January 1993

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Magee, Patrick A., "13.3.14. Detrital Accumulation and Processing in Wetlands" (1993). *Waterfowl Management Handbook*. 20.
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Wetlands are among the most productive ecosystems on earth (Fig. 1) and are often characterized by lush growths of hydrophytes. However, direct consumption of wetland plants by animals is relatively low, and, therefore, much of the biomass and energy assimilated by hydrophytes becomes detritus or senesced plant litter. Nutrients released by detritus into the water and soil are assimilated by microorganisms, algae, plants, and small aquatic animals. Through this process, energy is transferred from detritus to other biotic components of a wetland. Plant litter ultimately decomposes.

Litter processing is regulated by environmental factors, microbial activity, the presence and abundance of aquatic invertebrates, and in some wetlands by vertebrate herbivores, such as muskrats, nutria, fishes, and snow geese. Microbes usually contribute most significantly to litter decay through oxidation of organic matter. Large numbers of invertebrates may feed and live on plant litter after microbial conditioning. Detritus is one of several important substrates and energy sources for wetland invertebrates that in turn provide forage for vertebrates, such as fishes, waterfowl, shorebirds, and wading birds. When their dietary needs for animal proteins are high (e.g., during molt and reproduction), waterbirds forage heavily on invertebrates. Therefore, the role of invertebrates in detrital processing is of particular interest to wetland managers and waterbird biologists.

Understanding the dynamics of litter processing promotes a broader perspective of wetland functions and more specifically enhances an understanding of detrital-based invertebrate ecology. Here I discuss the production of litter, some details of decomposition and nutrient cycling, and the role of invertebrates in detrital processing.

Production of Detritus

Along with algae, detritus fuels secondary production in temperate regions during the dormant season. In many temperate and arctic wetlands, residual litter provides an initial energy source for secondary consumers at the beginning of the growing season. In contrast, in tropical systems, productivity is high, litter decays rapidly, and, therefore, organic substrate for invertebrate colonization is scarce. Productivity is reduced in some arctic wetlands and slow decomposition favors deep, acidic peat accumulations that support few invertebrates. An optimal quantity of litter from balanced primary production and decomposition favors invertebrate communities on wetland substrates. The amount of produced litter varies tremendously among wetlands (Fig. 1) and depends on a myriad of biotic and abiotic factors.

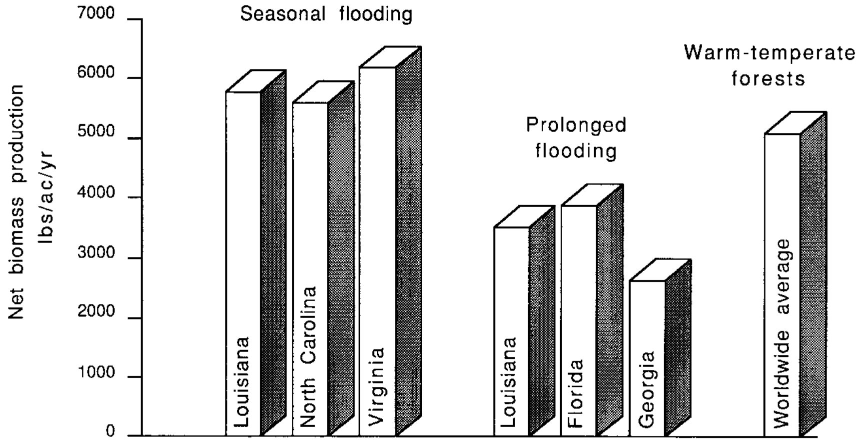

Fig. 1. Litter production varies greatly among wetlands depending on factors, such as plant species, climate, and hydrology. Dynamic hydrology in contrast to prolonged flooding promotes net biomass production in cypress–tupelo forested wetlands. Data presented for Virginia (Great Dismal Swamp) also includes red maple litter production. The worldwide average for warm-temperate forests is shown for comparison.

In temperate regions, deciduous trees and herbaceous plants enter dormancy or die during autumn. Before senescence, large trees and perennial herbs with well-developed root or rhizome systems resorb the nutrients from their leaves and stems for future use. Therefore, plant litter is composed largely of nonnutritive, structural compounds, such as lignin and cellulose. In prairie glacial marshes, litter may enter the system throughout the year. Nearly three fourths of bulrush shoots die before the first killing frost, whereas 80% of cattail shoots are killed by the frost. During the dormant season, wind, waves, and ice formation topple standing litter. Decomposition is most dynamic in fallen litter.

Decomposition

Decomposition is a complex process that is regulated by characteristics of the litter and by external environmental factors (Table). The process can be described as a series of linked phenomena in which one step does not occur until preceding steps make it possible (Fig. 2, also see Fig. 2 in Leaflet 13.3.1.).

The rate of decomposition is important because it affects the release rate of nutrients, the accumulation rate of litter, and the state or quality of the litter substrate. Litter from many submergent and floating plants, such as watershield, decays rapidly (Fig. 3). On the other

Table. *Some factors of litter decomposition rate.*

	Rate of decomposition	
Properties	Fast	Slow
Intrinsic	Low lignin	High lignin
	High phosphorus	Low phosphorus
	High nitrogen	Low nitroge
	Low carbon to nitrogen	High carbon to nitrogen
	Low carbon to phosphorus	High carbon to phosphorus
	Low tannic acid	High tannic acid
	Few polyphenols	Many polyphenols
	Leaf tissue	Woody tissue
Environmental	Microbes present	Low microbial biomass
	Shredders present	Low shredder biomass
	Water present	Water absent
	Flowing water	Stagnant water (less O_2)
	High water temperature	Low water temperature
	Water with high pH	Water with low pH
	Low latitudes	High latitudes
	Low elevations	High elevations

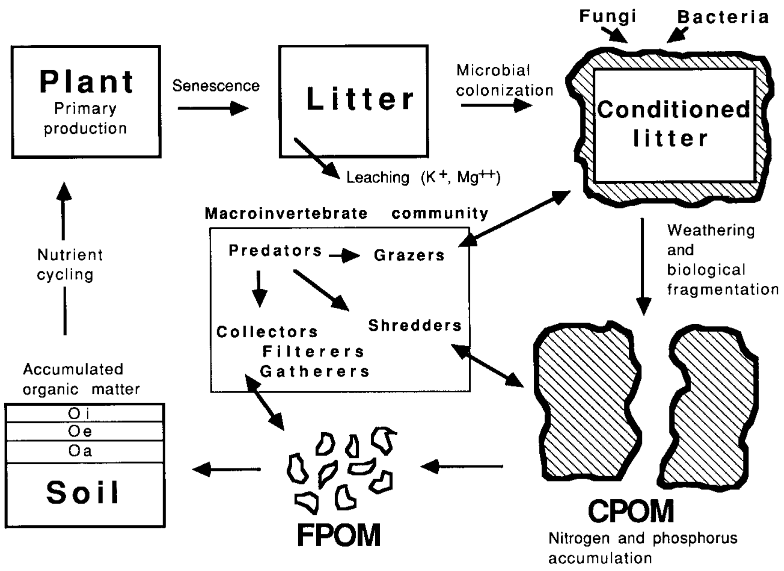

Fig. 2. Litter decomposition is a complex, dynamic process in which detritus is slowly fragmented to fine organic matter and eventually to minerals. Detritus provides energy and nutrients that support microorganisms and macroinvertebrates. Oi, Oe, and Oa refer to organic litter horizons. FPOM = fine particulate organic matter, CPOM = coarse particulate organic matter.

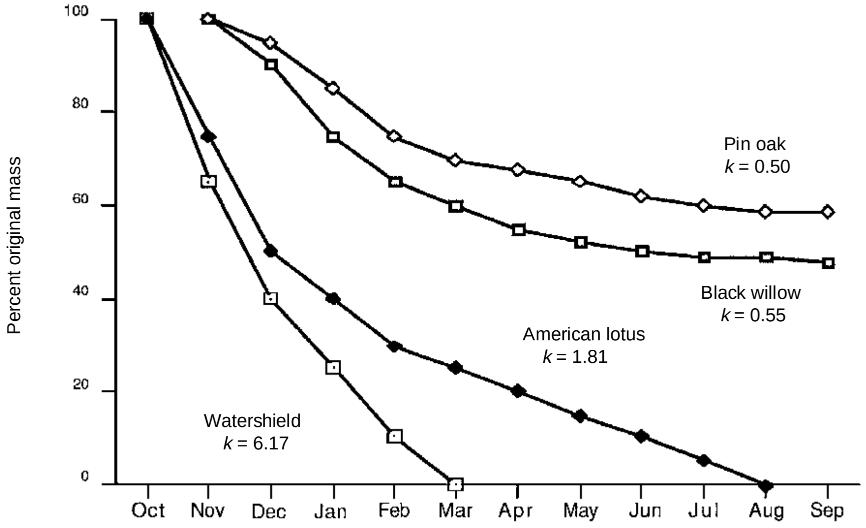

Fig. 3. Decay rates of the leaves of four common wetland plants over a 12-month interval starting from senescence. The annual decay coefficients (*k*) are determined from a negative exponential decay model and represent a single value that can be used to compare decay rates among species.

hand, robust emergent plant litter and leaves from certain trees decay slowly. The leaves of pin oaks, for example, require 4–7 years to completely mineralize (Fig. 3). In forested wetlands with slowly decaying leaves, accumulated layers of litter reflect each year's growth and state of decay. The result is a substrate with a diverse vertical profile. Plant parts decay at different rates; leaves decompose more rapidly than stems or woody tissues. Furthermore, plants with high quantities of lignin, such as common reed and burreed, have the slowest decay rates. Decomposition is usually slow in northern wetlands (i.e., >50% of plant litter remains after 3 years of decay) partly because of cold temperatures. In contrast, in a warm, tidal wetland, more than three fourths of the litter decayed within 3 months. Because of the interactions between the environment and a plant's characteristics, the composition of litter substrate varies.

Decomposition of litter by a complex interaction of physical, chemical, and biological processes has at least two phases. In the first phase of decomposition (leaching), loosely bound nutrients, such as calcium, potassium, and magnesium, are rapidly released from newly senesced plant litter. Cattail, for example, lost 76% of sodium, 93% of potassium, 70% of calcium, and 65% of magnesium after 1 month of decay. Black willow leaf litter lost 85% of its potassium within the first 2 weeks of decay. Sometimes the leaching phase is so rapid that labile nutrients are flushed from the litter within 48 h of flooding.

Not all nutrients immediately escape from the litter. Nitrogen (Fig. 4) and calcium, for example, may accumulate in the litter as a result of immobilization and colonization by microbes. Litter can act as an important sink for these nutrients, which are slowly released during the second phase of decomposition.

The second phase of decay consists of mechanical fragmentation of litter by ice, wind and wave action, and biological fragmentation by invertebrates called detritivores (Fig. 2). Most importantly, however, biologically mediated chemical transformations of litter by microbes promote gradual loss of recalcitrant litter tissues, such as lignin and cellulose. All of these processes convert litter from large, structurally complex forms to smaller, simpler materials. Largely intact litter with a >1-mm diameter is called coarse particulate organic matter (CPOM), whereas highly fragmented litter is fine particulate organic matter (FPOM). Eventually, plant litter is converted to its simplest forms and becomes incorporated into the soil or dissolved in the water column.

The Role of Microbes and Invertebrates

Before most invertebrates begin processing litter, microbes colonize litter surfaces at densities of 410,000–410,000,000 individuals /cm2. These microbes are the fungi (e.g., phycomycetes) and bacteria (e.g., actinomycetales, eubacteriales, myxobacterales, pseudomonaiales) that digest cellulose.They are the key organisms that erode the structural framework of the litter. Their abundance and activity reflect environmental conditions; bacteria are more numerous on submerged than on standing dead litter, although water temperature and oxygen availability affect bacterial response. In many wetlands, microbes regulate decay and account for as much as 90% of litter weight loss. Many fungi produce external enzymes that break down cellulolytic tissues in detritus. In this process, sucrose is broken down into glucose and fructose, but only a portion of these sugars are assimilated by microbes. The remainder are available to protists, zooplankton, and macroinvertebrates.

Macroinvertebrates are a diverse group and fill many niches in wetland communities. As litter decomposes, these niches become available sequentially by size of litter fragments and by the activities of other invertebrates and microorganisms (Fig. 2). Litter is food and habitat for many aquatic invertebrates. Followmg leaching, litter is primarily composed of nonnutritive,

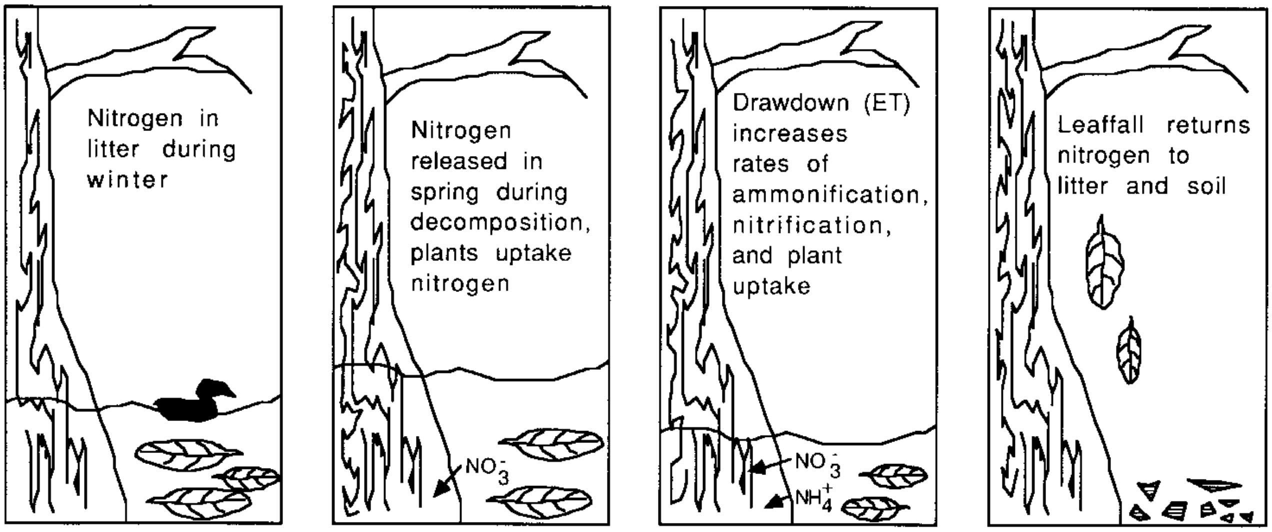

Fig. 4. Nitrogen cycling in wetlands involves a labyrinth of chemical transformations of nitrogen into forms that may or may not be available to plants. Microorganisms play a key role in mediating nitrogen availability in the benthos and soil.

complex carbohydrates that are difficult or impossible for detritivores to digest. Therefore, the key link between macroinvertebrates and litter processing is the presence of microbes. Not only do these bacteria and fungi break down litter directly, they also condition litter by making it palatable to invertebrates.

Detritivores, called shredders, are the first to fragment CPOM because they are voracious feeders with low assimilation rates; much of the litter they consume is excreted in a highly fragmented state. The surface area increases after the litter passes through the digestive tract of invertebrates and thereby enhances microbial growth. Crustaceans, such as aquatic sowbugs, freshwater scuds, and crayfish, are prominent shredders in many forested wetlands. Crayfish and many insects are common shredders in moist-soil wetlands in Missouri.

Grazers, another group of detritivores, scrape algae and microbes off surfaces of CPOM, allowing recolonization by new microbes. Grazing tends to increase microbial growth and activity. Snails, such as the pond and orb snail, are the most conspicuous grazers in wetland systems.

Collectors feed on fine particulate organic matter (FPOM) that is produced mainly by shredders. One group of collectors is mobile and gathers FPOM from sediments. For example, some midge larvae and mayflies, called collector–gatherers, obtain nutrients and energy by foraging on small litter fragments. Another group of collectors, including fingernail clams, filters FPOM from the water column.

A dynamic invertebrate community develops in detrital-based systems as water temperatures increase and litter processing is most active. Shredders reach peak density and biomass and create more foraging opportunities for collectors. Given these conditions, highly mobile, predaceous invertebrates, such as dragonflies, respond to available prey (i.e., shredders and collectors).

Considerations in Management

Wetlands are productive because the base of the biotic pyramid is large and diverse and nutrient cycling is dynamic. Because energy flows from the lowest levels of the pyramid, detritus sustains much of the biomass and structure of the community (Fig. 5). Furthermore, detrital processing releases and transforms nutrients tied up in plant tissues and makes them available for uptake by wetland flora and fauna. Management, particularly hydrological manipulations, may enhance energy and nutrient flow in wetlands.

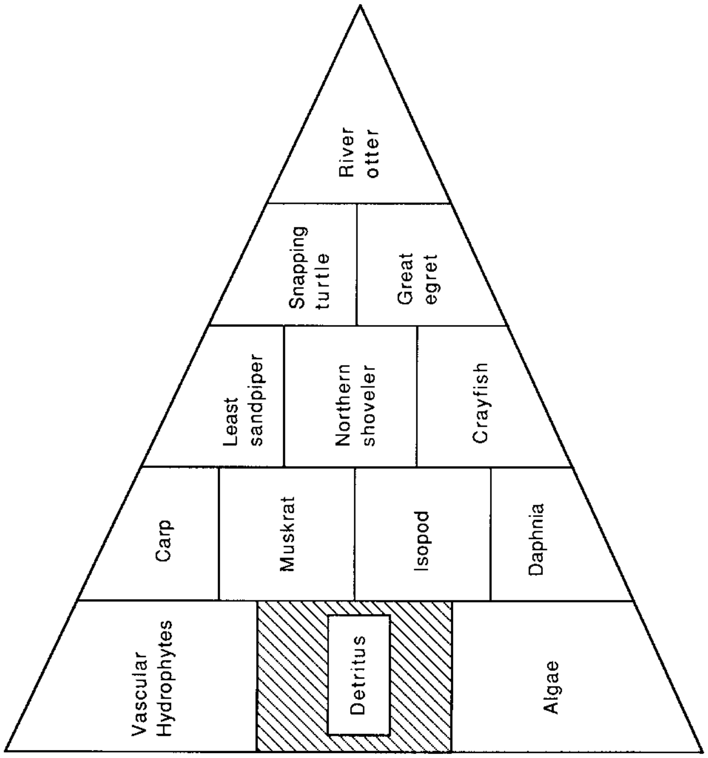

Fig. 5. Detritus is a fundamental component of food–energy pyramids in wetland ecosystems. During the dormant season in temperate wetlands, only detritus and algae supply energy and nutrients to sustain higher trophic levels.

Detritus becomes an important energy source when wetlands are flooded. Inundation triggers the dynamic process of litter decomposition. Decay rates are often much higher in wetlands than in adjacent uplands, indicating in part the level of activity and the biomass of aquatic biological decomposers. Maintenance of long-term hydrological regimes is the key to maintaining the balance between litter decay and accumulation and to sustaining the biotic components of detrital processing and wetland productivity. For example, aquatic invertebrates have evolved diverse adaptations for living in seasonally flooded environments, and, without dynamic flooding regimes, many of these organisms are incapable of completing their life cycles. In the short term, the annual timing, rate, depth, and duration of flooding affect the diversity and abundance of invertebrates at a particular site.

Hydrology also influences nutrient cycling in wetlands. Because of leaching and subsequent decomposition, the water column is rich in nutrients for several months after flooding. Therefore, rapid drawdowns when nutrient content is high can flush nutrients from the system. Slow and delayed drawdowns retain nutrients and enhance long-term wetland productivity.

Stabilized flooding regimes may harm detrital nutrient dynamics. Anaerobic conditions can develop in detritus, especially when water is stagnant. Subsequently, denitrification, which is the loss of nitrogen from the litter, may result in a net export of nitrogen from the system. Denitrification is less common in aerated litter layers than in wetland soils and is minimal under dynamic flooding strategies.

Secondary production in wetlands may be hindered by runoff of sediments and chemicals from agricultural lands or storm flow. When sedmients envelop litter, the substrate is less hospitable to the epifauna because oxygen is deficient. Furthermore, as more sediments are suspended in the water column, penetration of light is reduced and chemical imbalances may occur. Although hydrophytes are excellent purifiers of polluted waters, excessive amounts of fertilizers and pesticides may have a direct detrimental effect on wetland biota. Maintaining upland borders that filter sediments and chemicals before they settle in wetland basins is important for sustained detrital processing.

Litter quality and quantity also affect secondary production. Mechanical fragmention of litter increases the surface area for microbial and invertebrate colonization. Hydrophytes, such as American lotus, with its large, round leaves, have relatively small surface areas and low invertebrate densities. Mowing or shallowly disking lotus increases the surface area of this simple substrate by artificially hastening litter fragmentation. Such control of nuisance vegetataon enhances short-term production of invertebrates.

The balance between litter removal and accumulation affects wetland productivity. Small litter accumulations may not provide adequate substrate for invertebrates; however, large accumulations may alter surface hydrology through peat formation or nutrient binding. Litter removal may be accomplished by flooding if surface flow is sufficiently great to simulate this natural function. Prescribed burns not only remove excess organic matter but release minerals bound in the litter.

Habitats with diverse litter layers in various stages of decay are optimal for the management of invertebrates. Where litter accumulation is scant or heavy, however, invertebrate production may be impeded because of unfavorable conditions associated with hydrology, substrate, and nutrient availability.

Suggested Readings

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Appendix. *Common and Scientific Names of the Plants and Animals Named in the Text.*

Plants

Red maple	*Acer rubrum*
Watershield	*Brasenia schreberi*
American lotus	*Nelumbo lutea*
Water tupelo	*Nyssa aquatica*
Common reed	*Phragmites australis*
Pin oak	*Quercus palustris*
Black willow	*Salix nigra*
Bulrushes	*Scirpus* spp.
Burreeds	*Sparganium* spp.
Baldcypress	*Taxodium distichum*
Cattails	*Typha* spp.

Invertebrates (by function)

Shredders	
Aquatic sowbug	Asellidae
Crayfish (omnivore)	Cambariidae
Freshwater scud	Gammaridae
Collectors	
Mayfly (gatherer)	Baetidae
Midge (gatherer)	Chironoraidae
Water flea (filterer)	Daphnidae
Fingernail clam (filterer)	Sphaeriidae
Grazers	
Pond snail	Physidae
Orb snail	Planorbidae
Predator	
Dragonfly	Aeshnidae

Vertebrates

Northern shoveler	*Anas clypeata*
Least sandpiper	*Calidris minutilla*
Great egret	*Casmerodius albus*
Snapping turtle	*Chelydra serpentina*
Snow goose	*Chen caerulescens*
Common carp	*Cyprinus carpio*
Hooded merganser	*Lophodytes cucullatus*
River otter	*Lutra canadensis*
Nutria	*Myocastor coypus*
Muskrat	*Ondatra zibethicus*

March 3, 1849

UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
Fish and Wildlife Leaflet 13
Washington, D.C. • 1993