with a fluctuating hydroperiod, by drying the leaves in an oven at 70° C for approximately 1 h between each soaking interval. The controls for the two treatments contained no leaves. The leachate was filtered through glass fiber filters, acidified for preservation, stored at 4° C, and analyzed within 48 h. The leachate was digested and analyzed for nitrogen, phosphorus, potassium, calcium, and magnesium by the methods described for the microcosm experiment. Leaching rates were expressed as milligrams of nutrient appearing in the water per gram of leaf dry mass per hour. The leaves were oven dried, weighed, ground in a Wiley Mill, and analyzed for nitrogen, phosphorus, potassium, calcium, and magnesium. Mass and nutrient losses from the leaves were computed. The experiment was repeated with green *Acer rubrum* leaves collected from a single tree on the maple-gum site on July 17, 1980.

## Results

### Decomposition Rates

By chance, a large population of chironomids developed in microcosm B1. Decay rates in B1 were higher than in all treatments; however, tests for statistical significance were influenced by the small sample size. By day 215, leaves collected from B1 had lost 70% of their original mass, and unlike the leaves in all other microcosms, they were observed to be highly skeletonized. As indicated in Table 2, statistical analyses were conducted with and without B1 and the results involving treatment B were unaffected.

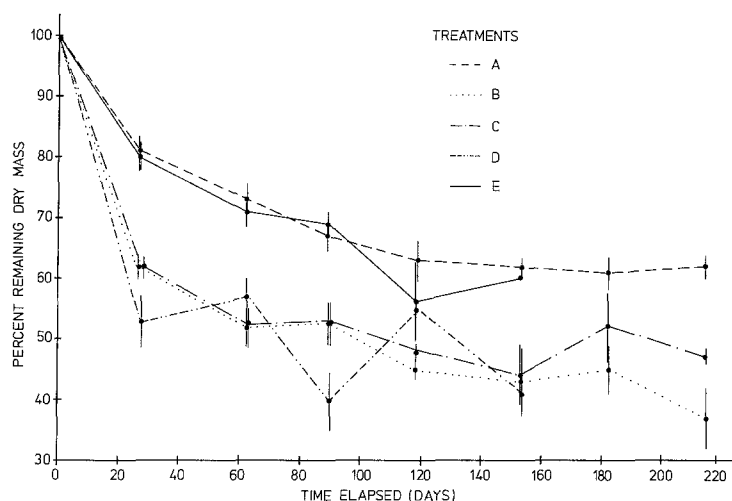
Decomposition through day 154 in treatment B and C (both continuously flooded at that time) was significantly faster than in treatment A (continuously unflooded) (t test,  $P \leq 0.05$ ) (Table 2). Leaves were not recovered from treat-

**Table 2.** Daily decomposition rates ( $-k$ ) for senescent *Acer rubrum* leaves based on the exponential decay model. Leaves were not recovered from treatments D and E after day 154, so two sets of rates were computed

Elapsed time (days)	Treatment	Daily $-k$ ( $\times 10^{-3}$ )	$r^*$	F*	$n$
154	A	2.89	0.847	96	40
	B	4.65	0.781	50	34
	B w/o B1	4.39	0.778	43	30
	B1 <sup>a</sup>	9.36	0.916	10	4
	C	4.60	0.788	48	31
	D	5.58	0.623	14	24
215	E	3.70	0.782	54	36
	A	1.68	0.725	71	66
	B	3.58	0.755	56	44
	B w/o B1	3.17	0.752	46	37
	B1 <sup>a</sup>	4.85	0.790	8	7
	C	2.58	0.669	30	39

\* All correlation coefficients ( $r$ ) and F - statistics are significant ( $P < 0.05$ )

<sup>a</sup> Microcosm B1 contained a large population of chironomids



**Fig. 1.** Decomposition of *Acer rubrum* leaf litter in microcosms measured as percent dry mass remaining. Treatments are described in Table 1. Error bars are  $\pm 1$  SE

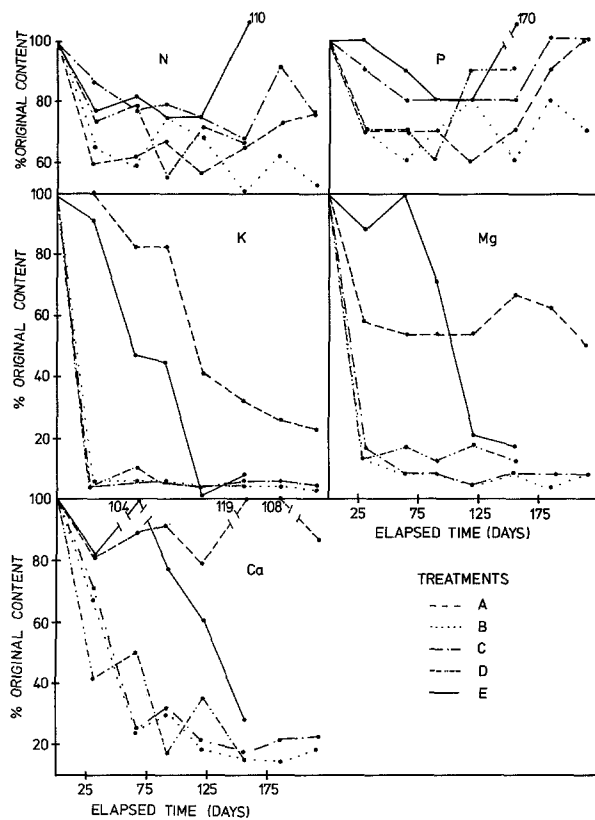


Fig. 2. Percent of original nutrient content in decomposing *Acer rubrum* leaf litter in microcosms. Treatments are described in Table 1

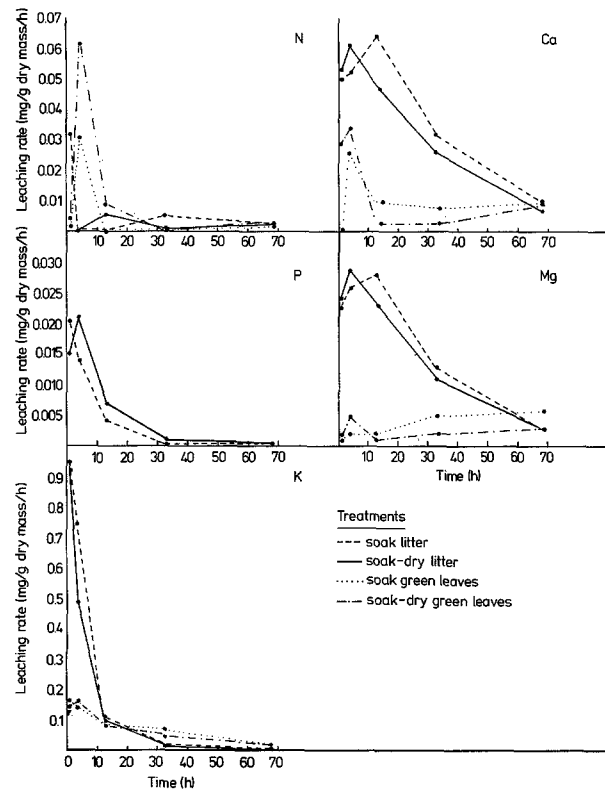


Fig. 3. Leaching rates of nutrients from *Acer rubrum* leaf litter and green leaves. Data points represent midpoint of successive leaching intervals. Note scale differences on y-axes

Table 3. Total losses of dry mass and nutrients from *Acer rubrum* leaves in the leaching experiment. Total soaking time was 93 h. Error terms are 1 S.E. ( $n=5$ )

Treatment	Oven-dry mass loss (%)	N loss (%)	P loss (%)	Ca loss (%)	Mg loss (%)	K loss (%)
Soak litter	$30.8 \pm 1.1$	$18.7 \pm 3.3$	$35.1 \pm 2.7$	$38.1 \pm 2.7$	$65.6 \pm 1.3$	$98.1 \pm 0.4$
Soak-dry litter	$30.6 \pm 7.6$	$16.5 \pm 9.0$	$38.5 \pm 7.5$	$28.1 \pm 10.0$	$55.8 \pm 6.3$	$99.6 \pm 0.2$
Soak green leaves	$22.6 \pm 0.7$	$2.7 \pm 1.7$	$31.4 \pm 2.6$	$34.2 \pm 2.8$	$61.4 \pm 0.3$	$87.2 \pm 1.3$
Soak-dry green leaves	$20.0 \pm 6.7$	$13.4 \pm 6.5$	$31.1 \pm 5.5$	$25.4 \pm 7.5$	$39.2 \pm 5.1$	$83.3 \pm 2.5$

ments D and E after day 154 of the experiment, so decomposition rates ( $-k$ ) were computed for two time periods, through day 154 and day 215 respectively. Through day 215, decay in only B was greater than in A ( $t$  test,  $P \leq 0.01$ ). There were no other significant differences in decay rates between treatments over these two periods. Treatments E to day 154 and C to day 215 exhibited intermediate decay rates and both were periodically flooded during those time spans. Treatment D simulated a highly fluctuating hydroperiod and had the highest decay rate through day 154. However, high variability in the data apparently masked any possible significant differences with the other treatments. All three periodically flooded treatments (C, D, E) exhibited variability in mass loss dynamics during the study (Fig. 1). Flooding apparently promoted decomposition with aerobic conditions persisting (based on comparisons between the unflooded and flooded microcosms), but varia-

tions in hydroperiod were not demonstrated to have a significant effect.

#### Microcosm Nutrient Dynamics

Nitrogen and phosphorus were released from the decaying leaves initially and then were immobilized in all but the B treatment (continuously flooded) (Fig. 2). Treatment E (unflooded initially, then flooded) was the only one to show a net gain of nitrogen and phosphorus. Potassium, calcium and magnesium were released throughout the study in all treatments except A (continuously unflooded), which was variable but exhibited net accumulation of calcium. Trends in leaf cation levels in E approximated those in A until E was flooded, after which cation levels in E dramatically dropped to levels found in the other flooded treatments. Cation levels (indicated by percent of original content) were

highest in treatment A (continuously unflooded); this suggests that leaching is an important mechanism of losses from leaf litter in flooded conditions.

#### *Leaching Losses*

Losses of mass and nutrients from leaves in the leaching experiment were substantial and were generally greater in senescent leaves than green leaves (Table 3). Most potassium in the leaves was lost during the 93 h of leaching. Mass loss due to leaching (31% in senescent leaves) could explain most of the difference in decay rates between flooded and unflooded conditions.

Nutrient leaching rates decreased sharply, following initial increases, during the experiment with senescent leaves and showed less change with green leaves (Fig. 3). Values were corrected for nutrient levels in the controls which did not change. Phosphorus levels in the green leaf leachate were too low to detect by the methods used. The decrease in senescent leaves was gradual for calcium and magnesium and very rapid and high for potassium. Leaching rates were greater in senescent leaves than in green leaves, except for nitrogen (ANOVA and Duncan's Multiple Range test,  $P \leq 0.01$ ). Loss of structural integrity in senescent leaves likely results in greater leaching losses. There was no significant difference between treatments (soak and soak-dry). The drying treatment appeared to be harsher than what might occur in the field, but it apparently had no effect on leaching rates.

## **Discussion**

### *Effects of Hydroperiod on Decomposition*

The results of the present study indicate a direct relationship between flooding and decomposition rates. Decay was faster in the microcosms than in the field (probably due to the constant mild temperatures of the microcosms); however acceleration of the decay processes probably did no more than accentuate the differences between flooded and unflooded conditions in the relatively short term study. The progress of decay was compressed in time.

Flooding promoted higher leaf litter decomposition rates in the microcosms (Table 2). Slow decay is frequently attributed to water logged litter due to anaerobic conditions (Williams and Gray 1974). However, the litter environment in the microcosms remained aerobic, as it does in shallow water seasonal swamps. Apparently though, the higher decay rates were due primarily to high leaching losses from continuous soaking (Table 3) rather than greater microbial activity. McDowell and Fisher (1976) and Brinson (1977) have noted large mass losses due to leaching after a few days in a stream and riverine swamp respectively. Witkamp and Frank (1969) found greater mass loss from litter in an aquatic habitat than in a terrestrial one, and they attributed the primary cause of higher mass loss in the aquatic habitat to leaching. Brinson et al. (1981) suggest that a fundamental difference between leaching in wetland and upland ecosystems lies in constant soaking in the wetland versus leaching by periodic rainfall in the upland. There was no attempt in the present study to evaluate the role that microorganisms and invertebrates play in the leaching process. Their importance was certainly greatly minimized in the leaching experiment itself. Decay organisms do im-

mobilize nutrients from the litter and they also increase the surface area of the litter from which physical leaching occurs. However, much of the initial, rapid loss of nutrients and organics is apparently the result of physical leaching (Willoughby 1974; Witkamp and Ausmus 1976; Brinson et al. 1981).

I had hypothesized that fluctuating hydroperiods would result in the highest decay rates because of increased physical weathering and leaching due to wetting and drying and flushing action. Anderson (1973) suggested that leaching was perhaps accentuated in aerial litter bags as a result of frequent wetting and drying. Treatment D (highly fluctuating hydroperiod) did exhibit the highest decay rate (Table 2), but it was not significantly different from the unflooded treatment (A) because of the great variability in treatment D. There were also no significant differences between the soak and soak-dry treatments in the leaching experiment (Fig. 3). Wetting and drying apparently had no effect on mass and nutrient losses. Flushing effects of fluctuating hydroperiods could still be an important factor as both leaching treatments involved changes of water (flushing); however, the present study indicated variation in hydroperiod had no significant effect on decomposition rates. Temporal changes in decay trends obviously occurred in response to changing hydroperiod (Fig. 1).

Microcosm B1, with the chironomid population, indicates the importance of dipteran larvae in the decay process in wetlands (Table 2). The leaves in B1 were visually more physically altered than leaves from the other microcosms. Other studies have indicated the importance of macroinvertebrates in litter processing in streams and swamps (Reice 1977; Merritt and Lawson 1979; Short et al. 1980; Yates 1981).

### *Microcosm Nutrient Dynamics*

The loss and subsequent immobilization of nitrogen and phosphorus in litter in the microcosms, except in treatment B (continuously flooded), (Fig. 2) was quite different from dynamics observed in the field. Net accumulations in the field were probably due to immobilization from external sources (primarily throughfall) by decomposer microorganisms (Day 1982). The main difference between field and microcosm conditions was the lack of inputs of nitrogen and phosphorus and more rapid decay in the microcosms; thus, net losses occurred. The microcosm soil may have been the source for the later immobilizations. Treatment B was continuously flooded, and perhaps conditions in the constantly waterlogged soil were not adequate for such releases. Anaerobic conditions may have developed within the waterlogged soils of treatment B, even though the water column was aerobic.

Potassium, magnesium and calcium were lost from the litter in the microcosms, except in treatment A (continuously unflooded), which apparently accumulated calcium. Release of calcium, primarily a structural element, might be expected to be slow with slower decay and a lack of leaching, conditions which existed in treatment A. All cations were lost more slowly in treatment A, probably due to these conditions. However, it is difficult to explain why net accumulations of calcium occurred.

The closed microcosms demonstrate internal cycling and redistribution of nutrients, but results of this study indicate the importance of external inputs to litter nutrient relations.

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