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Plant litter decomposition in mitigated and reference wetlands

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ABSTRACT

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Decomposition of plant litter in wetlands influences many processes and is driven by a complex web of interacting forces. This makes litter decomposition a useful measure of wetland function and a possible means of judging wetland functional replacement in compensatory mitigation projects. However, the web of interacting forces that intricately connect decomposition to wetland function also make it difficult to identify the importance of individual variables. In order for decomposition to be used as a metric to judge wetland function, its driving forces must be better understood.

This study examined some of the variables that drive decomposition. Specifically, decomposition rates were studied in-depth at 3 mitigated and 3 reference wetlands, and more broadly at 8 created and 8 reference wetlands, located in the Allegheny Mountain ecoregion of West Virginia. Decomposition rates were measured using the litter bag technique and incorporated five different litter types. Four types of single species bags were created from common wetland litter species and included broadleaf cattail (*Typha latifolia* L.), common rush (*Juncus effusus* L.), brookside alder (*Alnus serrulata* (Ait.) Willd.), and reed canary grass (*Phalaris arundinacea* L.). The fifth litter type was created from a mix of common rush, brookside alder, and reed canary grass. Environmental measurements were taken throughout the study to determine their effect on decomposition and invertebrates were collected from litter bags to study the importance of biotic communities. Fungal biomass was estimated by measuring the amount of ergosterol extracted from leaf litter.

Decomposition rate constants were similar between mitigated and natural wetlands. Reed canary grass had the fastest decomposition rate constant and broadleaf cattail had the slowest. Of the environmental parameters tested, models that included air (AT) and soil temperature (ST), water pH (WPH), hydroperiod (HP, proportion of days flooded), and the number of transitions between flooded and exposed conditions (FET) were best able to predict decomposition rate constants. Overall, AT, ST, and WPH were directly related to decomposition rate constant, while HP was inversely related. The FET was directly or inversely related to the decomposition rate constant depending on the litter type.

For biological variables, invertebrate taxonomic groups had the strongest associations with decomposition trends compared to functional feeding groups or invertebrate metrics (abundance, richness, diversity). Shredders, collector/gatherers, and omnivores were more strongly associated with early phases of decomposition, while oligochaetes and omnivores were most strongly associated with trends in decomposition during the later phase. Ergosterol levels indicated that fungi colonized bags quickly, peaked at 35 days, and then decreased and leveled off by 300 days, but were not useful predictors of decomposition rate.

This study helps demonstrate the importance of both environmental and biological variables in naturally functioning systems and ultimately helps to improve wetland mitigation by expanding our understanding of wetland function.

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CHAPTER 1

Introduction and Justification for the Use of Litter Decomposition to Assess Wetland Function

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Written in the style of:
Wetlands

INTRODUCTION

Wetland History and Law

Wetlands provide many functions within an ecosystem including floodwater storage and retention, groundwater recharge, biological productivity, biogeochemical cycling and storage, wildlife and community habitat, sediment trapping, and water purification (Richardson 1994; Smith et al. 1995). However, these functions have not always been recognized and valued. Between the 1780s and 1980s, 42 million ha (53%) of wetlands were lost in the contiguous United States (Dahl 1990).

Starting in the 1970s, awareness concerning wetlands and their functions within the landscape began to curb widespread filling and conversion (USNRC 2001). In 1988, the National Wetlands Policy Forum brought to the forefront the continued loss of wetlands in the United States and recommended a policy of "no net loss" of wetlands (Mitsch and Gosselink 2007). This recommendation was adopted by the administration of President George H. W. Bush, and along with the "no net loss" policy, came the requirement for the mitigation of wetlands to compensate for the government-approved destruction of an existing wetland. Wetland mitigation is intended to replace an existing wetland, or its functions, by creating a new wetland, restoring a former wetland, or enhancing or preserving an existing wetland. After the mitigated wetland's creation, there is a requirement for 5 years of monitoring to determine the success of the project (Votteler and Muir 1996). Sections 401 and 404 of the Clean Water Act (CWA) grant regulatory control of most wetlands to the U.S. Army Corps of Engineers (USACOE) and the U.S. Environmental Protection Agency (USEPA) and require permits to be obtained and mitigation to be performed when dredging or filling a wetland. A Memorandum of

Agreement between the USEPA and US Department of the Army, signed in 1990, clarified that wetland function must be replaced in addition to lost acreage (USEPA 1990).

On Earth Day in 2004, President George W. Bush called for a goal beyond the "no net loss policy," calling for the restoration, improvement, and protection of more than 1.2 million hectares of wetlands in five years. To track this progress, he directed the US Fish & Wildlife Service to conduct an updated wetland status and trends survey. The findings are presented in a document titled, *Status and Trends of Wetlands in the Conterminous United States 1998 to 2004*. It found that between 1998 and 2004 a net gain of 77,630 ha of wetlands were created in the United States (Dahl 2006).

This finding suggests two questions, the first being whether correct acreage is being created and reported. Though Dahl (2006) found a net gain in acreage using aerial photography and field verification, it cannot be assumed that this implies acreage is being met for permitted projects. Robb (2002) inventoried 345 permitted mitigation projects in Indiana and found that 71% of palustrine forested wetlands (Cowardin et al. 1979) and 78% of wet meadow wetlands failed to meet the acreage requirements of their permits. Morgan and Roberts (2003) found that 72% of 50 mitigation projects in Tennessee had less acreage than stipulated. Brown and Veneman (2001) studied 391 project files and 114 field sites in Massachusetts and found that 64.9% failed to meet acreage requirements. Allen and Feddema (1996) looked at 75 wetland projects with Section 404 permits and found that of 111.6 ha of required wetland mitigation, only 77.3 ha (69.3%) were created. To ensure this criterion is met requires relatively straightforward site visits that involve delineating the wetland boundary to ensure proper acreage.

The second question is whether wetland function is adequately being replaced. According to Dahl (2006) open water and depressional wetlands were the most frequently

created types of wetlands contributing to the net gain in acreage. However, 364,540 ha (4.9%) of freshwater shrub wetlands were lost at the same time. Estuarine vegetated wetlands decreased by 13,120 ha from 1998 to 2004, while estuarine non-vegetated wetlands had a net gain of 1,620 ha. The report states that, "There was a substantial increase in the number of open water ponds as pond area increased by an estimated 12.6 percent. Without the increased pond acreage, wetland gains would not have surpassed wetland losses." The study also states that it does not draw any conclusions regarding "trends in the *quality* of the nation's wetlands" [emphasis added] (Dahl 2006).

These trends in wetland types emphasize the importance of performing functional assessments of mitigated wetlands and ensuring adequate replacement of lost functions. Previous studies suggest that overall success is mixed. Landscape placement of mitigated wetlands does not always match that of lost wetlands and affects wetland type and function (Bedford 1996; Hoeltje and Cole 2007, 2009). Minkin and Ladd (2003) studied 60 mitigated sites to determine if they successfully met their permit objectives and found that 40 (67%) of the wetlands met the criteria of their permits, but that only 10 mitigated sites (17%) were adequate functional replacements for the impacted wetlands. Zedler and Callaway (1999) monitored soil organic matter, soil nitrogen, plant growth, and plant canopies at the Sweetwater Marsh National Wildlife Refuge for 10 years at a 12-year-old site and found that wetland development was not trending towards surrounding natural conditions. Sudol and Ambrose (2002) performed qualitative assessments of habitat quality at 55 projects associated with 126 ha of lost habitat and found that only 26 ha of mitigation was considered successful.

In response to concerns over compensatory mitigation projects' low functional success rates, the ACOE and USEPA issued updated regulations in 2008 that required measurable,

enforceable ecological performance standards and regular monitoring of mitigated wetlands (USDOD and USEPA 2008). It will take time to determine if this new legislation is able to enforce successful functional replacement.

Assessing Wetland Function through Litter Decomposition

For functional performance to be fully assessed each function needs to be addressed; however, not all wetland functions have received equal attention. A wide range of indicators have been studied to compare mitigated wetlands with reference sites, including vegetative communities, functional groups, and zonation (Galatowitsch and van der Valk 1996; Seabloom and van der Valk 2003; Balcombe et al. 2005a; Spieles 2005; Bouchard et al. 2007), wildlife presence and use (Brown and Smith 1998; Ratti et al. 2001; Snell-Rood and Cristol 2003; Balcombe et al. 2005b), fish presence and use (Shreffler et al. 1992; Williams and Zedler 1999), invertebrate presence (Scatolini and Zedler 1996; Brown et al. 1997; Stanczak and Keiper 2004; Balcombe et al. 2005c), soil composition (Bishel-Machung et al. 1996; Anderson et al. 2005; Bruland and Richardson 2006) or a combination of these (Confer and Niering 1992; Campbell et al. 2002; Edwards and Proffitt 2003; Balcombe et al. 2005d). Far less focus has been put on functions such as sediment retention, biogeochemical cycling and storage, hydrologic flux and storage, groundwater recharge, and water purification.

Litter decomposition has gained attention in recent years as a means of assessing wetland function. Decomposition is an important component of wetland function (Richardson 1994; Spieles and Mora 2007) and is linked to many other wetland processes. Physical and chemical properties of wetland soils are, in part, determined by the process and rate of decomposition (Mitsch and Gosselink 2007). The rate and pattern of decomposition can influence nutrient availability and cycling (Prentki et al. 1978; Facelli and Pickett 1991), primary productivity

(Brinson et al. 1981), litter/organic matter accumulation (Gambrell and Patrick Jr. 1978; Xiong and Nilsson 1997), and seed germination (Xiong and Nilsson 1997; Taylor and Middleton 2004). These processes then support many other aspects and benefits wetlands provide. Mitsch and Gosselink (2007) suggested that a common feature of wetland development is a shift from a detritus-poor to a detritus-based system over time.

Litter decomposition also exerts influence at the ecosystem level by supporting major flows of energy that occur along detrital pathways (Brinson et al. 1981; Webster and Benfield 1986). Organic matter collecting in wetlands during the growing season or deposited during bankfull discharge events of nearby streams is broken down into coarse and fine particulate organic matter (CPOM and FPOM respectively) and dissolved nutrients that are then released back into streams during later flooding events. These are important riparian wetland exports because they provide a nutrient source for aquatic organisms downstream (Richardson 1994; Dodds 2002; Mitsch and Gosselink 2007). Additionally, waste organics and pollutants are deposited and decomposed in wetlands, which leads to improved water quality (Walbridge 1993; Mitsch and Gosselink 2007).

Finally, decomposition can have effects on a global scale. Decomposition is an indicator of a wetland's organic matter storage potential (Richardson 1994). Since decomposition is an important component in nutrient cycles, it is the only process enabling the massive recycling of chemical elements on the scale of whole ecosystems (Richardson 1994; Björn and Laskowski 2006). Slow litter decomposition in wetlands therefore contributes to global climate by sequestering carbon and balancing the atmospheric CO_2 pool and rate of CO_2 returning to the atmosphere (Richardson 1994; Björn and Laskowski 2006). This is especially important in

wetlands because, although less than 4% of the earth's surface is covered in wetlands, wet soils contain about one-third of all organic matter stored in the world's soils (Dodds 2002).

Phases of Decomposition

Decomposition typically goes through three stages (Godshalk and Wetzel 1978; Brinson et al. 1981). The first phase is rapid loss of mass from leaching and occurs within 48-92 hrs of inundation (Nykvist 1962; Webster and Benfield 1986). Depending on temperature, turbulence, and the litter species, up to 29% of mass can be lost during the leaching phase (Petersen and Cummins 1974; Brinson 1977; Howard-Williams and Howard-Williams 1978). Anderson (1973) attributed up to 75% of the weight losses from sweet chestnut (*Castanea sativa* Mill.) to leaching in a 31 month study, showing that though it defines the first stage, leaching can continue to contribute to weight loss through the second and third phases.

The second phase of decomposition begins as rapid leaching ends and involves the colonization of litter by microbial organisms, which break down soft tissues. Depending on the time of year and stage of the second phase, bacteria (Howard-Williams and Davies 1978; Robb et al. 1979) and fungi (Barlocher and Kendrick 1974; Gessner and Chauvet 1994; Findlay et al. 2002) can drive decomposition rates. It has been suggested that litter exposed to the air is mostly decomposed by fungi (Holland and Coleman 1987; Facelli and Pickett 1991) and submerged litter is processed by bacteria. However, fungi can be important in submerged conditions as well (Mason 1976; Gessner and Chauvet 1994; Bauer et al. 2003). Petersen and Cummins (1974) estimated that microbial activities caused about 30% weight loss from the original leaf mass in streams. Hieber and Gessner (2002) attributed 15% and 18% mass loss of black alder (*Alnus glutinosa* (L.)Gaertn.) and crack willow (*Salix fragilis* L.) respectively to fungi, and 7% and 9% mass loss to bacteria.

The third and final phase of decomposition involves mechanical fragmentation of the litter by environmental forces, abrasion, and invertebrates (Webster and Benfield 1986; Fazi and Rossi 2000; Hieber and Gessner 2002; Hutchens Jr. and Wallace 2002). Heard et al. (1999) found that mechanical abrasion and biological agents had similar levels of influence on litter decomposition rate in streams. Many studies have shown differences in decomposition rates and attributed them to macroinvertebrate and detritivore presence or absence (Mason and Bryant 1975; Coulson and Butterfield 1978; Kemp et al. 1985; Kirby 1992; Hutchens Jr. and Wallace 2002). Merritt and Lawson (1979) looked at litter processing in a Michigan floodplain woodland and found at least 29-32% of original litter weight loss was from macroinvertebrate activity. Hieber and Gessner (2002) attributed 64% of black alder and 51% crack willow leaf litter loss to invertebrates. Many controlled studies have directly observed decomposition rate increasing with macroinvertebrate density (Cummins et al. 1973; Petersen and Cummins 1974; Herbst 1982; Fazi and Rossi 2000).

Variables Determining Decomposition Rate

Decomposition is driven by three categories of variables: biotic (microorganisms and invertebrates that break down litter), physical (environmental conditions the litter is in), and chemical (physical and nutrient composition of the litter) variables (Aerts and de Caluwe 1997). Physical variables exert additional control on decomposition by influencing the biotic communities that are present and their levels of activity (Meentemeyer 1978; Rejmánková and Houdková 2006; Inkley et al. 2008).

Hydroperiod and temperature are often credited as being the two most significant factors that drive decomposition (Brinson et al. 1981; Webster and Benfield 1986; Batzer and Sharitz 2006). Temperature is positively correlated with decomposition rate (Morris and Lajtha 1986;

Middleton et al. 1992; Álvarez and Bécares 2006), but hydrology's influence is less certain. Battle and Golladay (2001) showed that multiple flooding and exposure events yielded faster decomposition rates than permanently flooded conditions or a single flooded period followed by a dry period. However, van der Valk et al. (1991) determined that more rapid decomposition occurred when litter experienced a single, longer flooded period and then dried. Though there is not agreement about what type of hydrology yields the fastest decomposition rates, many studies have shown the importance of wet-dry cycles (Neckles and Neill 1994; Lockaby et al. 1996; Atkinson and Cairns 2001; Anderson and Smith 2002).

Along with temperature and hydroperiod, many other physical variables have been hypothesized as influencing decomposition; however, for most alternatives studies exist both supporting and showing no influence on litter decomposition. Water nutrients and quality have been found to increase (Davis 1991; Verhoeven and Arts 1992; Qualls and Richardson 2000) or be uncorrelated (Deghi et al. 1980) with decomposition rates. pH has been shown to retard (Day Jr. 1987; Kittle et al. 1995; Taylor and Middleton 2004) or have no effect (Harper and Bolen 1995) on decomposition. Sedimentation can inhibit decomposition (Vargo et al. 1998) or have no effect (Atkinson and Cairns 2001). Dissolved O_2 may influence decomposition (Schipper and Reddy 1995) and soil moisture may be important in wetlands that have significant intervals of exposure (Battle and Golladay 2007).

The chemical variables driving decomposition, sometimes referred to as litter quality, can be broken into 3 additional categories: abundance of essential nutrient elements like nitrogen, potassium and phosphorus; fiber content and lignin; and presence of chemical inhibitors such as waxes, cutins (one of two waxy polymers that make up a plant's cuticle), or tannins (Bell et al. 1978; Webster and Benfield 1986). Of all litter quality factors, increases in litter nitrogen and

the nitrogen:carbon ratio (Coulson and Butterfield 1978; Aerts and de Caluwe 1997; Poi de Neiff et al. 2006) and phosphorus and the phosphorus:carbon ratio (Bartsch and Moore 1985; Aerts and de Caluwe 1997; Rejmánková and Houdková 2006; Guo et al. 2008) are most often cited as causes of increased decomposition rates. An increase in lignin is most often cited as a cause of depressed decomposition rates (Schwintzer 1984; Bartsch and Moore 1985; Poi de Neiff et al. 2006). Several studies also have shown that higher potassium and the potassium:carbon ratio (Bartsch and Moore 1985; Ohlson 1987) are associated with faster decomposition rates.

Decomposition Study Design

Decomposition has been studied using a variety of methods. Leaf litter has been put out in enclosed mesh bags (Figure 1 & 2), called litter bags (Hodkinson 1975; Bell et al. 1978; Kittle et al. 1995; Battle and Golladay 2007), fastened together and anchored to mimic a natural obstruction's debris accumulation, called a leaf pack (Boulton and Boon 1991; Ryder and Horwitz 1995), and at least one study involved unconfined litter (Cummins et al. 1980). The tagging of standing dead leaves (Kuehn et al. 1999) and suspended woody debris (Rice et al. 1997) also have been used. Since litter quality, in part, determines decomposition rates, some studies have measured the decomposition of cotton strips to standardize the nutrient content of material between sites (Harrison et al. 1988; Trettin et al. 1996; McLaughlin et al. 2000; Penton and Newman 2007). Each technique has different strengths and weaknesses, but, overall, the litter bag technique is most commonly used, especially in wetlands, with leaf packs being more common in stream studies (Webster and Benfield 1986). The litter bag technique is the best method for determining and comparing decomposition rates and patterns for different plant species and when studying chemical changes (Berg et al. 2006).

Litter bag studies have a number of variables that need to be chosen and requires detailed planning. Litter bag size, bag material, method of sealing the bag, litter type, litter amount, and mesh size are all considerations that have to be planned based on the goals of the research. Polyester and fiberglass meshes are commonly used. Nylon meshes also are sometimes used, but contain nitrogen and cannot be used if litter nitrogen is going to be studied (Berg et al. 2006). Bags usually range from 10 x 10 cm to 20 x 20 cm and are sealed in a variety of ways. Hot glue (Arp et al. 1999), plastic cable ties (Bedford 2005), rotex tape (Brock et al. 1985), staples (Deghi et al. 1980; Harper and Bolen 1995), Velcro® strips fitted to the bag (Grout et al. 1997), and sewing (Thormann and Bayley 1997; Anderson and Smith 2002) have all been used to shut the sides.

One of the most important factors is mesh size. Mesh size has varied from as small as 0.25 mm (Bedford 2005) to as large as 5 x 5 cm (Cuffney and Wallace 1987) with an average coarse mesh size being around 5 mm and a fine mesh size around 1 mm. Studies have shown that different mesh sizes can have no effect on decomposition rate (Coulson and Butterfield 1978; Benfield et al. 1979; Brock et al. 1985; Murray-Gulde et al. 2005), but many studies have shown decomposition rates to be faster in larger mesh sizes (Mason and Bryant 1975; Merritt and Lawson 1979; Merritt and Lawson 1992; Bedford 2005). The difference is often attributed to two main effects: the size of the mesh limiting invertebrate access to the litter and allowing larger litter fragments to escape the bag (Brinson et al. 1981; Stewart and Davies 1989). However, Petersen and Cummins (1974) looked at decomposition rates in streams and suggested that bags with a small mesh may reduce gas and nutrient exchange rates and create an environment more prone to anaerobic conditions. It also has been suggested that leaves within a

finer mesh are less exposed to leaching, abrasion, and fragmentation and therefore subject to lower loss of particles (Webster and Benfield 1986).

Leaf Litter

Litter type and amount help determine the size of the bag that is going to be used. Species common to wetlands are most often used and have an order of decreasing decomposition rates, when put into categories, of soft leaves > hard leaves and shrub shoots > mosses, lichens, and wood (Heal and French 1974). Studies often involve anywhere from one to a dozen different species. Litter bags may contain a single species or multiple species representing a natural mix of litter. Some studies have shown that single-species decomposition rates do not accurately reflect ecosystem level decomposition rates as well as mixed-species litters (Gustafson 1943; Wardle et al. 1997; Gartner and Cardon 2004). Mixes with dissimilar litter types, such as litter from trees and dicotyledonous herbs, were found to increase litter decomposition and may suggest a synergistic effect (Gustafson 1943; Wardle et al. 1997).

Often, 5 to 20 g of leaf litter material is used, but as little as 0.5 to 1 g (Coulson and Butterfield 1978; Aerts and de Caluwe 1997) or as much as 300 g (Brock et al. 1985) have been used. Leaf litter is usually collected after the plant has senesced to mimic natural processes. Once the litter is collected, it has to be dried to a constant mass to allow for standardized initial measurements. Unfortunately, drying litter at a high temperature, such as 105 ^{o}C, can cause structural changes and loss of volatile compounds, such as terpenes (Berg et al. 2006). Even far lower temperatures allow for some chemicals to volatize. For this reason, many studies air-dry vegetation at room temperature for periods lasting from 24 hrs to 4 wk (Bartsch and Moore 1985; Hietz 1992; Aerts and de Caluwe 1997).

Mitigated versus Natural Wetland Litter Decomposition

Few studies have attempted to look at differences in decomposition rates between mitigated and natural reference wetlands. Atkinson and Cairns, Jr. (2001) compared litter decomposition of *Scirpus cyperinus* (L.)Kunth and *Typha latifolia* L. between eleven 20-year-old and six 2-year-old created wetlands in the Appalachian Mountains of Virginia. They found that the older wetlands had faster decomposition (76% of mass remained after 507 days) than the younger wetlands (85%), but that both were lower than rates reported for comparable natural wetlands (53%). Fennessy et al. (2008) found similar results when they conducted a study throughout Ohio. They used a litter mixture of *T. latifolia* with *Juncus effuses* L. or *J. tenuis* Willd. at 10 mitigated wetlands and 9 natural wetlands, 3 of which were highly disturbed and treated as "non-reference" sites. After one year, the litter in mitigated wetlands lost an average of 51.1% of their initial mass while litter in reference wetlands lost 62.6% on average. They also found that inundated litter at natural wetlands had faster decomposition rates than litter under similar conditions at mitigated wetlands and suggested that other factors such as microbial community and litter quality were affecting the difference in decomposition rates.

Not all studies have found litter decomposition to be slower in created wetlands. Schmidt (2002) compared adjacent mitigated and natural wetlands in the coastal plain of Virginia. Mixtures of vegetation were created by collecting all standing material from several 1 m^2 quadrats in a marsh and collecting litter in leaf traps in an upland forest. *Typha* sp. and *S. cyperinus* were the main marsh species and *Acer rubrum* L., *Liquidambar styraciflua* L., *Quercus biocolor* Willd., *Quercus michauxii* Nutt., and *Magnolia virginiana* L. were the main forest species. He found both marsh and forest litter decomposed more quickly in the created wetlands than the adjacent natural wetlands, despite similar moisture regimes. Schmidt (2002)

attributed some of the difference to increased temperature under the more sparsely shaded younger wetlands and suggested that other factors, such as differences in detritivore communities and direct contact with the soil at the mitigated site, may have contributed to the difference.

Taylor and Middleton (2004) studied a reference wetland compared to a reclaimed coal-slurry pond in the unglaciated Illinois Ozarks. They used single species litter bags of *Cyperus erythrorhizos* Muhl., *Phragmites australis* (Cav.) Trin. ex Steud., *Potamogeton nodosus* Poir., and *T. latifolia*. They found decomposition occurred more quickly in the coal slurry pond (k = 2.409 yr^{-1}, where k is the instantaneous exponential decay constant, as calculated by: $W = \exp^{-kt}$, where W is the proportion of mass remaining at time t [years]) than in the natural wetland (k = 1.570 yr^{-1}). Taylor and Middleton (2004) attributed this to lower levels of soil pH in the natural wetland (5.3) than the coal slurry pond (7.9).

Crawford et al. (2007) looked at decomposition of roots at restored and natural sites within the Great Dismal Swamp National Wildlife Refuge and the Alligator River National Wildlife Refuge in Virginia and North Carolina. They used commercially grown *Chamaecyparis thyoides* (L.) Britton, Sterns & Poggenb. roots as a standard and native roots from each site. *C. thyoides* roots had the same decomposition rate at all sites, but the native root decomposition was substantially faster on the restored sites. The differences in decomposition were not due to the different environmental conditions at restored versus the natural sites, but were instead a product of differing litter quality. Native roots on restored sites had lower lignin concentrations and higher phosphorus concentrations. These differences emerged from there being substantially more woody vegetation at the reference sites and herbaceous vegetation at restored sites. Crawford et al. (2007) hypothesized that once the canopy at the restored sites

closed and the vegetative community changed, decomposition rates would slow and eventually match the natural sites.

Spieles and Mora (2007) found that environmental conditions influence decomposition more than wetland age. They studied decomposition rates at three created wetlands of different ages, 4, 12 and 155 years, in Licking County, Ohio. They used new leaves of *Typha* spp. as their leaf litter and found that decomposition rate constants were highest in the 4-year-old wetland (k = 1.61 yr^{-1}), lowest in the 12-year-old wetland (k = 0.86 yr^{-1}) and intermediate in the 155-year-old wetland (k = 0.97 yr^{-1}). Spieles and Mora (2007) suggested that this finding was due to differences in hydrology. The youngest wetland had a significantly greater mean depth, shorter drawdown duration, and less total time of exposure than the other two wetlands.

At least one study has shown no difference between constructed and natural wetlands. Álvarez and Bécares (2006) studied a surface flow constructed wetland in Spain. They found that *T. latifolia* decomposition rate constants measured in their study (k = 0.511-1.898 yr^{-1}) were comparable to estimates reported from studies of natural wetlands. The small number of studies and seemingly contradicting results make it currently impossible to describe any trends when comparing decomposition in constructed or mitigated wetlands with similar reference sites.

Mitigated versus Natural Wetland Invertebrates

Similar to decomposition studies, there have been few studies comparing macroinvertebrate communities in constructed wetlands with those found in similar natural wetlands. The successful colonization of invertebrates have been mixed, with studies showing both comparable communities (Stanczak and Keiper 2004; Balcombe et al. 2005c; Meyer and Whiles 2008) and dissimilar communities (Scatolini and Zedler 1996; Fennessy et al. 2008). Several studies have found that dispersal ability hinders certain taxa. Clams (Scatolini and

Zedler 1996), snails (Balcombe et al. 2005c; Meyer and Whiles 2008), amphipods (Meyer and Whiles 2008), isopods (Balcombe et al. 2005c), leeches (Meyer and Whiles 2008), and some hemipterans (Brown et al. 1997) have all been found to have lower abundances in created wetlands, which were attributed to lower dispersal rates.

Similar abundance and diversity of species does not necessarily mean similar community compositions. Fennessy et al. (2008) compared mitigated and natural wetlands in Ohio and found that there were major differences in taxa richness and relative abundance of several invertebrate groups. Natural wetlands were high in numbers of dytiscid beetle, chironomids, dipterans and total taxa richness, while mitigated sites had higher mayfly and caddisfly taxa. This was mainly due to the two mayfly genera, *Caenis* and *Callibaetis,* which were found in high numbers at mitigated sites, are considered facultative to pollution tolerant, and were found in less than half of the natural wetlands. Even Balcombe et al. (2005c), who found that overall familial richness, diversity, density and biomass were similar between mitigated and reference wetlands, noted some differences in community composition. The few observed differences were attributable to differences in vegetative community composition and structure, but were not considered detrimental to the wetlands ability to support anuran and avian wildlife.

Success of Appalachian Mitigated Wetlands Compared to Natural Reference Wetlands

Trends for Appalachian mitigation projects seem to align with national trends, showing mixed results when observing different measures of success. Cole and Shafer (2002) studied 23 wetlands in central Pennsylvania and found that about 60% were considered successful based on their permit criteria. Hoeltje and Cole (2007) looked at hydrogeomorphic functional assessment models and found that created sites differed significantly from natural wetlands and that most of the differences observed were related to unnatural hydrologic regimes and to the characteristics

of the surrounding landscape. Hoeltje and Cole (2009) found that created wetlands were farther from natural wetlands and had smaller mean forest patch sizes within a 1-km-radius circle around them than did the reference sites, indicating less hydrologic connectivity. Created wetlands also had less microtopographic variation than reference wetlands. In each study they concluded that created wetlands were not fulfilling the criteria for successful wetland mitigation.

Hydrology has been shown to be both successfully and unsuccessfully replicated in Appalachian mitigated wetlands. Cole and Brooks (2000) conducted a study comparing hydrologic characteristics of natural and created floodplain wetlands in central Pennsylvania. The created wetlands were found to be generally wetter, and wetter for longer periods than natural sites, and had a larger component of open water at each site. The natural wetlands had deeper median depth to water, shorter periods where soils were saturated or inundated, and a lower percentage of time where water was in the root zone. Cole and Brooks (2000) suggested that in the haste to create wet sites, mitigation projects may be creating conditions that are more wet than naturally found in central Pennsylvanian wetlands. This contradicts Copen (2004), who studied hydrology in three mitigated and one natural wetland in West Virginia. He found that mitigated wetlands were performing well compared to the reference sites, with the exception of a few areas within the wetlands that were drier than natural sites. Copen (2004) also found that groundwater was the primary source of hydrologic inputs for areas where wetland conditions were successfully created.

Soil properties in Appalachian mitigated wetlands seem to be less successfully replicated. Bishel-Machung et al. (1996) studied soil properties in 20 reference wetlands and 44 wetland creation projects (age = 1-8 years, $\bar{x} = 4$) in Pennsylvania and found differences between wetland types. Wetland creation projects contained more sand and less clay than reference

wetlands at a depth of 20 cm, and reference wetlands were siltier and higher in organic matter content at 5 cm. The differences in soil organic matter contents resulted in reference wetlands having lower pH, bulk density, and matrix chroma and higher total nitrogen than created wetlands. Neither site landscape position nor dominant cover type accounted for the variation in soil organic matter between reference and created sites. Campbell et al. (2002) also looked at soil conditions in 14 natural and 12 created wetlands in Pennsylvania and found results similar to Bishel-Machung et al. (1996). Soils in created wetlands had less organic matter content, greater bulk densities, higher matrix chroma, and more rock fragments than reference wetlands. Soils in reference wetlands had clay loam textures with high silt content, while sandy clay loam textures predominated in the created sites.

Campbell et al. (2002) also studied vegetation features. Reference wetlands had greater species richness and total cover, while created wetlands included a greater proportion of upland species. They also noted that there were significant differences between ages, but the differences were not necessarily trending towards natural systems in older wetlands. In their study of Section 404 wetlands in Pennsylvania, Cole and Shafer (2002) note that estimates of the percent cover of emergent vegetation was the only success criterion specified in the majority of permits. However, despite this emphasis on vegetation, and a net gain of about 0.05 ha of wetlands per mitigation project, replacement of emergent, scrub–shrub, and forested wetlands with open water ponds or uplands had probably led to a net loss of vegetated wetlands.

In contrast to these results, Balcombe et al. (2005a) found favorable results when comparing vegetation at 11 mitigated and 4 natural wetlands in West Virginia. Mean total percent cover and mean weighted averages of plant communities were found to be similar between mitigated and natural sites. Species richness, evenness, and diversity were found to be

greater at mitigated wetlands; however, they also tended to have more pioneer species, non-native dominants, and species with relatively lower conservation quality. Balcombe et al. (2005a) concluded that mitigated sites adequately supported hydrophytic vegetation and appeared to be developing vegetation similar to reference standards.

Appalachian mitigated wetlands do seem to be successful at providing wildlife habitat, with studies showing that mitigated wetlands had higher anuran species richness, diversity, Wisconsin index calling values, and abundance (Petranka et al. 2003; Balcombe et al. 2005b) and similar avian species richness, diversity and abundance (Balcombe et al. 2005b) as reference wetlands. Balcombe et al. (2005d) evaluated invertebrate, avian, anuran, and vegetative communities along with habitat quality for eight wetland-dependent wildlife species (one reptile, one amphibian, three mammals, and three bird species). Wetland ranks were then assigned based on several parameters that included richness, abundance, diversity, density and biomass. Mitigated wetlands were found to consistently score lower (better) than reference wetlands across all communities (Balcombe et al. 2005d).

Similar numbers of individuals do not necessarily mean similar habitat use. Hartwig and Kiviat (2007) found that though Blanding's turtles (*Emydoidea blandingii*) used all constructed and adjacent natural wetlands in New York, they used the different types of wetlands for different purposes. Blanding's turtles appeared to be using the constructed wetlands to bask and forage in the spring and early summer, but moved to deeper wetlands in late summer when the constructed wetlands dried up or became too warm. Constructed wetlands provided good basking habitat due to shallower water, less tree cover, and abundant basking logs compared to the natural wetlands. Though the constructed wetlands were readily used by the turtles, they did

not provide the same habitat role as natural wetlands. Hartwig and Kiviat (2007) concluded that attributing a positive or negative value to their findings was impossible.

There is a need to briefly revisit the studies of Atkinson and Cairns, Jr. (2001) and Balcombe et al. (2005c) mentioned in previous sections because of their relevance to Appalachian studies. Atkinson and Cairns, Jr. (2001) studied decomposition rates between mitigated and natural wetlands in West Virginia and found that the older mitigated wetlands had faster decomposition than the younger mitigated wetlands, but that both were lower than rates reported for comparable natural wetlands. Balcombe et al. (2005c) studied invertebrates at 11 mitigated and 4 natural wetlands in West Virginia and found that they generally supported similar invertebrate assemblages, especially among benthic populations.

Overall, it appears that hydrology and soil composition seem to have mixed levels of success when compared to natural systems. These in turn influence wetland vegetation and lead to varying levels of success. Despite these differences, wildlife appears to have similar diversity and richness in mitigated and natural wetlands. However, community composition and how habitat is used may differ between the wetland types.

OBJECTIVES

This project was split into a primary and secondary study. The objective of the primary study was to assess wetland function by evaluating and comparing litter decomposition rates at freshwater palustrine mitigated (n = 3) and natural reference (n = 3) wetlands in West Virginia. The specific objects were:

1. To compare decomposition rates for mitigated versus natural wetlands.
2. To determine rates and trends of decomposition for five different litter types: broadleaf cattail (*T. latifolia*.), common rush (*J. effusus*), brookside alder (*Alnus serrulata*

(Ait.)Willd.), reed canary grass (*Phalaris arundinacea* L.), and a mix of common rush, reed canary grass, and brookside alder.

3. To determine the effect environmental variables (hydrology, soil moisture, temperature and pH) play in litter decomposition rates and compare results from mitigated to reference wetlands.
4. To determine the effect that biotic variables (macroinvertebrate familial diversity, abundance and biomass, along with fungal biomass) have on decomposition rates and compare this effect between mitigated and natural wetlands.
5. To investigate the feasibility of using decomposition of a known litter as a means of assessing wetland function.

Based on my literature review, I created the following hypotheses. I hypothesized that decomposition rates would be greater in mitigated than natural wetlands. I hypothesized that differences in hydrology, more frequent and longer inundation periods along with higher soil moisture at mitigated sites, would cause increased decomposition rates at mitigated wetlands. I believed the average soil moisture at the mitigated sites, in non-inundated areas, would be higher than the average soil moisture found at the reference wetlands and would cause faster decomposition. I also hypothesized that temperature and pH would be positively correlated with decomposition rate, but that these variables would be similar among sites.

I hypothesized that decomposition rates would vary between litter types. I hypothesized that brookside alder and the mixed litter would have faster decomposition rates and that cattail would have a slower decomposition rate. I hypothesized that the order of litter type decomposition rates would not vary greatly between wetlands.

I hypothesized that decomposition rate would change over time. I believed there would likely be an initial period of leaching with rapid mass loss, followed by an intermediate period of microbial decomposition and conditioning that would end with a slow period of mechanical and invertebrate fragmentation.

I hypothesized that fungal and macroinvertebrate presence would be positively correlated with decomposition, but to a lesser degree than hydroperiod or temperature. I believed that decomposition rates would correlate with differences in macroinvertebrate abundance, familial diversity and biomass, but would not vary between mitigated and natural wetlands. I hypothesized that fungal biomass would be greater in reference wetlands and would have a weak positive correlation with decomposition rates.

Based on the above statements, the following null hypotheses were analyzed:

1. There is no difference between average decomposition rates at reference and mitigated wetlands.
2. Decomposition rate does not change over time.
3. Decomposition rate is independent of litter type.
4. Decomposition rate is independent of environmental variables and there is no difference in environmental variables between mitigated and natural wetlands.
5. Decomposition rate is independent of biotic variables and there is no difference in biotic variables between mitigated and natural wetlands.

The objective of the secondary study was to assess wetland function throughout West Virginia by evaluating and comparing litter decomposition rates at freshwater palustrine created (n = 8) and natural reference (n = 8) wetlands. The specific objects were:

1. To compare decomposition rates for created versus natural wetlands.

2. To determine how decomposition rate changes with created wetland age.

I hypothesized that decomposition rates would be greater in mitigated than natural wetlands. I also hypothesized that younger created wetlands would have faster decomposition rates than older wetlands, and that decomposition rate would trend towards rates comparable with those found in natural wetlands.

Based on the above statements, the following null hypotheses were analyzed:

1. There is no difference between average decomposition rates at reference and mitigated wetlands.
2. Decomposition rate does not change with created wetland age.

STUDY SITES

This study was conducted in West Virginia, which is located in the mid-Atlantic region of the U.S. Study sites are broken up into two groups, primary study sites and secondary study sites. Six wetlands made up the primary study sites (Figure 3) and were comprised of three mitigated (Leading Creek, Sugar Creek, and Hazelton) and three reference wetlands (Meadowville, Upper Deckers Creek, and Bruceton Mills). Primary study sites were included in an in-depth decomposition study that included five litter types and ran from December 2007 through December 2009, along with a secondary study that used only *T. latifolia* in litter bags and ran from November 2008 through November 2009. Ten additional wetlands were used in the secondary study (Figure 4) and were comprised of five created (Enoch Branch, Pedlar Wildlife Management Area [WMA], Upper Deckers Creek WMA, Elk Run, and VEPCO) and five reference wetlands (Muddlety, Indian Creek, Kanes Creek, Thomas Airfield, and Glade Run).

All but 2 of the study sites (Indian Creek and Pedlar Wildlife Management Area) were located in the Allegheny Mountains ecoregion, which runs up the middle of West Virginia and separates the Allegheny Plateau ecoregion from the Ridge and Valley ecoregion (Bailey 1983). In the Allegheny Mountain ecoregion, mountain ridges can reach between 1,200 and 1,375 m in elevation. The remaining 2 study sites were located on the edge of the Allegheny Mountains, in the Allegheny Plateau ecoregion of the state, which is the unglaciated ecoregion to the west. Most of the ridges in this part of the state are 450 m or less in elevation.

Reference wetlands were chosen based on their proximity to mitigated sites; similarity in elevation, size, and wetland classification; and their relative degree of disturbance. Reference wetlands ranged in elevation from 275 to 965 m ($\bar{x}$ = 596, S.E. = 84) and in size from 0.7 to 11.7 ha ($\bar{x}$ = 5.0, S.E. = 1.6) (Table 1). Created wetlands ranged in age from 2 to 40 years ($\bar{x}$ = 15.1, S.E. = 4.5), in elevation from 335 to 1,020 m ($\bar{x}$ = 615, S.E. = 75), and in size from 0.1 to 17.0 ha ($\bar{x}$ = 5.9, S.E. = 1.9). Relief was minimal in all wetlands, most of which were located in floodplains. Almost all created wetlands had some level of disturbance on their edge in the form of roads with moderate to heavy traffic, houses, grazing, or cultivated land. Many of the reference wetlands also had some amount of disturbance adjacent to them in the form of roads with light to heavy traffic, tree plantations, railroad tracks converted to a hiking/biking trail, grazing, or cultivated land.

Primary Study Sites

Upper Deckers Creek

The Upper Deckers Creek wetland (Figure 5 & 6) is a reference site located about 1 km southwest of Masontown, Preston County. The site is a 2.1 ha oxbow wetland off Deckers Creek and is comprised mainly of palustrine aquatic bed, unconsolidated bottom, emergent persistent

and scrub-shrub wetland types. The wetland is long and narrow, with a forested slope on its east side and a narrow fallow field separating it from Deckers Creek on the west side. During wetter portions of the year, Deckers Creek overflows its banks and fills the wetland, causing its water levels to be flashy at times. Reed canary grass, cowlily (*Nuphar lutea ssp. advena* (L.)Sm.(Ait.)), marsh purslane (*Ludwigia palustris* (L.)Ell.), and buttonbush (*Cephalanthus occidentalis* L.) are dominant species.

Meadowville

The Meadowville wetland (Figure 7 & 8) is a reference site located in Meadowville, Barbour County. It is 6.6 ha and is part of a bottomland wetland complex that straddles Glady Fork, a tributary of Sugar Creek. The site was historically grazed, but became too moist and grazing was stopped about 40 years ago (Copen 2004). Meadowville wetland is long and narrow, with a wooded slope running most of its west side and State Route 92 on its eastern edge. Groundwater, direct rainfall, and surface water runoff are the primary sources of water (Copen 2004). It is comprised of both emergent persistent and scrub-shrub habitat dominated by cattail, tussock sedge (*Carex stricta* Lam.), rice cutgrass (*Leersia oryzoides* (L.)Sw.), blue-joint grass (*Calamagrostis canadensis* var. *canadensis* (Michx.)Beauv.), and brookside alder.

Bruceton Mills

The Bruceton Mills wetland (Figure 9 & 10) is a reference site located about 2.9 km north of Bruceton Mills, Preston County. The site is the remnant of a beaver (*Castor canadensis*) pond and is comprised mainly of emergent persistent and scrub-shrub wetland. The wetland is surrounded by a spruce plantation on the north, wooded hill slopes on the east and south, and grazed scrubland and farmland to the west. An unnamed tributary of Glade Run flows through the wetland and is a primary source of water along with hillside runoff. Reed canary

grass, rice cut grass, cattail and brookside alder are all present in good numbers, but reed canary grass is by far the dominant species.

Leading Creek

The Leading Creek wetland (Figure 11 & 12) is a mitigated site that was built in 1996 by the West Virginia Division of Highways (DOH) as a mitigated wetland for the Appalachian Corridor H highway project. It is located about 4 km south of Montrose in Randolph County. The wetland is 8.6 hectares in size and has wetland cells (unconnected portions of a single wetland complex) on both sides of Leading Creek. It is bordered by a wooded hillside to the west, the Allegheny Highlands Trail and US Route 219 to the east, and farmland to the north and south. Leading Creek wetland is a mix of unconsolidated bottom, aquatic bed, emergent persistent, scrub-shrub, and young forested wetland types. The wetland receives water from a culvert that runs under US Route 92, surface runoff from the hillside, a natural seep, occasional overbank flooding, and groundwater (Copen 2004). Hop sedge (*Carex lupulina* Muhl. ex Willd.), common and woodland rushes (*J. subcaudatus* var. *subcaudatus* (Engelm.) Coville&Blake), smartweed (*Polygonum hydropiperoides* Michx; *P. persicaria* L.), rice cutgrass, and brookside alder are dominant species.

Sugar Creek

The Sugar Creek wetland (Figure 13 & 14) is a mitigated site that was built in 1995 by the DOH as a mitigated wetland for the Appalachian Corridor H highway project and is located about 3 km southwest of Meadowville in Barbour County. Sugar Creek wetland is comprised of multiple unconnected cells on both sides of Sugar Creek and has emergent, open water, and scrub-shrub area. Groundwater, surface flow, rainfall, and occasional overbank flooding are the primary sources of water (Copen 2004). The wetland is surrounded by wooded hills with a sliver

of cleared fallow slope to the north. Reed canary grass, wool grass (*Scirpus cyperinus* (L.) Kunth), woodland rush, American burreed (*Sparganium americanum* Nutt.) and brookside alder are all dominant species.

Hazelton

The Hazelton wetland (Figure 15 & 16) is a mitigated wetland located at the Hazelton exit (exit 29) of Interstate 68. The wetland was created in 2006 as a mitigated site for the Mon-Fayette Expressway system project. Two stream channels, Cherry Run and Mill Run, converge into Little Sandy Creek within the main cell. Two additional cells are located adjacent to County Route 5/7 in the northwest corner of the site. Interstate 68 runs south of the wetland, County Route 5 runs to the east, County Route 5/7 runs to the north, and a small amount of wooded and scrubland lies to the west. Flooding from the three streams is the primary source of water, along with runoff from roads. It is primarily palustrine unconsolidated bottom, aquatic bed, and emergent types. Broadleaf cattail, common and narrowpanicle rush (*J. brevicaudatus* (Engelm.) Fernald), white and red clover (*Trifolium repens* L.; *T. pretense* L.), and beggar-tick (*Bidens sp.*) are all dominant species.

Secondary Study Sites

Muddlety

The Muddlety reference wetland (Figure 17 & 18) is about 4.0 km north of Summersville in Nicholas County. It is a semipermanently to permanently flooded bottomland complex dominated by shrub thickets consisting of swamp rose (*Rosa palustris* Marsh.) and silky cornel (*Cornus amomum* P.Mill.), as well as emergent marshes of American burreed and cattail (Balcombe 2003). US Route 19 and County Route 19/41 run to the northwest and scattered fields and wooded hills lie to the north, east and south.

Indian Creek

The Indian Creek reference wetland (Figure 19 & 20) is about 4.0 km southeast of Arnettsville in Monongalia County. The wetland lies in the confluence of Indian Creek and Monongahela River and is a delta wetland. It lies between Indian Creek to the south and County Road 45 and a wooded hillslope to the north. It is an emergent persistent wetland and broadleaf cattail is the dominant species.

Kanes Creek

The Kanes Creek reference wetland (Figure 21 & 22) is about 0.75 km southeast of Reedsville in Preston County. The wetland is a forested semipermanently flooded to permanently flooded bottomland complex that lies along Kanes Creek. The Mon River Rail Trail System: Deckers Creek Trail follows the wetland complex along its north end and there is forest and scattered fields around the wetland. The Kanes Creek is impacted by acid mine drainage (AMD), but no visual evidence of AMD, associated with other portions of the stream, were present at the study site.

Thomas Airfield

The reference wetland at the Thomas airfield (Figure 23 & 24) is about 0.7 km northwest of Thomas in Tucker County. The land is privately owned by Western Pocahontas Properties. The wetland complex is a series of beaver impoundments, with the largest impoundment being about 1.8 ha. An unnamed tributary of the North Fork Blackwater River runs through the site. It is primary unconsolidated bottom, aquatic bed, and emergent wetland. The wetland is surrounded by a pine plantation to the south and wooded hills to the east, west, and north.

Glade Run

The Glade Run wetland (Figure 25 & 26) is a reference beaver impoundment wetland in the Canaan Valley National Wildlife Refuge and is about 9.0 km east of Davis in Tucker County. It is connected to a larger 1,672 ha wetland complex. Glade Run flows through the wetland and is the primary source of water. It is aquatic bed and emergent and is surrounded by scrub-shrub, emergent, and aquatic bed wetland along with forested slope.

Enoch Branch

The Enoch Branch mitigated wetland (Figure 27 & 28) was created by DOH in 1997 as compensatory mitigation for the construction of US Route 19 (Corridor L). It is located about 4.0 km north of Summersville in Nicholas County and contains 2 main cells totaling 3.4 ha in size. It consists of 1.0 ha of emergent, 2.0 ha of open water and aquatic bed, and 0.4 ha of scrub-shrub wetland (Balcombe 2003). Both cells are semipermanently to permanently flooded open water ponds with patches of common rush and the western cell contains brookside alder along its perimeter. The wetland is surrounded by forested hill slope and a gravel road runs to the south.

Pedlar Wildlife Management Area

The Pedlar WMA wetland (Figure 29 & 30) was created in 2006 by the WV Division of Natural Resources (DNR) to create wildlife habitat in the Pedlar WMA (Mike Peters, per. comm.). It is located about 4.2 km from Cassville in Monongalia County. It is a small wetland purposely created on the upslope side of a road cut into a hillside. The road lies to the north and forested hillside surrounds the remainder of the wetland. It is an aquatic bed and emergent wetland and hillside runoff is the primary source of water.

Upper Deckers Creek Wildlife Management Area

The Upper Deckers Creek WMA created wetland (Figure 31 & 32) is a reservoir open water wetland that was created through the impoundment of Dillan Creek. It was constructed in 1968 by the Monongahela Soil Conservation District, but it is unclear whether or not it was part of a mitigation project (Mike Peters, per. comm.). Two impoundments (2.6 ha and 3.9 ha) were created and in 1974 DNR acquired the property. It is located 1.9 km northwest of Reedsville in Preston County and is primarily unconsolidated bottom and aquatic bed with some emergent wetland area. Along the southwestern portion of the wetland are a narrow forested stand and private residence and farm fields are scattered on all sides.

Elk Run

The Elk Run mitigated wetland (Figure 33 & 34) was constructed in 1981 as mitigation for the Island Creek Coal Company's creation of the Alpine Mine Complex Treated Water Impoundment (Balcombe 2003). The site is now owned and managed by Consol Energy. The site represents the enhancement and expansion of existing wetlands, associated with Elk Run, through the creation of water control structures. It is located about 10.0 km north of Davis in Grant County. It consists of two cells connected by a large dike. The first cell is a large permanently flooded open water pond, while the second cell is temporarily flooded and dominated by rough arrowwood (*Viburnum dentatum* L.) and cattail (Balcombe 2003). It is 3.8 ha in size and consists of 0.4 ha emergents, 3.3 ha open water, and 0.1 ha scrub-shrub areas (Balcombe 2003). The wetland is near mine land, but is surrounded by forest, with only a narrow stand of forest separating the wetland from the grassy contoured mine land to the north. Elk Run is impacted by acid mind drainage, but it does not seem to flow into the wetland.

VEPCO

The Virginia Electric and Power Company (VEPCO) wetland (Figure 35 & 36) was constructed in 1995 as mitigation for the creation of the Phase A Flue Gas Desulfurization By-Product Facility at the Mount Storm Power Station (Balcombe 2003). The site is now owned and managed by Dominion Resources Inc. It is located 10.3 km from Davis in Tucker County and is 0.4 km off State Route 93 on A-frame Road. The total mitigation area is 7.0 ha in size, consisting of 5.9 ha emergents, 0.9 ha open water, and 0.2 ha scrub-shrub areas (Balcombe 2003). The 3 cells are separated by a series of dikes and each consists of 1 or 2 open water areas separated by temporarily flooded emergent vegetation. The wetland is surrounded by forest on all sides.

STUDY SPECIES

Four common wetland species were used in this study: broadleaf cattail, common rush, brookside alder, and reed canary grass. Cattail is a native wetland species that is an erect, rhizomatous, perennial aquatic growing to 3 m tall, with creeping rhizomes up to 70 cm long and from 0.5 to 3 cm in diameter (Mitich 2000). Cattail is common throughout the United States and temperate and tropical places worldwide. It occurs in coastal and valley marshes at elevations lower than 2,000 m (Hickman 1993). Its ubiquitous distribution has led to it being used extensively in decomposition studies. Previous studies have measured decomposition rate constants ranging from 0.17 to 1.50 yr^{-1} (Middleton 1994; Álvarez and Bécares 2006; Spieles and Mora 2007) using the exponential decay model $y_t / y_o = e^{-kt}$, where y_o = initial litter mass, y_t = litter mass at time *t*, and *k* is the decomposition rate constant (Olson 1963).

Common rush is a slow spreading, clump forming, grass-like perennial with short, finely divided rhizomes that are 15 to 25 centimeters long, growing from 0.6 to 5 centimeters beneath

the soil surface (Stevens 2003). It is a wetland species that has a range including much of North America, Mexico, and Eurasia (Hickman 1993). Common rush has decomposition rate constants that range from 0.36 to 2.04 yr^{-1} (Kittle et al. 1995; Kuehn et al. 2000). Kittle et al. (1995) compared common rush and broadleaf cattail decomposition rates in three wetlands receiving acid mine drainage in West Virginia and found that broadleaf cattail decomposed faster at all three sites.

Brookside alder is a native nitrogen-fixing, thicket-forming shrub or small tree with dark, green foliage. It can grow up to 3.5 m tall and produces nitrogen through the activity of nitrogen-fixing bacteria located in its root nodules. Brookside alder has a distribution that covers the eastern U.S., from Florida to Maine and west to Oklahoma, Missouri and Illinois (Northeast Plant Materials Program 2006). There are no decomposition rate constants for brookside alder in the literature, but stream studies have reported values of 0.908-2.701 yr^{-1} for European alder (*Alnus glutinosa* (L.) Gaertn.) (Chauvet 1987; Scheiring 1993; Pereira et al. 1998). Stream studies have shown that alder leaves in general break down more rapidly that other species, despite the fact that they are woody (Hart and Howmiller 1975; Sedell et al. 1975; Gessner et al. 1991). Wedderburn and Carter (1999) found that deciduous N-fixing tree species decomposed faster than other species in a silvopastoral system and attributed it to low lignin and C concentrations and high N content. These results agree with many wetland litter decomposition studies (Coulson and Butterfield 1978; Bartsch and Moore 1985; Neely and Davis 1985; Ohlson 1987; Aerts and de Caluwe 1997; Poi de Neiff et al. 2006).

Reed canary grass is a rhizomatous perennial grass that can reach 0.9 to 1.8 meters in height (Weinmann et al. 1984). It is possible that it was native to North America, but European cultivars have been widely introduced for use as hay and forage and there are no easy traits to

differentiate between the native and European cultivars (White et al. 1993). Reed canary grass forms dense, highly productive single species stands that inhibit and suppress many other wetland species (Apfelbaum and Sams 1987). Hough and Cole (2009) measured reed canary grass decomposition rate constants of 1.55-4.19 yr^{-1} at 14 wetlands in Pennsylvania and Kao et al. (2009) measured 68% mass remaining at the end of 150 d in New York. Kao et al. (2009) also measured decomposition rates for common rush and found they were similar to reed canary grass. They found that reed canary grass exhibited a strong capacity for N and P accumulation, but had a low capacity for retention of nutrients in aboveground litter. This contrasted with common rush, which had high accumulation and retention of N and P (Kao et al. 2009).

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Table 1. List of 8 created and 8 reference wetland study sites in West Virginia, including site name, year constructed, size (ha), source builder, elevation (m above sea level), Universal Transverse Mercator (UTM) coordinates, basin, and watershed, 2007-2009.

Site name	Year	Size (ha)	Source	Elev. (m)	UTM Y	UTM X	Basin	Watershed
Created Wetlands								
Leading Creek	1995	17.0	Division of Highways	600	4321563	602550	Tygart Valley	Leading Creek
Sugar Creek	1995	11.0	Division of Highways	490	4328850	591470	Tygart Valley	Laurel Creek
Hazelton	2006	2.7	Division of Highways	560	4390990	625708	Cheat River	Little Sandy Creek
Pedlar WMA	2006	0.1	Division of Natural Resources	335	4393134	575877	Dunkard Creek	Dunkard Creek
Upper Deckers WMA	1968	3.5	Monongahela Soil Conservation District	520	4375719	602837	Monongahela River	Upper Deckers Creek
Elk Run	1981	3.8	Island Creek Coal Co.	830	4341542	636104	North Branch of the Potomac	Elk Run
VEPCO	1995	5.7	Virginia Electric Power Co.	1020	4338218	641309	Cheat River	Blackwater River
Enoch Branch	1997	3.4	Division of Highways	570	4248058	513819	Gauley River	Muddlety Creek
Reference Wetlands								
Meadowville	-	11.7	-	480	4330920	593940	Tygart Valley	Laurel Creek
Upper Deckers Creek	-	2.1	-	515	4377282	602193	Monongahela	Upper Deckers Creek
Bruceton Mills	-	1.4	-	515	4393306	615536	Cheat River	Big Sandy Creek
Indian Creek	-	0.7	-	275	4379544	580789	Monongahela River	Monongahela River
Kanes Creek	-	8.9	-	520	4373209	603528	Monongahela River	Upper Deckers Creek
Thomas Airfield	-	3.5	-	940	4335279	629233	Cheat River	Blackwater River
Glade Run	-	1.7	-	965	4328921	641158	Cheat River	Blackwater River
Muddlety	-	10.4	-	560	4248673	516774	Gauley River	Muddlety Creek

Figure 1. Photograph of litter bag with mixed litter type and coarse (2.8 mm) mesh.

Figure 2. Photograph of the 4 single species (reed canary grass, broadleaf cattail, brookside alder, and common rush) litter bags with fine (1.27 mm) mesh.

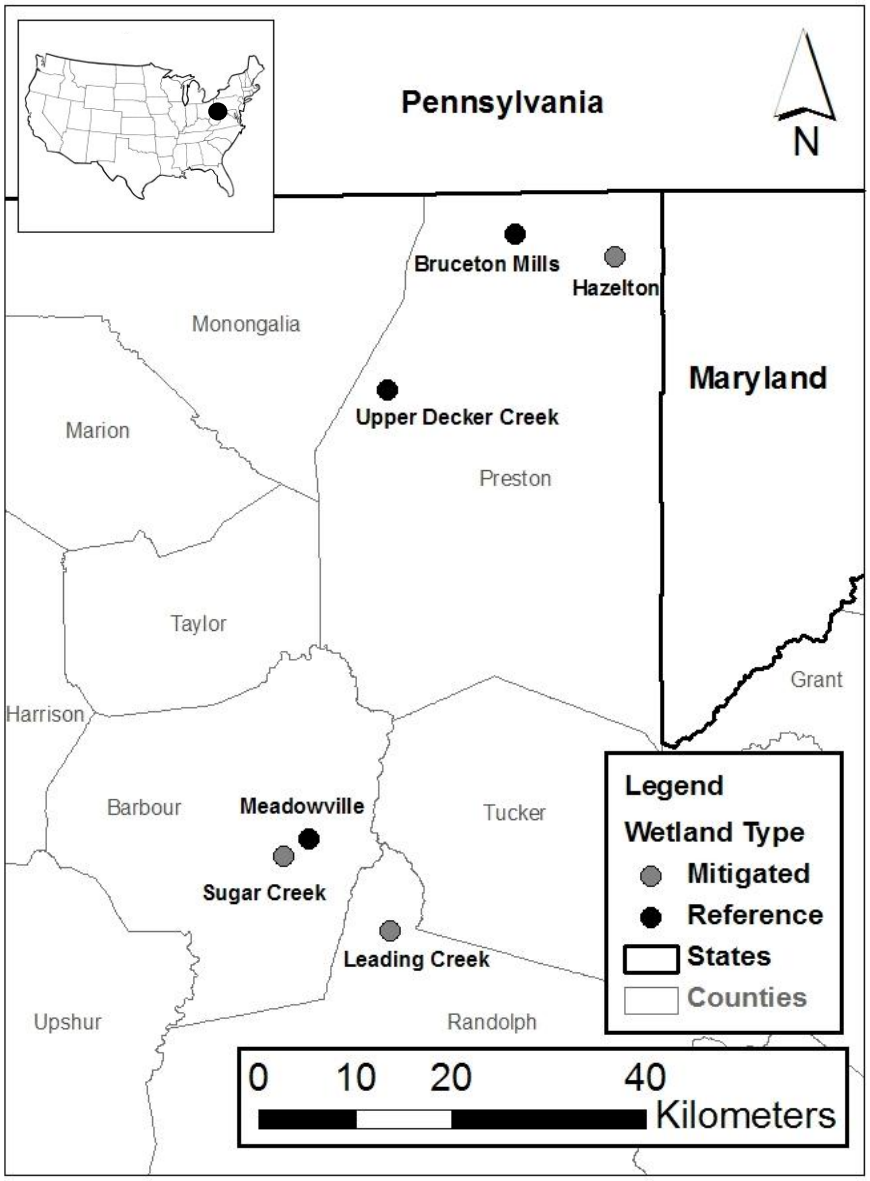

Figure 3. Six primary study sites included in the primary study that ran from December 2007 through December 2009. Wetland sites were comprised of three mitigated and three reference wetlands, in the Allegheny Mountain region of West Virginia, USA.

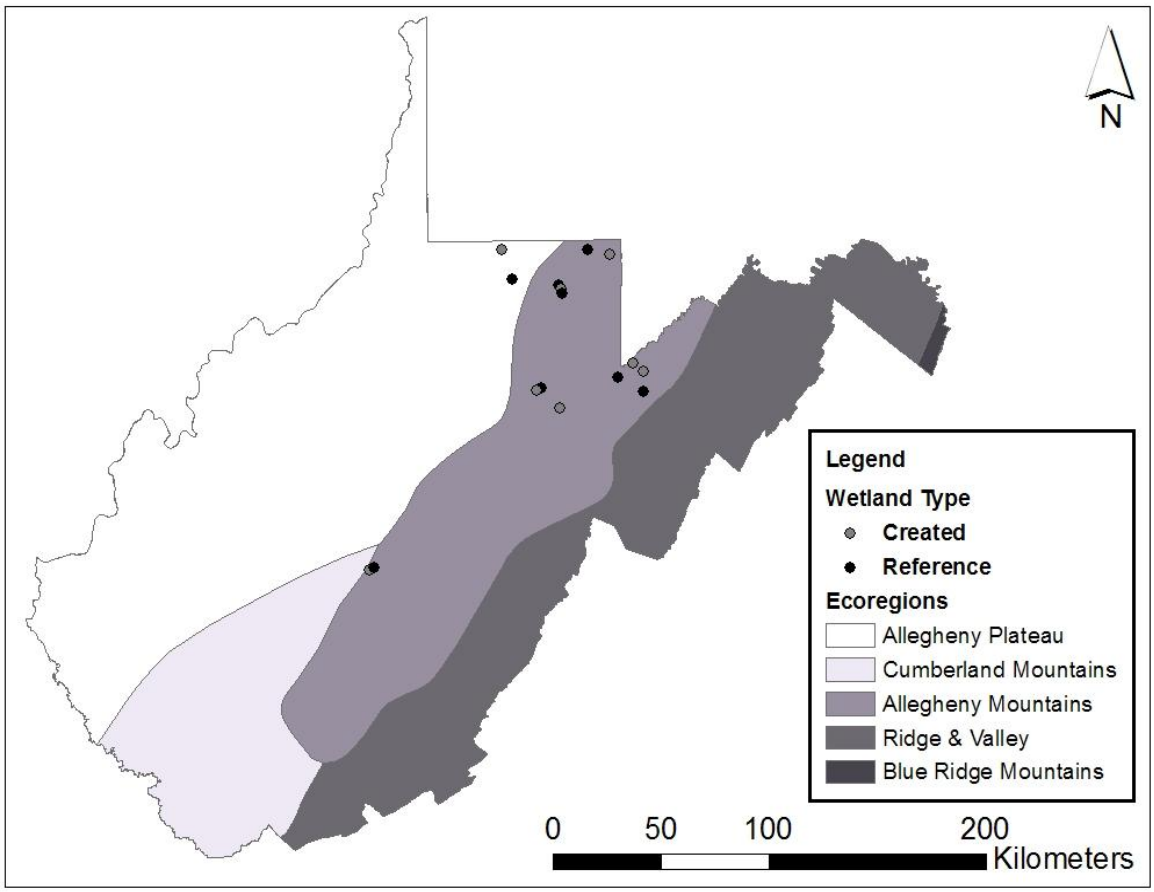

Figure 4. Sixteen study sites included in the secondary study that ran from November 2008 through November 2009. Study sites were comprised of eight created and eight reference wetlands located primarily in the Allegheny Mountain ecoregion of West Virginia, USA.

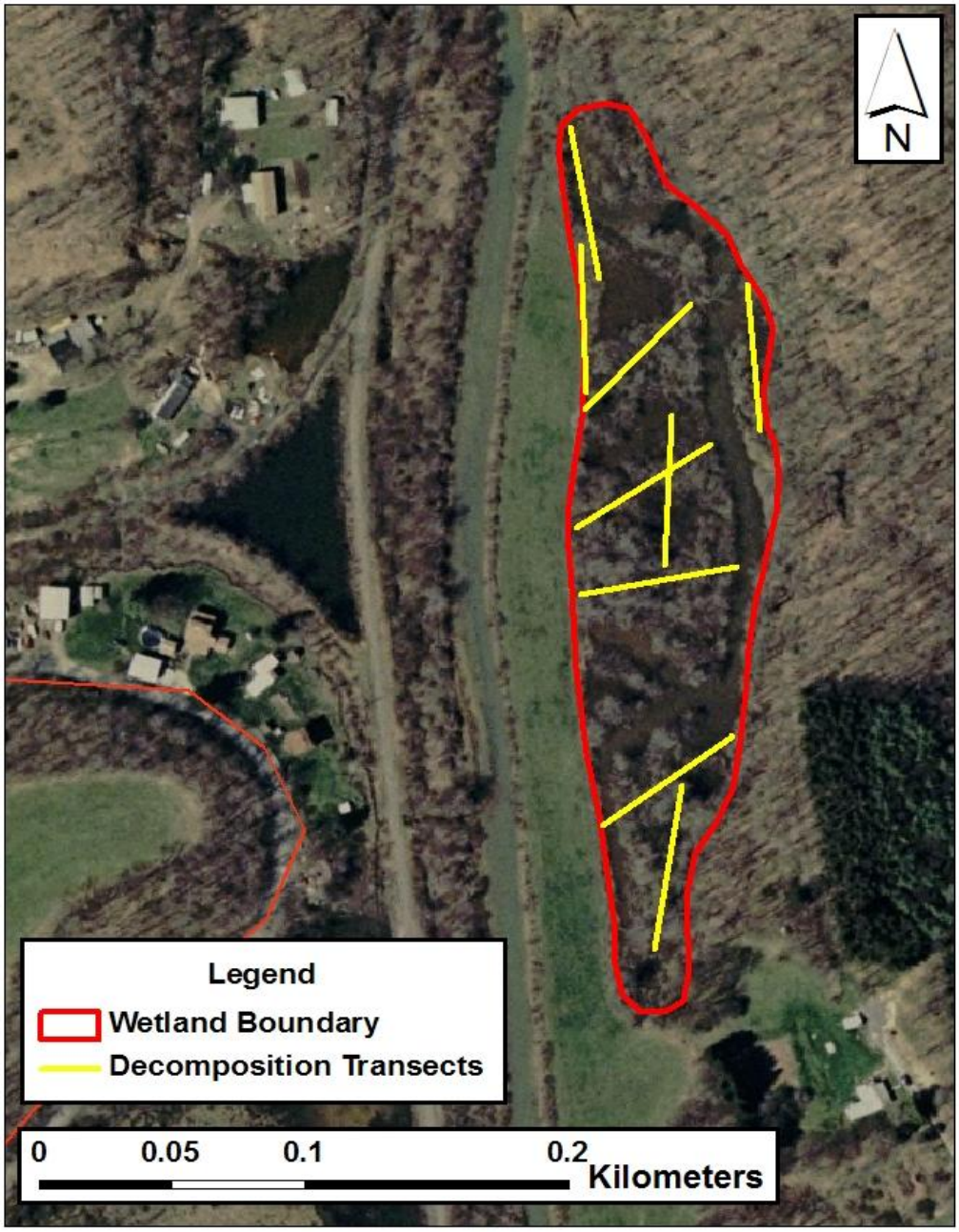

Figure 5. Aerial photograph of Upper Deckers Creek reference wetland showing wetland perimeter and litter decomposition transects. (Aerial photograph provided by WV GIS Tech Center)

Figure 6. Photograph of Upper Deckers Creek reference wetland, West Virginia, taken in October 2007. (Photo taken by Ann Anderson.)

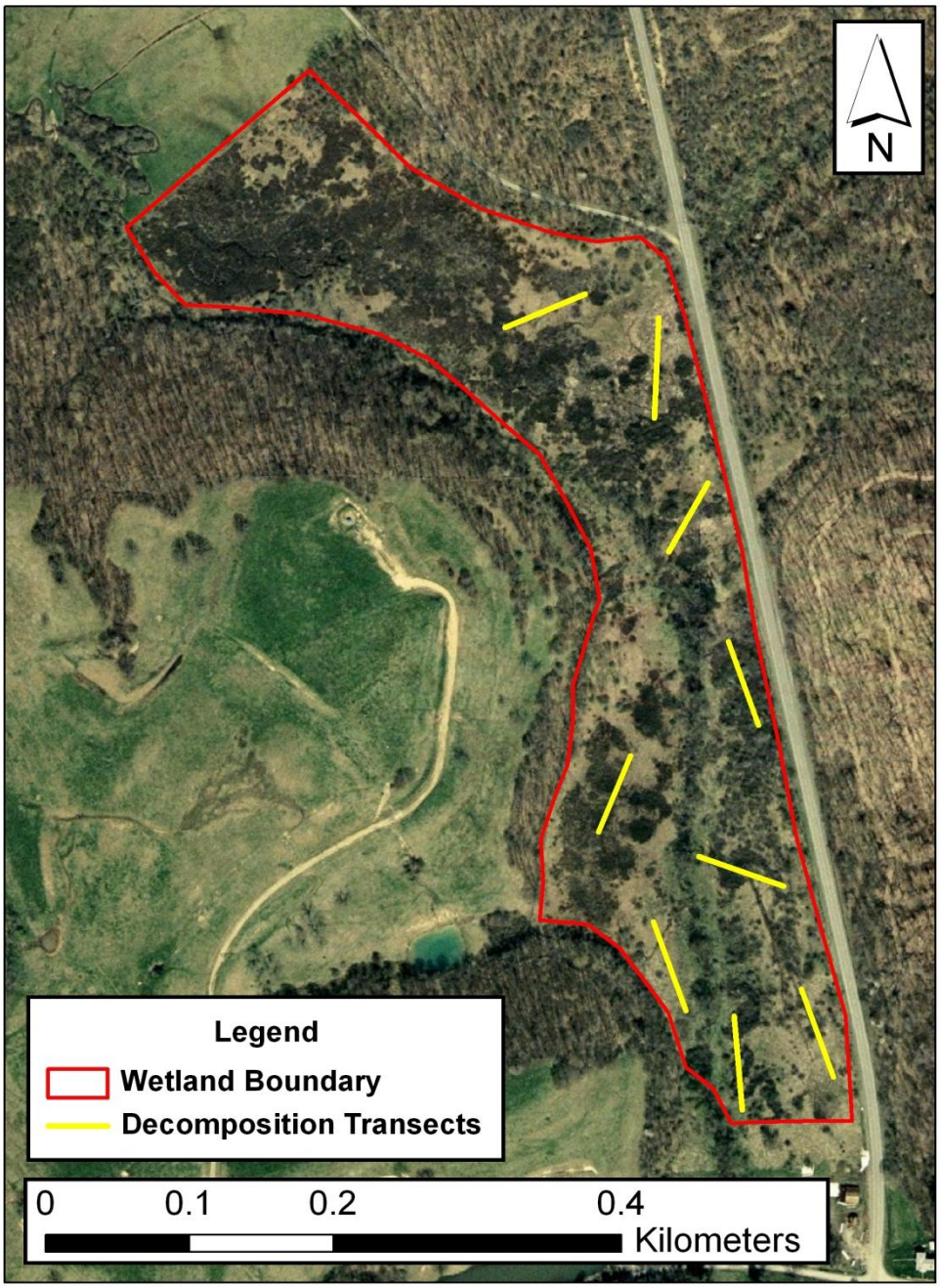

Figure 7. Aerial photograph of Meadowville reference wetland showing wetland perimeter and litter decomposition transects. (Aerial photograph provided by WV GIS Tech Center)

Figure 8. Photograph of Meadowville reference wetland, West Virginia, taken in August 2009.

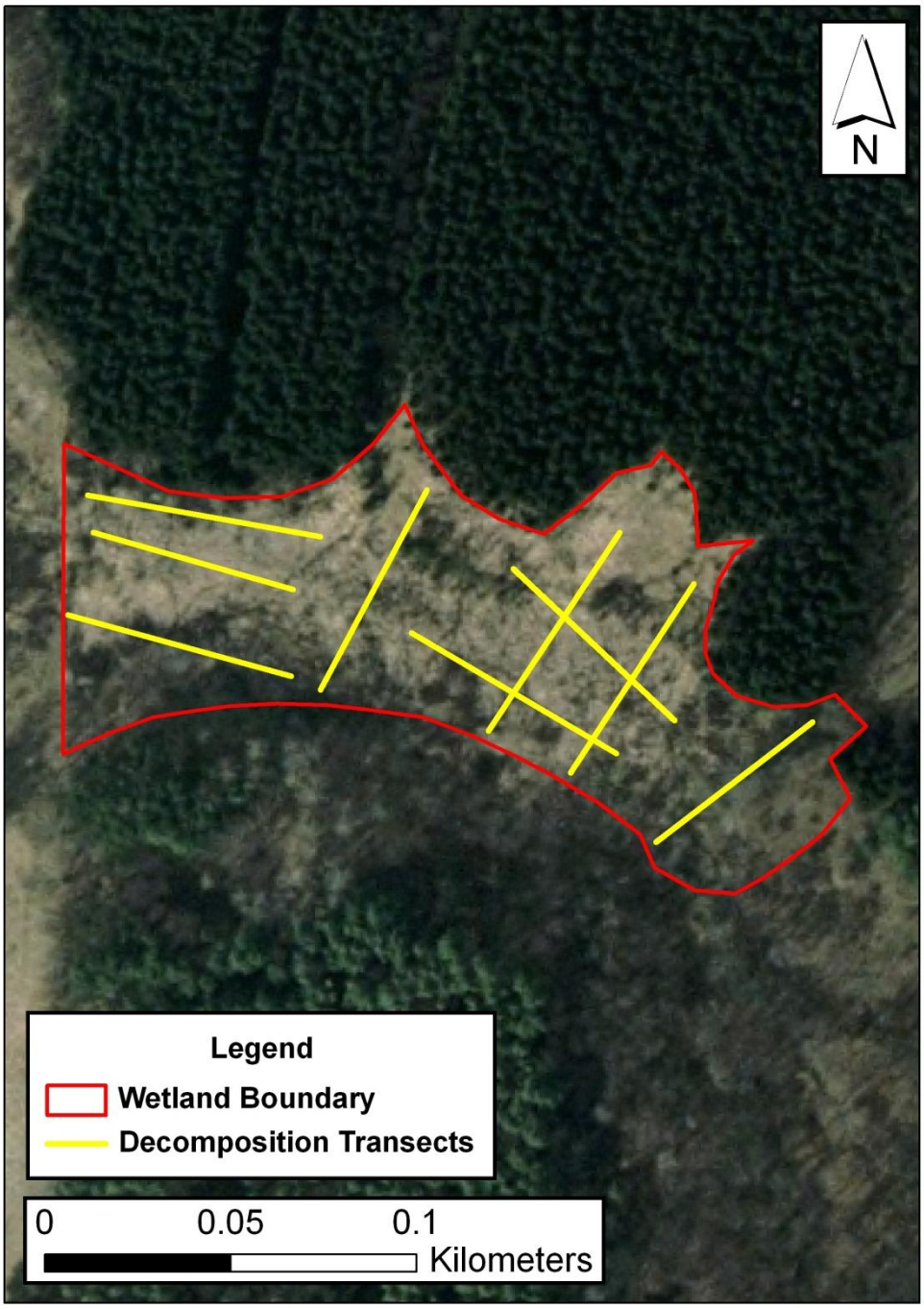

Figure 9. Aerial photograph of Bruceton Mills reference wetland showing wetland perimeter and litter decomposition transects. (Aerial photograph provided by WV GIS Tech Center)

Figure 10. Photograph of Bruceton Mills reference wetland, West Virginia, taken in February 2009.

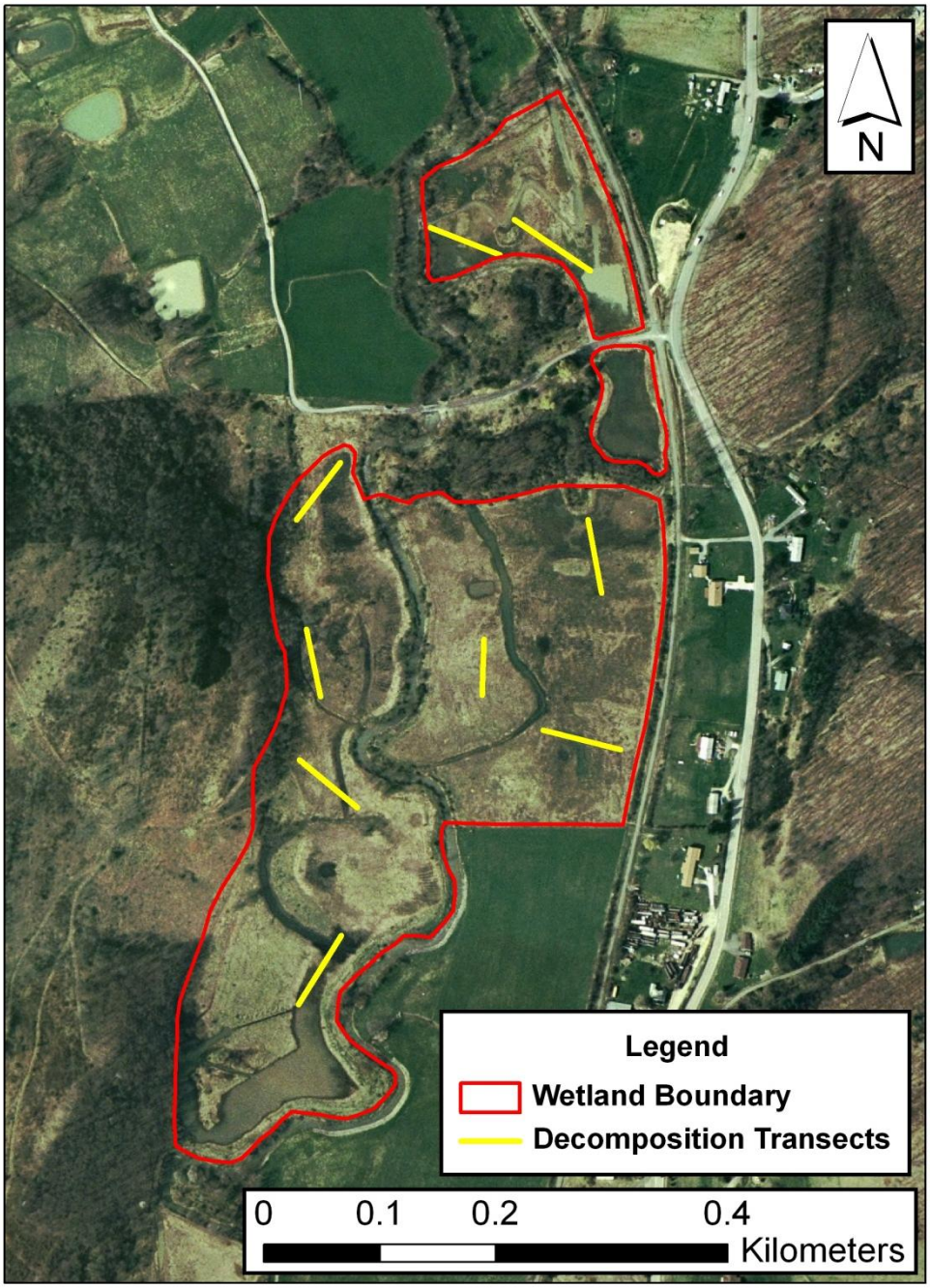

Figure 11. Aerial photograph of Leading Creek mitigated wetland showing wetland perimeter and litter decomposition transects. (Aerial photograph provided by WV GIS Tech Center)

Figure 12. Photograph of Leading Creek mitigated wetland, West Virginia, taken in July 2008.

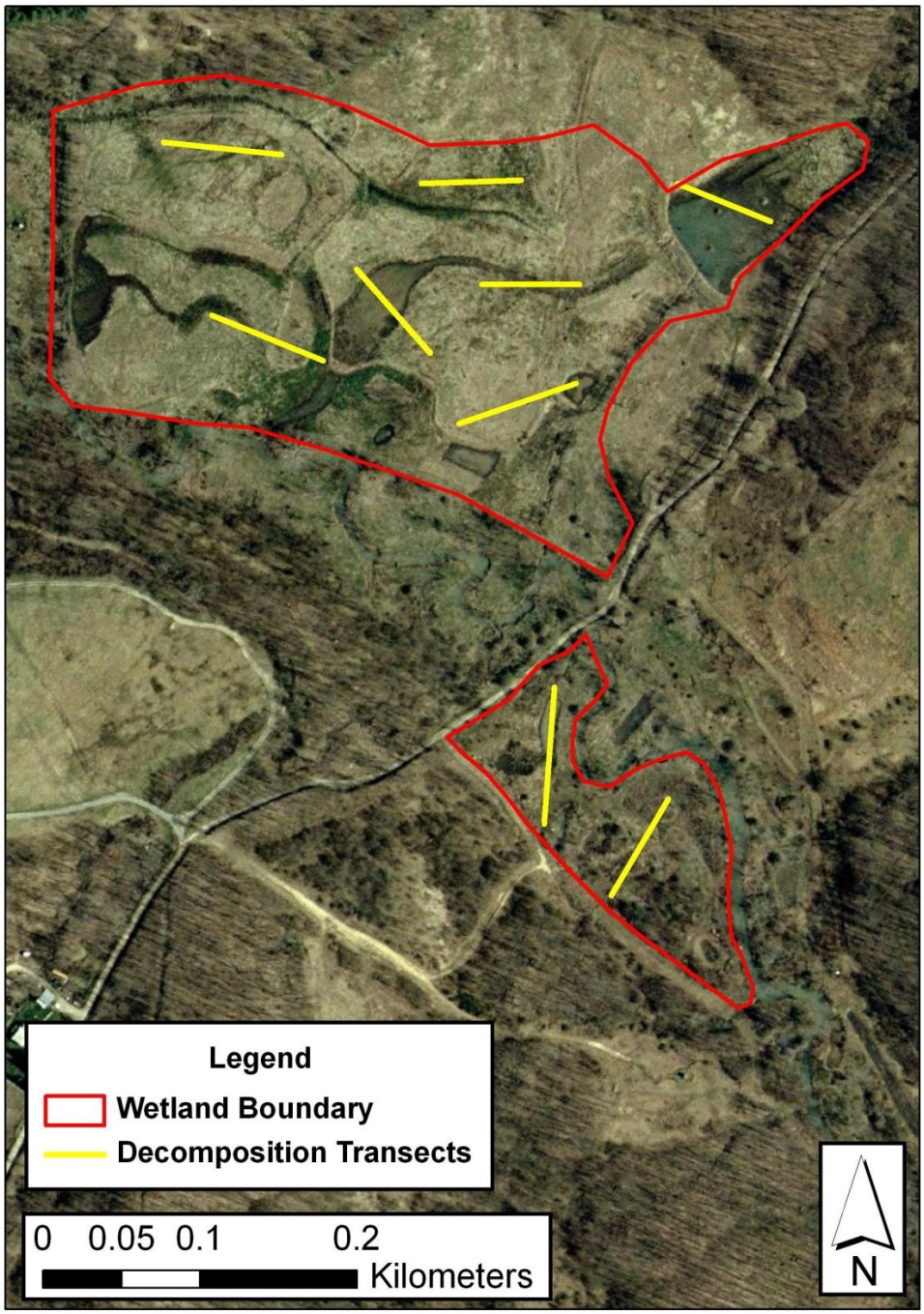

Figure 13. Aerial photograph of Sugar Creek mitigated wetland showing wetland perimeter and litter decomposition transects. (Aerial photograph provided by WV GIS Tech Center)

Figure 14. Photograph of Sugar Creek mitigated wetland, West Virginia, taken in July 2008.

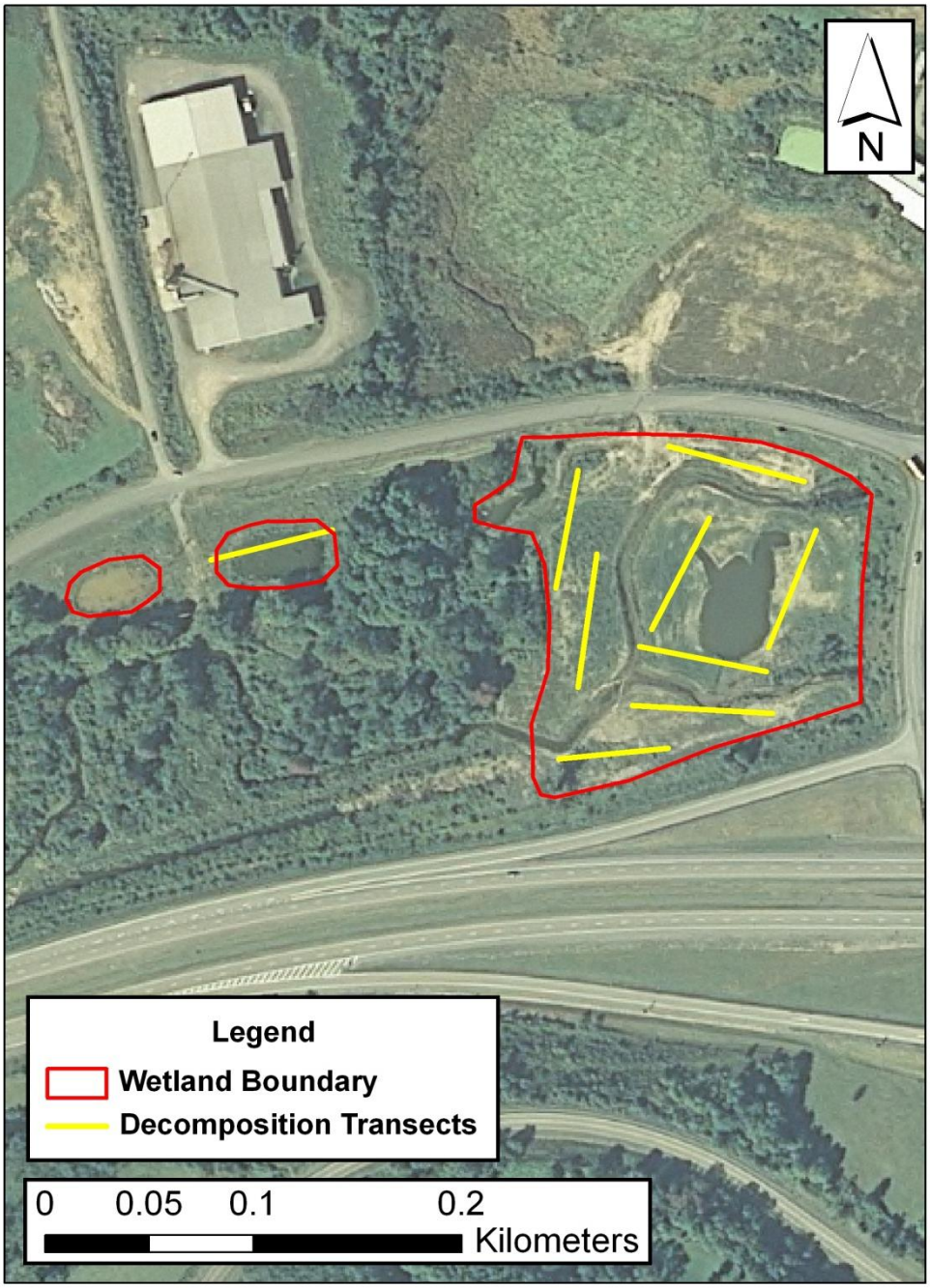

Figure 15. Aerial photograph of Hazelton mitigated wetland showing wetland perimeter and litter decomposition transects. (Aerial photograph provided by WV GIS Tech Center)

Figure 16. Photograph of Hazelton mitigated wetland, West Virginia, taken in October 2007.

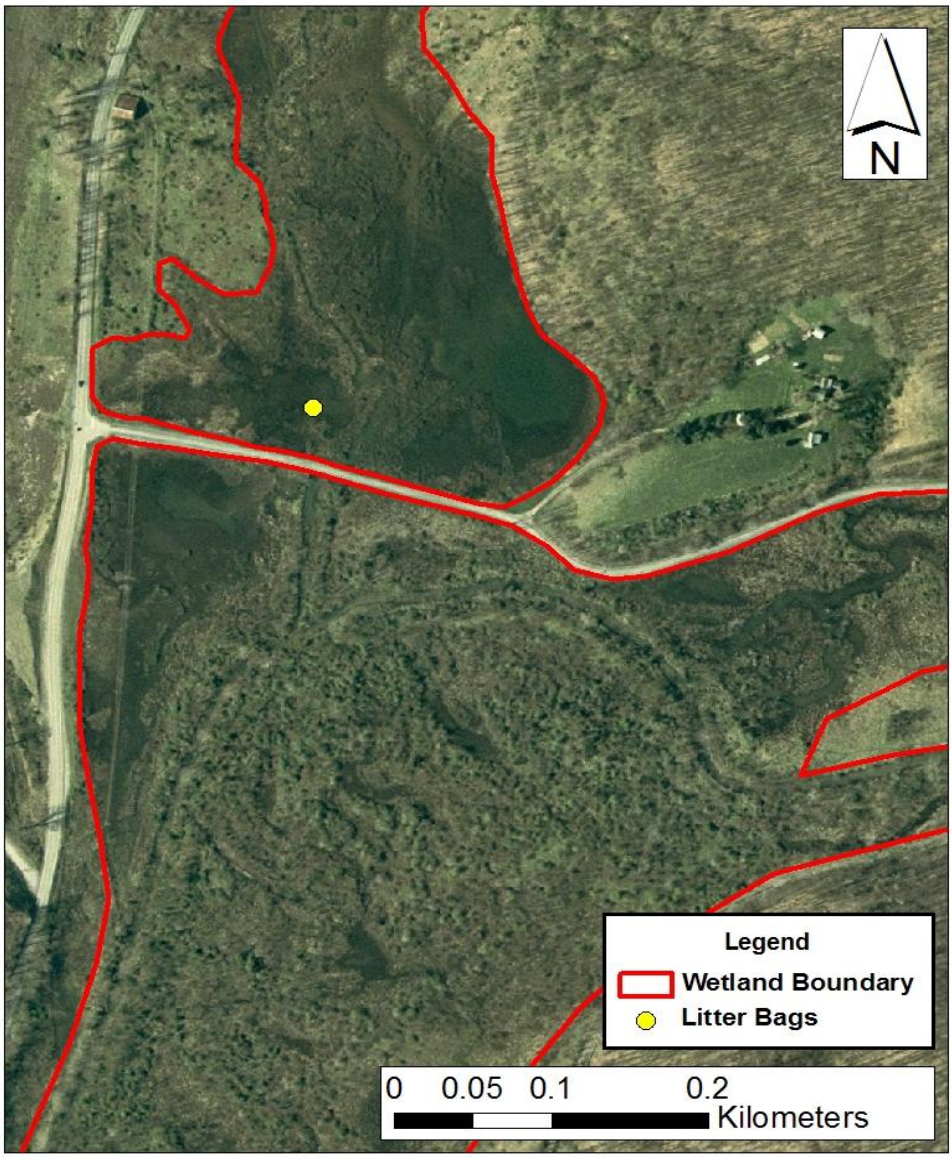

Figure 17. Aerial photograph of Muddlety reference wetland showing wetland perimeter and placement of litter decomposition bags. (Aerial photograph provided by WV GIS Tech Center)

Figure 18. Photograph of Muddlety reference wetland, West Virginia, taken in August 2009.

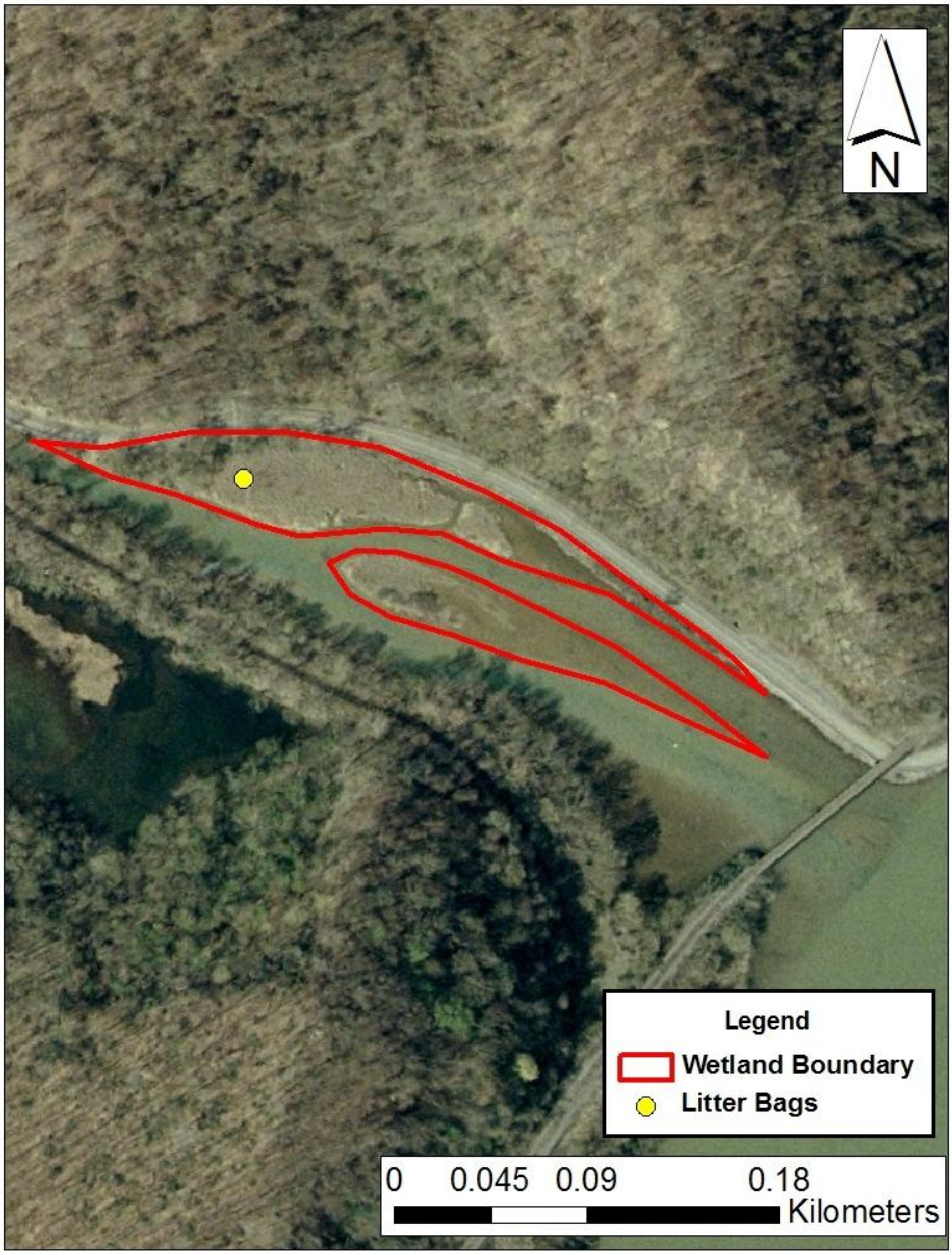

Figure 19. Aerial photograph of Indian Creek reference wetland showing wetland perimeter and placement of litter decomposition bags. (Aerial photograph provided by WV GIS Tech Center)

Figure 20. Photograph of Indian Creek reference wetland, West Virginia, taken February 2009.

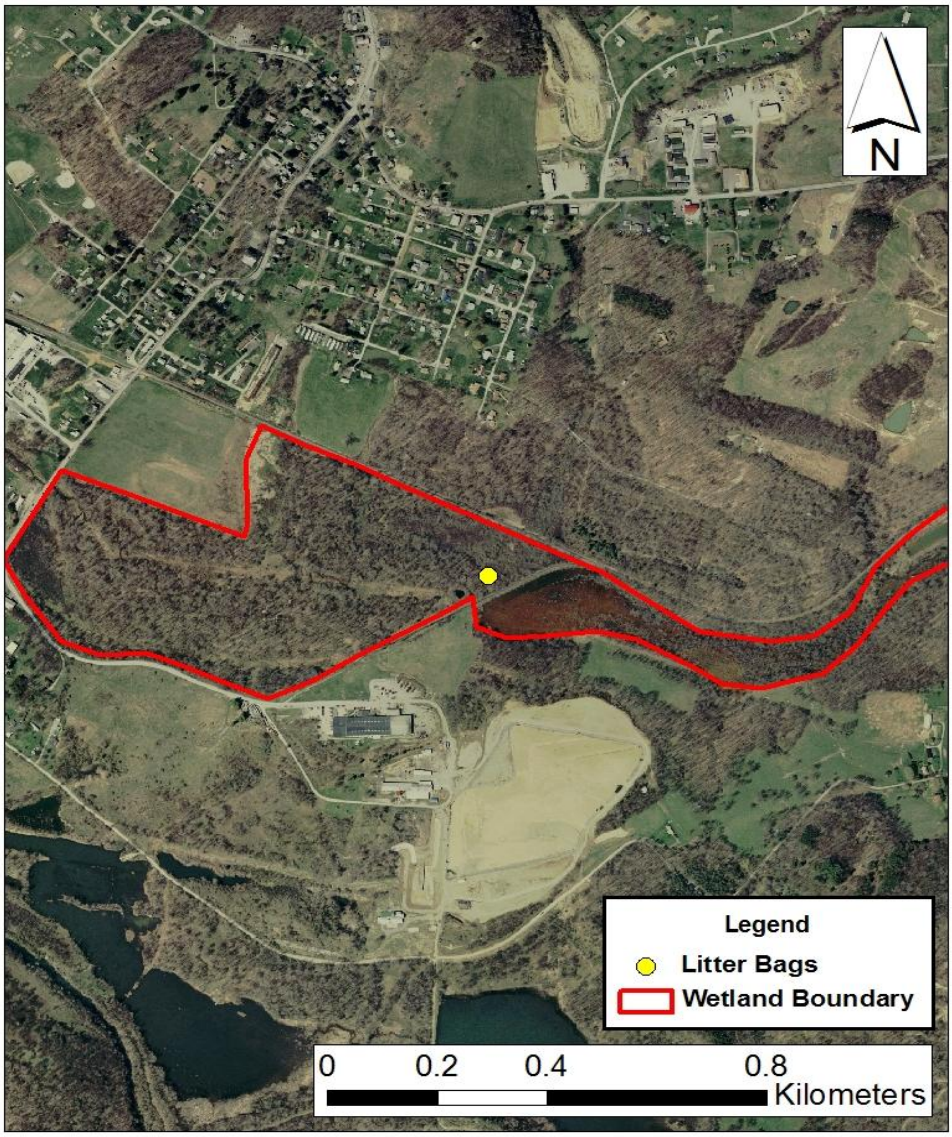

Figure 21. Aerial photograph of Kanes Creek reference wetland showing wetland perimeter and placement of litter decomposition bags. (Aerial photograph provided by WV GIS Tech Center)

Figure 22. Photograph of Kanes Creek reference wetland, West Virginia, taken in February 2009.

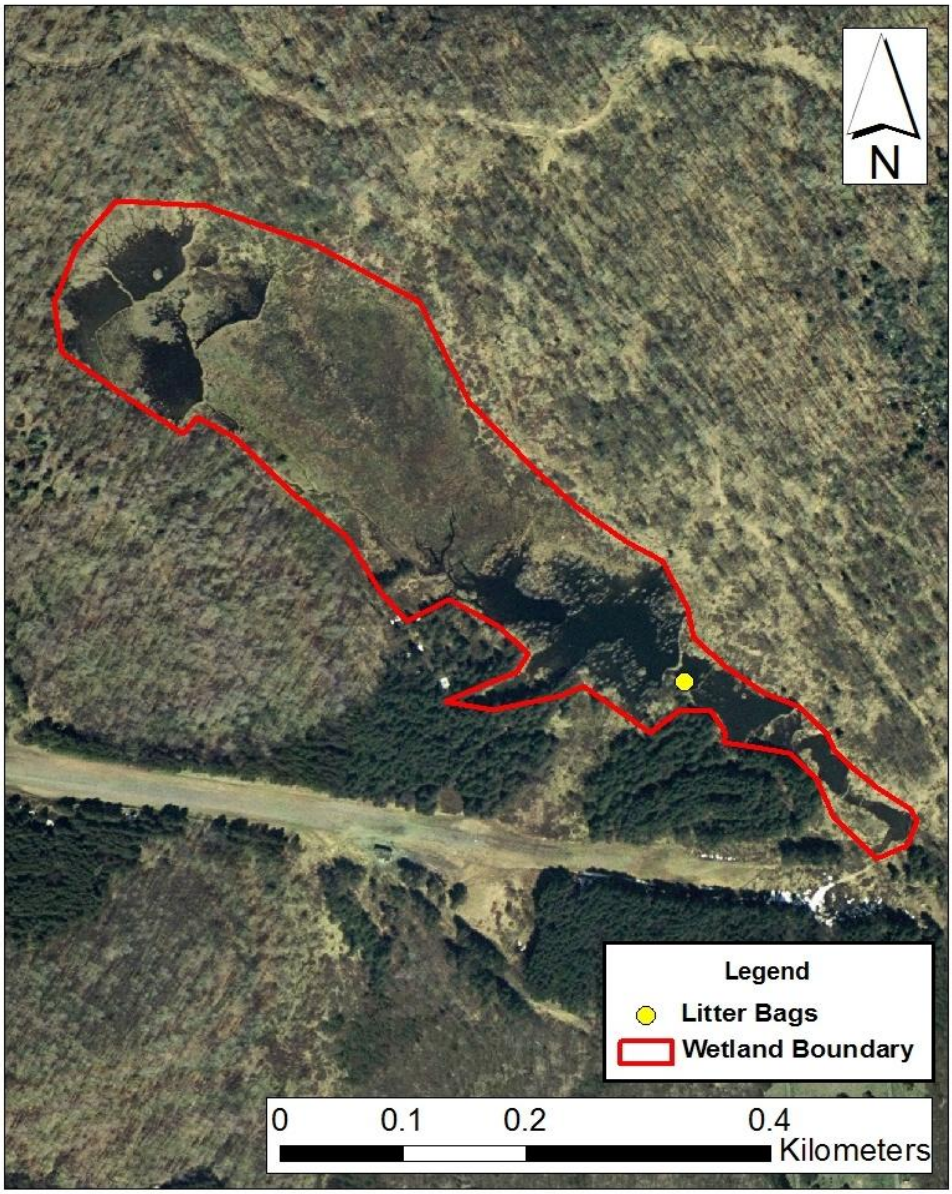

Figure 23. Aerial photograph of Thomas Airfield reference wetland showing wetland perimeter and placement of litter decomposition bags. (Aerial photograph provided by WV GIS Tech Center)

Figure 24. Photograph of the Thomas Airfield reference wetland, West Virginia, taken in August 2009.

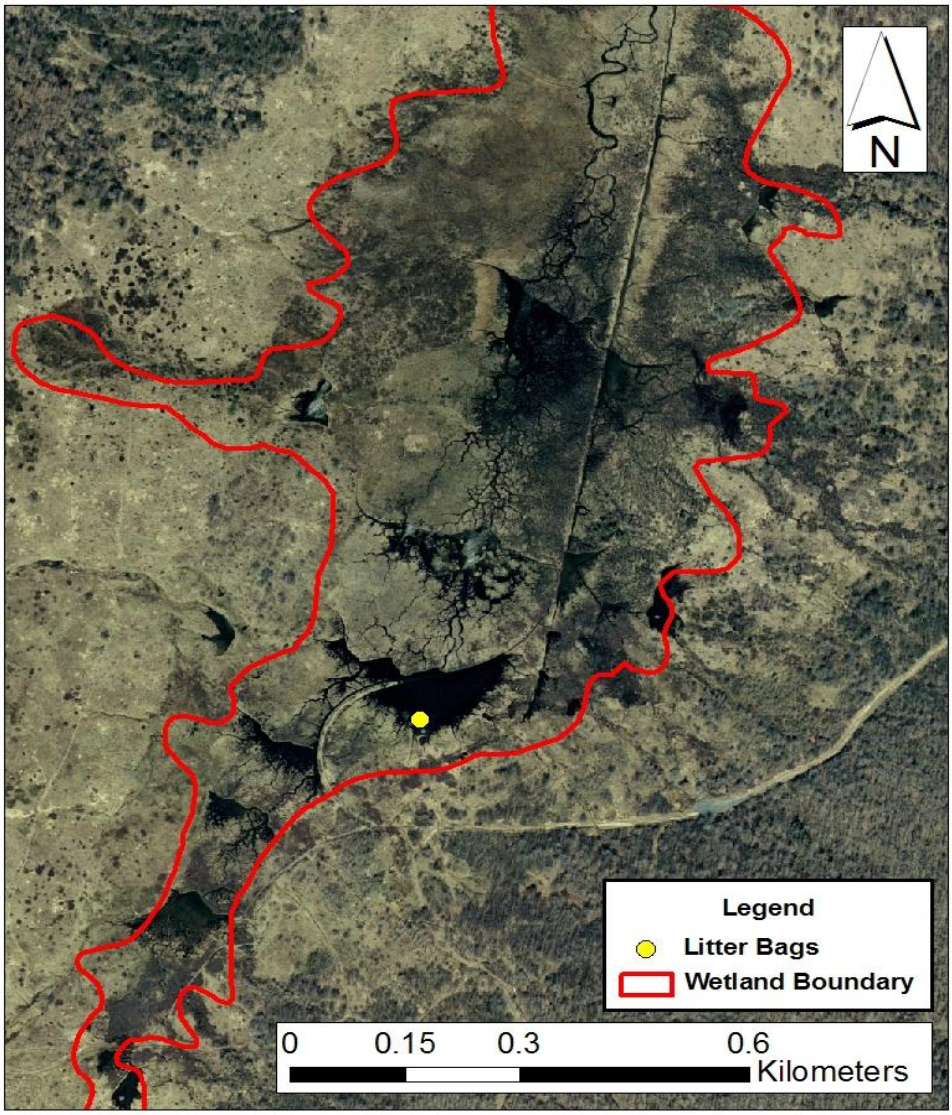

Figure 25. Aerial photograph of Glade Run reference wetland showing wetland perimeter and placement of litter decomposition bags. (Aerial photograph provided by WV GIS Tech Center)

Figure 26. Photograph of Glade Run reference wetland, West Virginia, taken in September 2008.

Figure 27. Aerial photograph of Enoch Branch created wetland showing wetland perimeter and placement of litter decomposition bags. (Aerial photograph provided by WV GIS Tech Center)

Figure 28. Photograph of Enoch Branch created wetland, West Virginia, taken in May 2008.

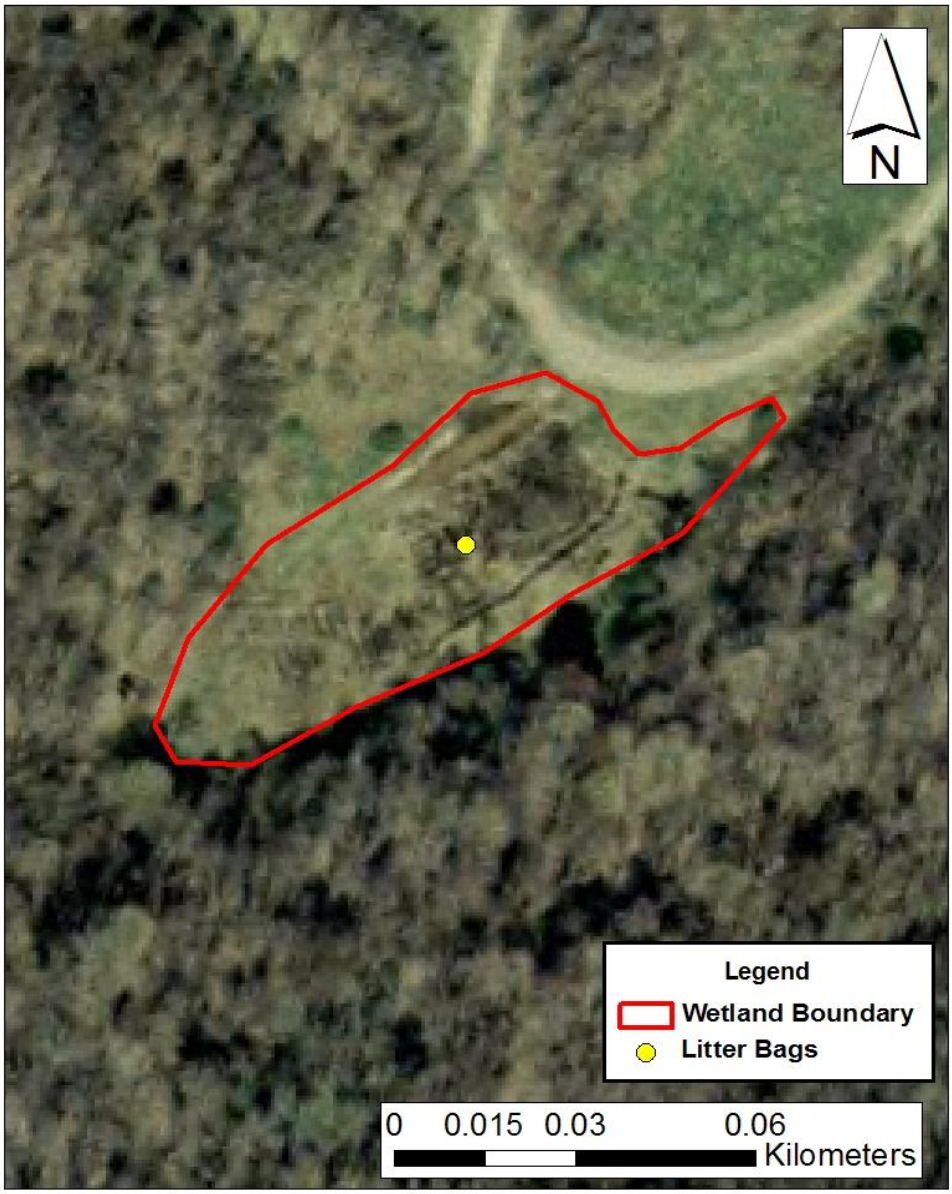

Figure 29. Aerial photograph of Pedlar Wildlife Management Area created wetland showing wetland perimeter and placement of litter decomposition bags. (Aerial photograph provided by WV GIS Tech Center)

Figure 30. Photograph of Pedlar Wildlife Management Area created wetland, West Virginia, taken in February 2009.

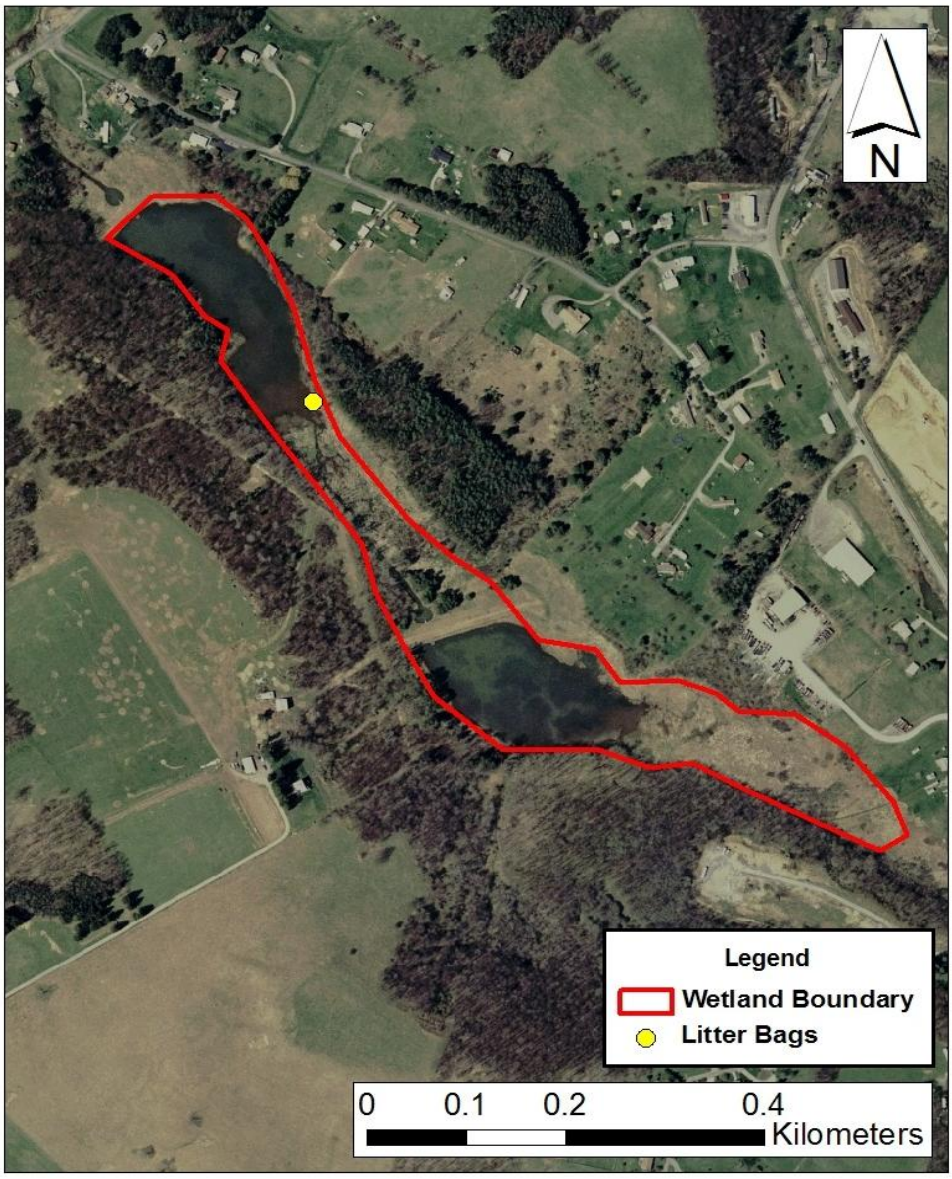

Figure 31. Aerial photograph of Upper Deckers Creek Wildlife Management Area created wetland showing wetland perimeter and placement of litter decomposition bags. (Aerial photograph provided by WV GIS Tech Center)

Figure 32. Photograph of Upper Deckers Creek Wildlife Management Area created wetland, West Virginia, taken in February 2009.

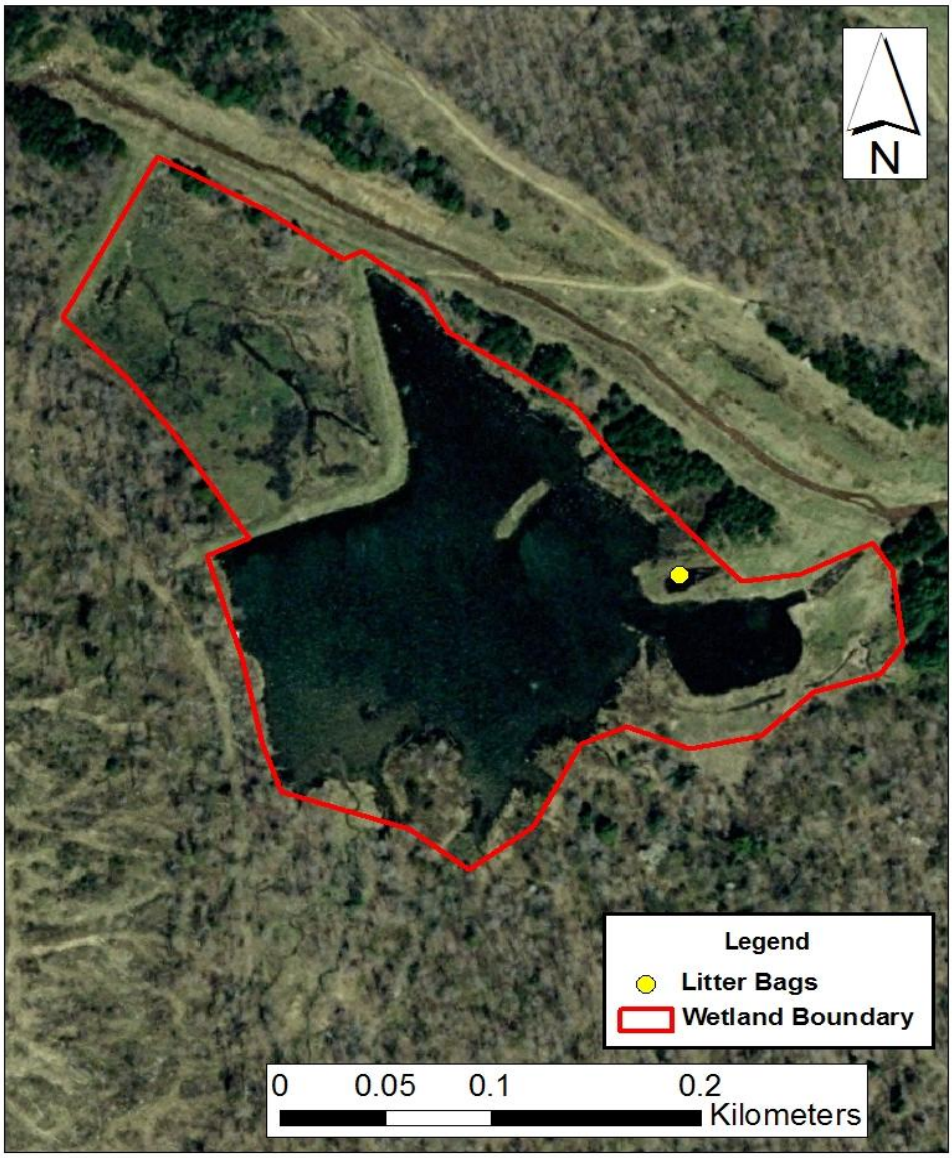

Figure 33. Aerial photograph of Elk Run created wetland showing wetland perimeter and placement of litter decomposition bags. (Aerial photograph provided by WV GIS Tech Center)

Figure 34. Photograph of Elk Run created wetland, West Virginia, taken in August 2009.

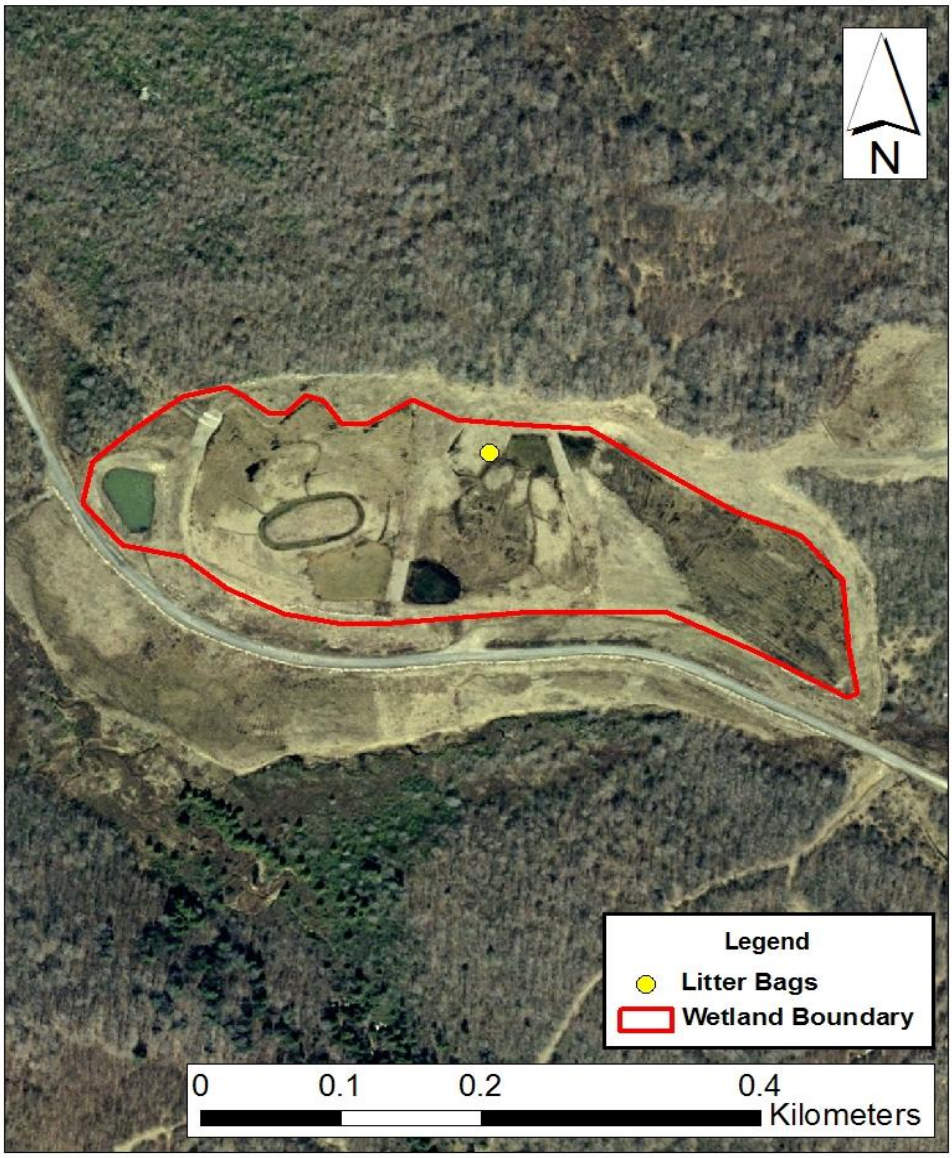

Figure 35. Aerial photograph of VEPCO created wetland showing wetland perimeter and placement of litter decomposition bags. (Aerial photograph provided by WV GIS Tech Center)

Figure 36. Photograph of VEPCO created wetland, West Virginia, taken in August 2009.

CHAPTER 2

Decomposition Trends of Five Plant Litters in Mitigated and Reference Wetlands in West Virginia, USA

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ABSTRACT

Decomposition of organic matter in wetlands is linked to numerous wetland functions, making it a useful metric to assess wetland function. We measured plant litter decomposition rates in three mitigated and three reference wetlands located in the Allegheny Mountains of West Virginia, from 2007 to 2009. Four common wetland litter species were used: broadleaf cattail (*Typha latifolia* L.), common rush (*Juncus effusus* L.), brookside alder (*Alnus serrulata* (Ait.)Willd.), and reed canary grass (*Phalaris arundinacea* L.). A fifth litter type was created from a mixture of common rush, brookside alder, and reed canary grass. Decomposition rate constant and percent mass remaining were statistically similar between mitigated and reference wetlands. Reed canary grass had the lowest percent of mass remaining at the end of the study, and was significantly lower than cattail, which was the species with the largest percent mass remaining, on 8 of the 14 collection dates. Decomposition rate constants were similar among litter types for 11 of the 14 days, with the rate for reed canary grass being significantly faster than the rate for broadleaf cattail on two of the dates and significantly faster than the rate for brookside alder and broadleaf cattail on the third date. Our study indicates that mitigated wetlands had similar function, with regards to litter decomposition rate, as reference wetlands. Additionally, reed canary grass, an invasive species, had comparable decomposition rate constants to the native common rush.

INTRODUCTION

Mitigation for lost wetlands, required under Sections 401 and 404 of the Clean Water Act, created an average annual gain of 12,900 ha of wetlands between 1998 and 2004 (Dahl 2006). Freshwater, shrub wetlands had the highest losses (4.9%) during that time period while open water ponds composed the largest portion of wetland gain (12.9%) (Dahl 2006). This offset in gain by wetland type leads to the question of whether wetland function is being created along with increased acreage, or if high-quality functional wetlands are being replaced by mitigated wetlands with reduced complexity and function. Race and Fonseca (1996) surveyed mitigation projects nationwide and found that the success rate of permit-linked mitigation projects was low overall, which agrees with other studies (Holland and Kentula 1992; Zedler and Callaway 1999; Robb 2002; Morgan and Roberts 2003), but not all (Shreffler et al. 1992; Brusati et al. 2001; Stanczak and Keiper 2004; Balcombe et al. 2005a; Álvarez and Bécares 2006).

Organic matter decomposition has long been recognized as an important function supported by wetlands (Simpson et al. 1983; Richardson 1994; Björn and Laskowski 2006). It is directly and indirectly linked to many other wetland processes. This makes it a useful tool for assessing the evolution of ecosystem function in created systems (Spieles and Mora 2007). Decomposition also is important as a driving force in nutrient cycling, supporting major flows of energy along detrital pathways in ecosystems (Brinson et al. 1981; Webster and Benfield 1986). Wetlands are especially important to ecosystem energy flow because they are the principal source of dissolved organic carbon for streams, rivers, and lakes (Dillon and Molot 1997; Mulholland 1997; Gergel et al. 1999).

Litter decomposition typically goes through three stages (Godshalk and Wetzel 1978; Brinson et al. 1981). The first phase is rapid loss of mass from leaching and occurs within 48-92

hrs of inundation (Nykvist 1962; Webster and Benfield 1986). Depending on temperature, turbulence, and the litter species, up to 29% of mass can be lost during the leaching phase (Petersen and Cummins 1974; Brinson 1977; Howard-Williams and Howard-Williams 1978). In a 31-month study, Anderson (1973) attributed up to 75% of the mass lost from sweet chestnut (*Castanea sativa* Mill.) to leaching, showing that in addition to defining the first stage, leaching can continue to contribute to weight loss through the second and third phases of decomposition. The second phase of decomposition begins as rapid leaching ends and involves the colonization of litter by microbial organisms which break down soft tissues. Depending on the time of year and stage of the second phase, bacteria (Howard-Williams and Davies 1978; Robb et al. 1979) and fungi (Barlocher and Kendrick 1974; Gessner and Chauvet 1994; Findlay et al. 2002) can drive decomposition rates. The third, and final phase, of decomposition involves mechanical fragmentation of the litter by environmental forces and invertebrates, which can contribute significantly to decomposition (Fazi and Rossi 2000; Hieber and Gessner 2002; Hutchens and Wallace 2002).

Few studies have compared decomposition at mitigated wetlands with natural wetlands, but the few that have often find significantly different rates. Atkinson and Cairns (2001) compared litter decomposition between eleven 20-year-old and six 2-year-old created wetlands in the Appalachian Mountains of Virginia and found that the older created wetlands had faster decomposition than the younger wetlands, but that both were lower than rates reported for comparable natural wetlands. Fennessy et al. (2008) found similar results when they conducted a study of 10 mitigated wetlands and 9 natural wetlands throughout Ohio. Taylor and Middleton (2004) found the opposite result, with a reclaimed coal-slurry pond in Illinois having higher decomposition rates than a reference wetland. Crawford et al. (2007) also found decomposition

of roots was substantially faster in restored Atlantic white cedar (*Chamaecyparis thyoides* (L.) B.S.P.) wetlands than in natural sites. Spieles and Mora (2007) studied decomposition rates at three created wetlands of different ages (4, 12 and 155 years) in Ohio and found that decomposition rates were highest in the 4-year-old wetland, lowest in the 12-year-old wetland and intermediate in the 155-year-old wetland. Álvares and Bécares (2006) found decomposition rates of *Typha latifolia* at a created wetland in Spain were similar to rates reported in the literature.

With so few studies and so much variance among results, it is difficult to generalize trends between mitigated and natural wetlands. To determine if mitigated wetlands in West Virginia were functioning similarly to reference sites, with respect to decomposition rate, we designed an experiment to measure decomposition rates in three of each wetland type (mitigated and natural) using five different litter types. Our objectives were to determine if decomposition rates were similar between mitigated and reference wetlands and to evaluate differences in decomposition rates between different common litter species found in West Virginia wetlands.

MATERIALS AND METHODS

Study Area

Leaf decomposition rates were measured at three created and three reference wetlands located in the Allegheny Mountain ecoregion (Bailey 1983) of West Virginia, USA (Figure 1; Table 1). The Allegheny Mountains run northeast in West Virginia, through Maryland, and into Pennsylvania.

The three created wetlands were formed by the West Virginia Division of Highways (WVDOH) to mitigate for wetland losses associated with the Corridor H and Mon-Fayette Expressway system projects. Leading Creek is 4 km south of Montrose in Randolph County. It

is a mix of palustrine unconsolidated bottom, aquatic bed, emergent persistent, scrub-shrub, and young forested wetland types (Cowardin et al. 1979). Hop sedge (*Carex lupulina* Muhl. ex Willd.), common and woodland rushes (*Juncus effuses* L.; *J. subcaudatus* var. *subcaudatus* (Engelm.) Coville&Blake), smartweed (*Polygonum hydropiperoides* Michx; *P. persicaria* L.), rice cutgrass (*Leersia oryzoides* (L.)Sw.), and brookside alder (*Alnus serrulata* (Ait.)Willd.) are dominant species. The Sugar Creek wetland is located 3 km southwest of Meadowville, Barbour County. It is comprised of multiple wetland cells and had palustrine aquatic bed, emergent persistent, and scrub-shrub types. Reed canary grass (*Phalaris arundinacea* L.), wool grass (*Scirpus cyperinus* (L.)Kunth), woodland rush, American burreed (*Sparganium americanum* Nutt.) and brookside alder are all dominant species. The Hazelton wetland is located at Exit 29 on Interstate 68. It is made up of one large wetland cell and two smaller cells (unconnected portions of a single wetland project) and is primarily palustrine unconsolidated bottom, aquatic bed, and emergent types. Broadleaf cattail (*Typha latifolia* L.), common and narrowpanicle rush (*J. brevicaudatus* (Engelm.) Fernald), white and red clover (*Trifolium repens* L.; *T. pretense* L.), and beggar-tick (*Bidens sp.*) are all dominant species.

The three reference wetlands were chosen based on their proximity to mitigated sites; similarity in elevation, size, and wetland classification; and their relative degree of disturbance. The Upper Deckers Creek wetland is located about 1 km southwest of Masontown, Preston County. The wetland is an oxbow wetland off Deckers Creek and is comprised mainly of palustrine aquatic bed, unconsolidated bottom, emergent persistent, and scrub-shrub wetland types. Reed canary grass, cowlily (*Nuphar lutea ssp. advena* (L.)Sm.(Ait.)), marsh purslane (*Ludwigia palustris* (L.)Ell.), and buttonbush (*Cephalanthus occidentalis* L.) are dominant species. The Meadowville wetland is located at Meadowville, Barbour County. The site was

historically grazed, but became too moist and grazing was stopped about 40 years ago. It is comprised of palustrine emergent persistent, scrub-shrub, and young forested types, which are dominated by cattail, tussock sedge (*Carex stricta* Lam.), rice cutgrass, blue-joint grass (*Calamagrostis canadensis* var. *canadensis* (Michx.)Beauv.), and brookside alder. The Bruceton Mills wetland is located about 2.9 km north of Bruceton Mills, Preston County. The site was the remnant of a beaver (*Castor canadensis*) pond and was comprised mainly of palustrine emergent persistent and scrub-shrub habitat types. Reed canary grass, rice cut grass, cattail and brookside alder are dominant species.

In general, the mitigated wetlands have more open water and ponded areas than the reference sites, and the reference sites tend to have more scrub-shrub areas than the mitigated sites. Leading Creek is the only mitigated site with a large portion of scrub-shrub and young forest. All wetlands have some level of disturbance on their edge in the form of roads, grazing, or cultivated land.

Decomposition (Litterbag) Procedures

Decomposition rates were measured using the litter bag method (Benfield 1996). We chose four litter types based on common dominant species at mitigated and reference sites in West Virginia (Balcombe et al. 2005b, along with unpublished vegetation surveys) and collected them in September and October of 2007. Litter included broadleaf cattail, common rush, brookside alder, and reed canary grass. Some studies have shown that litter mixes can have non-additive decomposition rates compared to single species (Gartner and Cardon 2004), so a fifth litter type was created with a mix of common rush, brookside alder, and reed canary grass. The ratio of species was 3:2:1 reed canary grass : common rush : brookside alder in an attempt to mimic ratios present in the wetlands (Balcombe et al. 2005b).

Many species of wetland vegetation have a standing dead period, during which some fungal colonization and decomposition can occur before it falls to the ground (Kuehn et al. 1999). To help ensure similar vegetation conditions, reed canary grass, common rush, and broadleaf cattail leaves and stems were clipped and collected as they senesced, but while still standing (Davis and van der Valk 1978; Hill 1985; Marsh et al. 2000; Bedford 2005). Brookside alder leaves were collected mechanically with a leaf blower (STIHL model SH 85 D Shredder Vacuum/Blower; Virginia Beach, Virginia) reversed to suck leaves into the tube. Brookside alder leaves that were not intact and any material other than alder leaves were discarded. Several studies have shown that nutrient dynamics and litter quality can influence decomposition (Aerts and de Caluwe 1997; Baker et al. 2001; Fennessy et al. 2008). To minimize differences in litter quality, each species was collected from only one area in a single wetland. Brookside alder and broadleaf cattail were collected from Meadowville, reed canary grass was collected from Sugar Creek, and common rush was collected from Leading Creek. All litter was air-dried for a minimum of 1 wk before being weighed and bagged.

Litter bags were constructed from 1.27 mm vinyl-coated fiberglass window mesh (Benfield 1996). The litter bags had external dimensions of 20 x 20 cm and were constructed with one folded side and three sides heat sealed. To reinforce the melted sides, bags were stapled shut at 5-cm intervals with stainless steel staples (Deghi et al. 1980). A small sealed plastic bag containing a plastic tag with a unique identification code was placed in each litter bag, along with the litter, to allow final masses to be matched with initial masses (Davis and van der Valk 1978; Vargo et al. 1998). For the single species litter bags with broadleaf cattail, common rush, and reed canary grass, 20 g of litter was placed in each bag. For brookside alder, 20 g would have required the litter to be crushed, so only 12 g of litter was used. The mixed

litter samples also had about 20 g (brookside alder [3.3 g], common rush [6.7 g], and reed canary grass [10 g]).

Nine transects were established using stratified sampling (Taylor and Middleton 2004), to represent aerial proportions of different environmental conditions, as represented by major vegetation communities, within each wetland (e.g., wetter portions of a wetland, dominated by *Polygonum sp.* and comprising 1/3 of the wetland by acreage, had 3 transects placed in it based on the proportion of wetland dominated by *Polygonum sp.*). Ten wooden stakes were installed at 7.5 m intervals along each transect and one type of each litter bag, five bags total, was attached to the base of each stake with 0.5 m lengths of nylon fishing line (Battle and Golladay 2001; Anderson and Smith 2002). Litter bags were placed prostrate on bare ground or on top of any existing litter to mimic natural litter deposition. If the stake was in standing water, the litter bag was first dunked to inundate the surface and minimize any hydrophobic effect the mesh might have contributed and then allowed to float or sink unimpeded.

Ninety of each type of litter bag (nine transects of 10 stakes) were placed for a total of 450 litter bags in each wetland and 2,700 litter bags overall. Six replicates of each litter type were retrieved the same day the bags were placed in the field to calculate the loss of mass due to handling (Benfield 1996). Four replicates were then retrieved on 14 different dates: 7 d (1 wk), 21 d (3wk), 35 d (5 wk), 49 d (7 wk), 77 d (11 wk), 119 d (17 wk), 168 d (24 wk), 224 d (32 wk), 294 d (42 wk), 364 d (52 wk), 455 (65 wk), 546 d (78 wk), 637 d (91 wk), and 728 d (104 wk). The four replicates were sampled by collecting all litter bags present at four randomly chosen stakes within a wetland. Stratified random sampling, with transects as strata, was used to ensure that two samples were never pulled from the same transect during a single, or two consecutive, collection dates.

When bags were collected, they were gently brought to the surface if submerged, then excess sediment and plant material was removed from the outside of the litter bag before they were placed in individual plastic bags and transported back to the lab on ice (Benfield 1996). Once back at the lab, any additional debris adhering to the outside of the bags was removed before it was opened. Litter was carefully removed from the interior of the bag and sediment was rinsed off. The litter was then oven-dried (65° C) for about 1 wk until a constant mass was reached (Morris and Lajtha 1986; Verhoeven and Arts 1992; Lockaby et al. 1996), the mass was recorded, and the litter was ground to a powder in a Wiley mill with a 2-mm mesh screen (Thomas® Scientific Wiley Cutting Mill model ED-5; Philadelphia, Pennsylvania). Three subsamples of 250 mg of powder were placed in an aluminum pan and ashed at 550^{o} C for 30 minutes. Once a sample cooled, it was weighed and the proportion of mass remaining was subtracted from the original 250 mg, averaged across the three samples, and used to calculate the ash-free dry mass (AFDM) of the litter bag. The AFDM was used during analysis to minimize error from sedimentation.

Data Analysis

Litter decomposition was the dependent variable and was analyzed using two different models. The first model was the percent of mass remaining. The second model was the exponential decay model, which expresses the decomposition rate as constant *k*: $y_t / y_o = e^{-kt}$, where y_t is the AFDM at time *t* (yr) and y_o is the initial AFDM (Olson 1963; Brock et al. 1985). In this model, *k* is expressed as yr^{-1} and represents the instantaneous mass loss rate. We averaged replicate bags from each wetland prior to analysis. Normality was tested using Program PROC UNIVARIATE (SAS® v9.1.3) and found to be violated for both proportion of mass remaining and *k*, therefore data were rank transformed (Conover and Iman 1981).

Analysis of variance (ANOVA) was run using Program PROC MIXED (SAS® v9.1.3), with wetland defined as a random effect, to test the significance of wetland type (n = 2), litter type (n=5), collection date (n=14), and their interactions. A series of models were run using differing covariance structures to determine which had the best fit, then the model with the lowest Akaike Information Criteria (AIC) value was chosen. AIC values represent the goodness of fit for a model, with lower values indicating a better fit, while penalizing models with more parameters. Differences in mean decomposition rates, at the wetland level, were compared using Tukey's least-square means. Tests were considered significant at $p < 0.05$.

RESULTS

Wetland Types

Overall plant litter decomposition, over the 728-d study, was similar (Table 2) between mitigated and reference wetlands for percent mass remaining and *k* (Table 3). Though not statistically significant, by 224 d the average mass of litter in reference wetlands was lower than mitigated wetlands and remained so throughout the rest of the study (Figure 2). This trend is matched with a slightly higher *k* in reference wetlands, signifying a slightly higher rate of decomposition (Figure 3). The highest *k* values, 2.069 and 1.779 yr^{-1} for reference and mitigated wetlands respectively, were observed during the first collection date at 7 d. They then continued to fall until they reached 0.364 and 0.353 yr^{-1} around 165 d. After that point *k* values rose again and roughly leveled off with an average around 0.590 and 0.506 yr^{-1}, for reference and mitigated wetlands respectively, from 290 d through the end of the study. Figure 2 also shows decomposition trends, with two plateaus that begin at 77 and 365 d and are captured by two collection dates in both mitigated and reference wetlands. The first spans 41 d and begins near the end of February, and the second spans 91 d and begins in December.

Litter Types

A significant interaction between litter type and collection date was found for both percent of mass remaining ($F_{52,208} = 1.70$, $P = 0.005$) and decomposition rate constant ($F_{52,208} = 0.59$, $P = 0.001$). Therefore, analyses between litter types were examined within each collection date (Appendix A). For every collection date, except 364 d, reed canary grass had the lowest percent of mass remaining, and for 11 of the 14 dates the mixed litter bags had the second lowest (Figure 4). Brookside alder and common rush generally had the third and fourth lowest percent of mass remaining respectively, but then switch ranks around 224 d. For every collection date except 21 and 637 d, broadleaf cattail had the largest percent of mass remaining.

Through 49 d there were no significant differences between percent of mass remaining for any of the litter types. However by 77 d, reed canary grass was significantly lower than broadleaf cattail and remained so through the rest of the study, with the exceptions of 364 and 728 d when their masses were similar. At 119 d, cattail had a significantly higher mass than all other species except common rush, and at 224 and 637 d, cattail had a significantly higher mass than reed canary grass and the mixed litter. At 546 d brookside alder had a significantly higher percent of mass remaining than reed canary grass and at 637 d brookside alder had significantly higher mass than reed canary grass and the mixed litter. At the end of the study, all litter types were similar.

For measures of *k*, all species of litter had their highest rate of decomposition measured in the first collection period at 7 d, except broadleaf cattail that had its highest decomposition measured at 21 d (Figure 5, Appendix B). Broadleaf cattail had the lowest *k* for 11 of the 14 collection dates and the lowest mean, minimum (0.121 yr^{-1}), and maximum (1.079 yr^{-1}) of all species. Reed canary grass had the highest *k* for every collection period, except 364 d, and had

the highest mean, minimum (0.534 yr^{-1}), and maximum (2.790 yr^{-1}) of all species. The mixed litter had the second highest *k* for 11 of the 14 collection dates, the second highest mean and minimum (0.407 yr^{-1}), and the third highest maximum (1.960 yr^{-1}) of all species. Decomposition rate constants were similar for all litter types for all collection dates except three. At 224 and 294 d, reed canary grass (224 d [0.773 yr-1]; 294 d [0.801 yr^{-1}]) and the mixed litter (224 d [0.718 yr^{-1}]; 294 [0.735 yr^{-1}]) were significantly higher than broadleaf cattail (224 d [0.0271 yr^{-1}]; 294 d [0.340 yr^{-1}]). At 637 d reed canary grass (0.724 yr^{-1}) was significantly higher than brookside alder (0.336 yr^{-1}) and broadleaf cattail (0.346 yr^{-1}).

DISCUSSION

Decomposition in Mitigated and Reference Wetlands

Our findings indicate that decomposition rate constants are similar between mitigated and reference wetlands. This suggests that functional equivalence may have been reached at these sites after a relatively short time (2-12 years after construction). Some studies have shown 10 to 25 years are needed for created wetlands to function similarly to natural sites (Mitsch and Wilson 1996; Simenstad and Thom 1996; Craft et al. 1999; Gutrich and Hitzhusen 2004), which places our wetlands on the young end of that timeline. Few studies have been performed comparing decomposition in mitigated and reference wetlands, but the majority that have been performed found differing rates (Atkinson and Cairns 2001; Taylor and Middleton 2004; Spieles and Mora 2007; Fennessy et al. 2008). Our results agree with Álvarez and Bécares (2006) who found similar decomposition rates when they compared broadleaf cattail in a constructed wetland in Spain with documented rates from natural wetlands. Our results also agree with Balcombe et al. (2005a) who looked at biotic indicators of wetland function in West Virginia mitigated wetlands,

including three of the wetlands used in this study, and found that they adequately supported ecological communities.

Our sample size for this study was small, with only three mitigated and three reference wetlands, but we are confident in our results because of the large number of samples collected, 280 per wetland and 1,680 total, and the relatively consistent trends observed over the two year study. Most decomposition studies allow leaf litter to decompose for a year or less, but our study observed trends in the second year, specifically that *k* levels off to a stable value, which shorter studies would have missed.

Litter Types

Broadleaf cattail has been studied extensively because it is a ubiquitous wetland species. Our *k* values for broadleaf cattail had a minimum that was lower than rates reported in other studies, but most values fell within the range reported (0.31 – 1.57 yr^{-1}) in other studies (Findlay et al. 1990; Álvarez and Bécares 2006). The standard error for broadleaf cattail samples was often higher than most other litter types which, in part, is due to initial drying of the litter. All litter was air dried, weighed, and bagged in the same manner. A subset of samples were then dried and ashed to calculate a correction factor for initial leaf masses to account for handling loss and conversion to ash-free dry masses. For the other four litter types, that correction factor ranged from 0.839 to 0.951, but for broadleaf cattail the correction factor ranged from 0.688 to 0.770. We attributed this large disparity to the broadleaf cattail not drying as well as the other litter types. When the initial litter samples were oven-dried and ashed, a larger proportion of initial weight was lost as water. This led to some samples having corrected initial weights equal to or less than the final weights for early sample dates and probably created deflated *k* values for cattail. Larger initial samples to calculate correction factors, longer periods of drying, or drying

under slight heat are possible corrections for this problem in future studies. Most studies do not report correction factors or implications of incomplete drying on results, but may contain similar errors in their results.

Brookside alder began the study with the second highest *k* value at 7 d, but ended being grouped with broadleaf cattail as having the second highest percent of mass remaining after 728 d. Alder are nitrogen-fixing woody plants and therefore have high amounts of nitrogen in their leaves. Nykvist (1962) looked at *Alnus glutinosa* (L.) Gaertn. leaching and decomposition under various conditions and found that the alder leaves were leached more easily than *Quercus robur* (L.) or *Fagus silvatica* (L.) leaves and that this contributed to faster decomposition rate constants. This likely explains the high *k* seen early in the study. Once the initial soluble nutrients were gone, decomposition rate constants decreased and were more comparable to the other species during the second phase of decomposition. During the third phase, the alder *k* value dropped again to rates similar to cattail. We suspect this is caused by alder having higher lignin content, similar to broadleaf cattail. By the end of the study, a noticeable proportion of alder leaves had their nutrient-rich, soft blades completely decomposed, but still had mostly intact petioles and veins. These tougher parts were more difficult to fragment and led to a lower average *k* during the third phase of decomposition.

We could not find any wetland studies that reported alder decomposition, but we found stream studies that reported values of 0.908-2.701 yr^{-1} for *A. glutinosa* (Chauvet 1987; Scheiring 1993; Pereira et al. 1998). Our rates for brookside alder were lower than the reported rates, but this may have been due to higher rates of mechanical fragmentation in lotic systems compared to lentic ones and differences in biotic communities.

Common rush had *k* values comparable to those reported in previous studies (0.36-2.04 yr^{-1}), but makes the minimum in our study a bit low (Kittle et al. 1995; Kuehn et al. 2000). Kittle et al. (1995) also looked at common rush decomposition and compared it to broadleaf cattail decomposition rates in three wetlands receiving acid mine drainage in West Virginia. They found that cattail decomposition rates were significantly higher over 155 d than common rush in each of their wetlands. In our study, common rush and broadleaf cattail had similar *k* values for all collection dates. Kittle et al. (1995) also found faster decomposition rates for both species than were measured in this study, despite pH impeding decomposition.

Our decomposition rate constant for reed canary grass were low compared to Hough and Cole (2009), who measured a range of 1.55-4.19 yr^{-1} at 14 wetlands in Pennsylvania and Kao et al. (2009) who measured 68% mass remaining at the end of 150 d in New York. Kao et al. (2009) studied common rush and reed canary grass and found no significant difference between decomposition rate constants, which agrees with our study. These rates are of special interest since reed canary grass is an invasive grass that aggressively colonizes wetlands. Several studies have shown that exotic species can change soil properties (Ehrenfeld 2003; Vanderhoeven et al. 2005; Dassonville et al. 2008) and differing decomposition rates could potentially be another way for invasive species to influence wetland function.

No other study that we found used a similar litter mix, so there are no comparable rates for our mixed litter samples. Wardle et al. (1997) looked at decomposition of 102 litter combinations made from 32 species and found that litter mixes had large and unpredictable effects that could both increase or decrease litter decomposition rate. Gartner and Cardon (2004) reviewed 30 decomposition studies that incorporated litter mixes and found that 67% had non-additive patterns of mass loss, with some studies finding mass loss 65% higher in mixes than

single species litter. No increased decomposition rates, due to mixing, were measured in this study. The mixed litter had statistically similar decomposition rates to the other four species.

Phases of Decomposition

The trend of decomposition we observed is typical of the three phases observed in past studies (Godshalk and Wetzel 1978; Brinson et al. 1981). The *k* value at 7 d was close to or exceeded double the value of any later date for reed canary grass, brookside alder, common rush and the mixed litter, suggesting rapid mass loss from leaching. Only broadleaf cattail had its highest decomposition rate at 21 d rather than 7 d and may be due, in part, to the fact that broadleaf cattail was the only litter that still had bags floating at 7 d. The lack of complete submersion until after 7 d could have postponed or extenuated the leaching phase and contributed to the higher *k* at 21 d. The second phase of decomposition appears to have continued until between 168 and 224 d, at which point decomposition began to proceed at a constant rate. The third phase of decomposition involves mechanical fragmentation of the litter by environmental forces and invertebrates and may explain the dip in *k* between 77 and 224 d. It is possible that there was a transition period between the end of the second phase, when fungi and some invertebrate functional feeding groups began to decline (Gingerich 2010: Chapter 5), and the point where oligochaetes and third phase decomposers reached adequate numbers to drive decomposition, sometime after 224 d. Between 224 and 728 d, *k* was fairly steady with a small amount of fluctuation that was probably seasonal and due to environmental factors such as temperature and hydrology (Morris and Lajtha 1986; Middleton et al. 1992; Gingerich 2010: Chapter 4). Lower *k* values were measured in the winter and early spring, when temperatures were low and sub-freezing conditions may have halted some biological processes.

Conclusions

Though past studies have found that permit-linked mitigation projects have a low overall success rate nationwide, wetland function, with regards to litter decomposition, is comparable between the reference and mitigated wetlands studied. Additionally, reed canary grass, an invasive wetland grass, had a similar decomposition rate and trend to the other native species. Our mixed litter bags showed no apparent synergistic decomposition rates compared to single species bags. Future monitoring efforts to determine mitigation success need to focus on the replacement of wetland function in addition to wetland acreage, and monitoring decomposition is one promising way of achieving this goal.

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Table 1. List of three mitigated and three reference wetland study sites in West Virginia, including site name, year constructed, size (ha), elevation (m above sea level), Universal Transverse Mercator (UTM) coordinates, basin, and watershed, 2007-2009.

Site name	Year	Size (ha)	Elevation (m)	UTM Y	UTM X	Basin	Watershed
Mitigated Sites							
Leading Creek	1995	16.99	600	4321563	602550	Tygart Valley	Leading Creek
Sugar Creek	1995	10.95	490	4328850	591470	Tygart Valley	Laurel Creek
Hazelton	2006	2.68	560	4390990	625708	Cheat	Little Sandy Creek
Reference Sites							
Meadowville	N/A	11.67	480	4330920	593940	Tygart Valley	Laurel Creek
Upper Deckers Creek	N/A	2.10	515	4377282	602193	Monongahela	Upper Deckers Creek
Bruceton Mills	N/A	1.41	515	4393348	615433	Cheat	Big Sandy Creek

Table 2. Analysis of variance results for decomposition, expressed as percent of ash-free dry mass remaining after 728 days and average decomposition rate constant *k* (yr^{-1}), in six wetlands (3 mitigated, 3 reference) in the Allegheny Mountains of West Virginia, December 2007 to December 2009. Wetland type (mitigated, reference), date (n=14), litter type (brookside alder, reed canary grass, common rush, broadleaf cattail, mixed litter), and their interactions were all tested.

		% Mass Remaining		*k*	
Effect	d.f.	F Value	P Value	F Value	P Value
Wetland (n=2)	1,4	2.93	0.162	2.39	0.197
Date (n=14)	13,52	249.88	< 0.001*	13.75	< 0.001*
Wetland*Date	13,52	0.93	0.533	1.01	0.452
Litter (n=5)	4,16	24.71	< 0.001*	17.75	< 0.001*
Wetland*Litter	4,16	0.39	0.814	0.59	0.673
Litter*Date	52,208	1.70	0.005*	1.87	0.001*
Wetland*Litter*Date	52,208	0.52	0.997	0.73	0.914

* Significant (α = 0.05)

Table 3. Mean, standard error (S.E.), and analysis of variance (ANOVA) results for decomposition of five litter types, expressed as percent of ash-free dry mass remaining after 728 days and *k* (yr^{-1}), in six wetlands (three mitigated and three reference) in the Allegheny Mountains of West Virginia, December 2007 to December 2009. P values were calculated using analysis of variance (ANOVA) to compare litter decomposition in mitigated and reference wetlands.

Litter	Reference		Mitigated		Overall		F value	P value
	Mean	S.E.	Mean	S.E.	Mean	S.E.	(d.f. = 1,4)	(α = 0.05)
Mass Remaining								
Brookside Alder	40.9	4.30	47.7	2.34	44.3	2.67	2.28	0.206
Reed Canary Grass	24.5	3.39	28.4	2.57	26.5	2.09	0.09	0.777
Common Rush	27.5	3.61	34.1	4.32	30.8	2.93	1.20	0.335
Broadleaf Cattail	43.6	6.49	48.0	8.25	45.8	4.79	0.00	0.974
Mixed Litter	24.4	2.59	32.1	2.67	28.3	2.39	1.03	0.367
Overall	32.2	4.17	38.1	4.09	35.1	4.12	2.93	0.162
Decomposition Rate Constant (*k*)								
Brookside Alder	0.744	0.196	0.603	0.122	0.673	0.158	1.48	0.291
Reed Canary Grass	0.942	0.163	0.898	0.143	0.920	0.153	0.29	0.619
Common Rush	0.634	0.075	0.584	0.093	0.609	0.083	1.05	0.363
Broadleaf Cattail	0.344	0.048	0.459	0.089	0.402	0.060	0.14	0.723
Mixed Litter	0.862	0.136	0.678	0.071	0.770	0.102	0.38	0.572
Overall	0.705	0.104	0.644	0.072	0.675	0.086	2.39	0.197

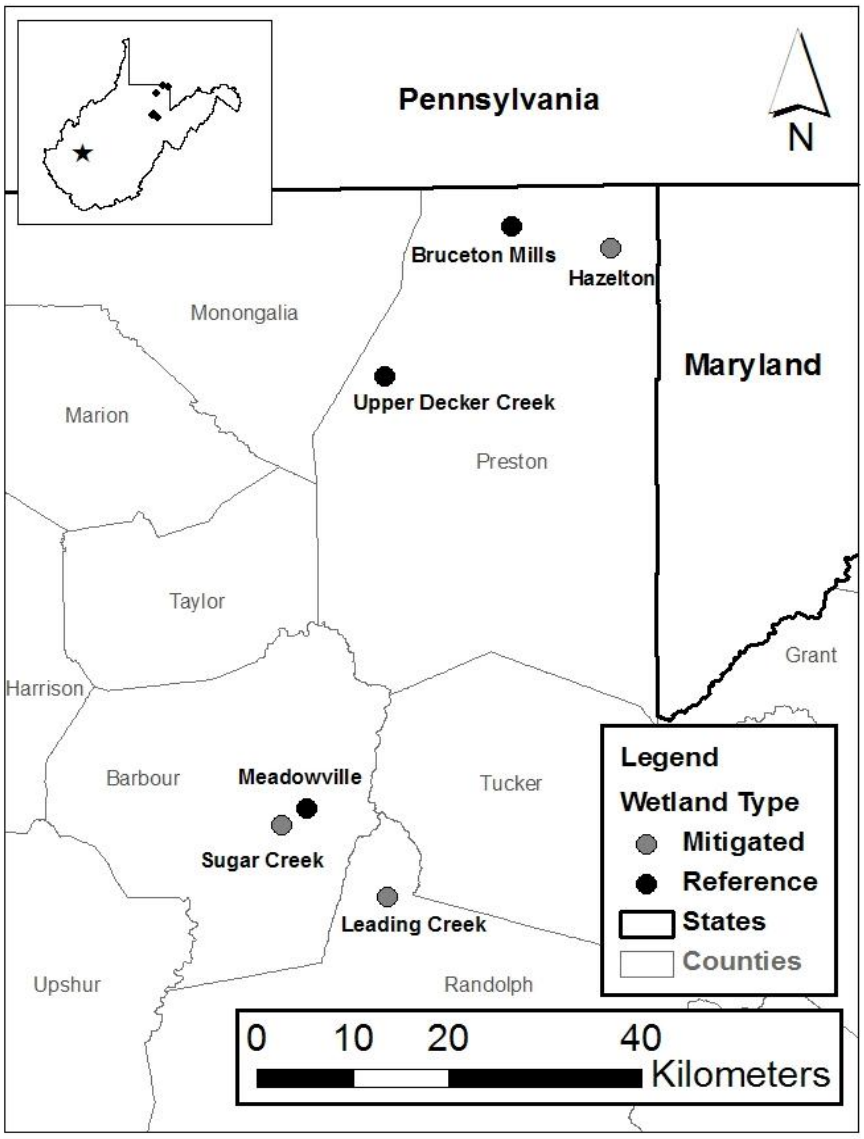

Figure 1. Six study sites, comprised of three mitigated and three reference wetlands, in the Allegheny Mountain region of West Virginia, USA, 2007-2009.

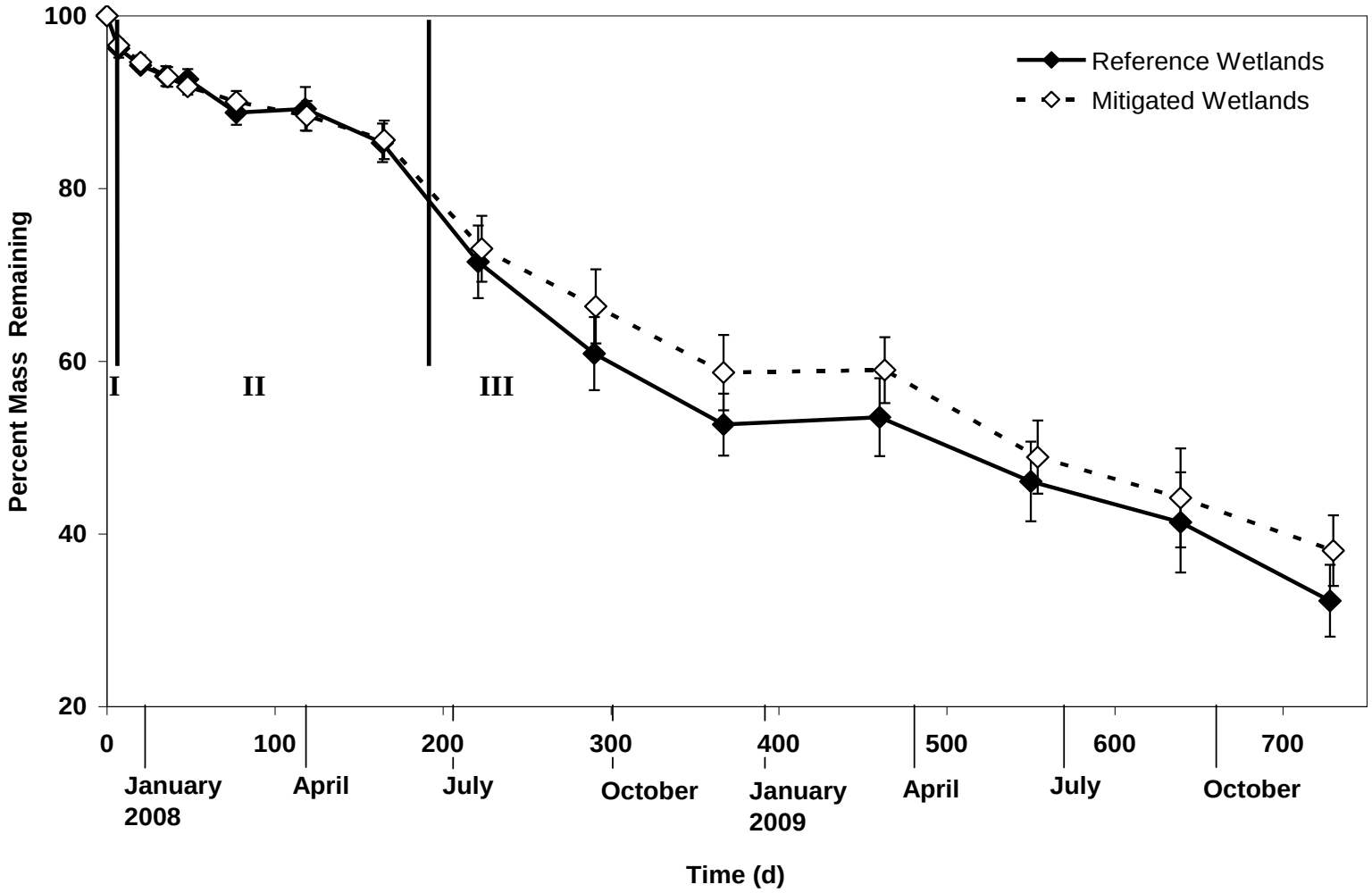

Figure 2. Mean (± S.E.) percent ash-free dry mass remaining for three mitigated and three reference wetlands in the Allegheny Mountain region of West Virginia, December 2007 through December 2009. The transitions between the first (I), second (II), and third (III) stages of decomposition are identified by vertical lines. The first stage is characterized by the rapid leaching of nutrients, the second phase is characterized by the colonization of the litter surfaces by microbial organisms and breakdown of soft tissues, and the third phase is mechanical fragmentation of remaining material by invertebrates and environmental processes.

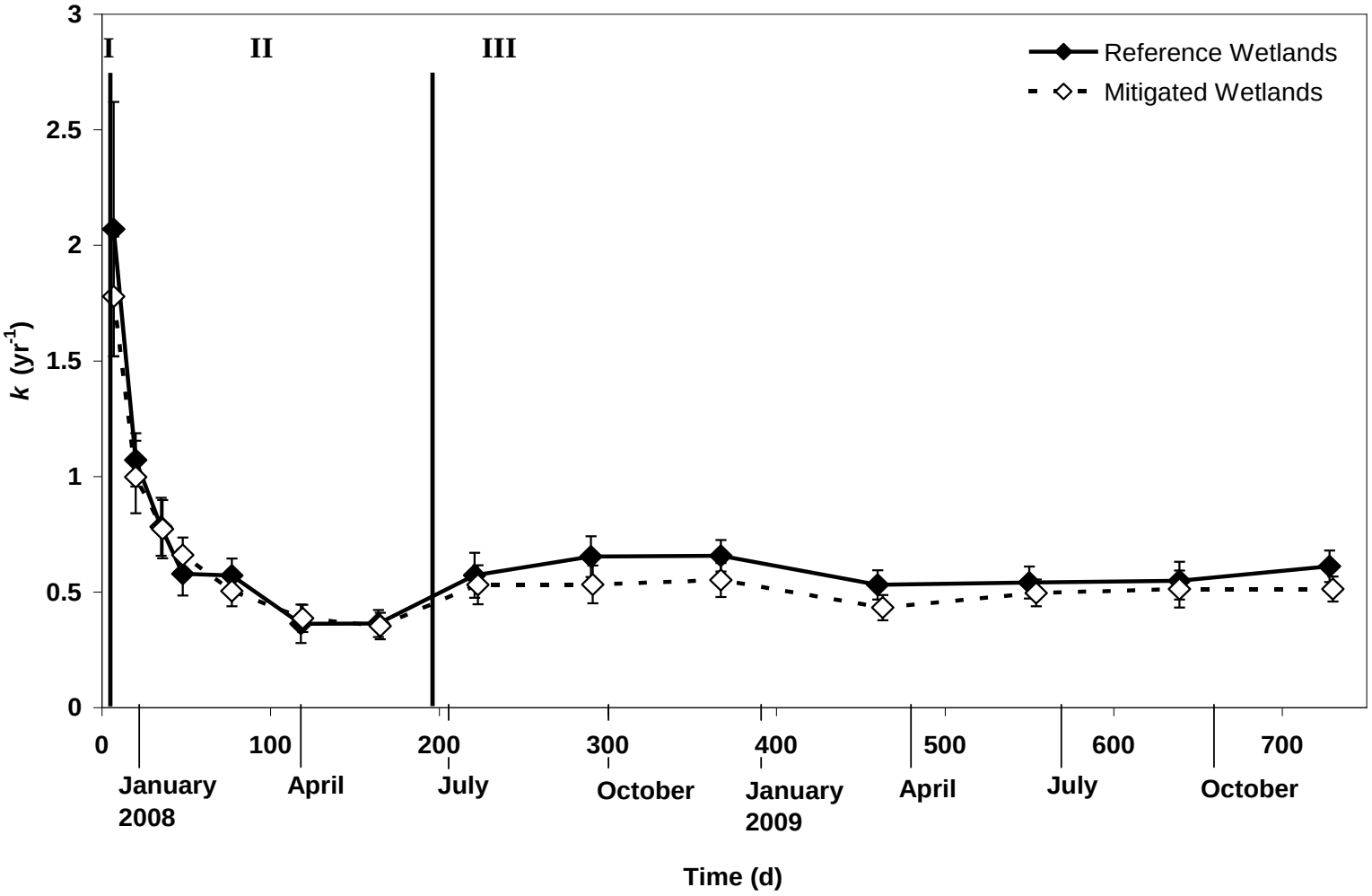

Figure 3. Mean (± S.E.) decomposition rate constants *k* (yr $^{-1}$) for three mitigated and three reference wetlands in the Allegheny Mountain region of West Virginia, December 2007 through December 2009. The transitions between the first (I), second (II), and third (III) stages of decomposition are identified by vertical lines. The first stage is characterized by the rapid leaching of nutrients, the second phase is characterized by the colonization of the litter surfaces by microbial organisms and breakdown of soft tissues, and the third phase is mechanical fragmentation of remaining material by invertebrates and environmental processes.

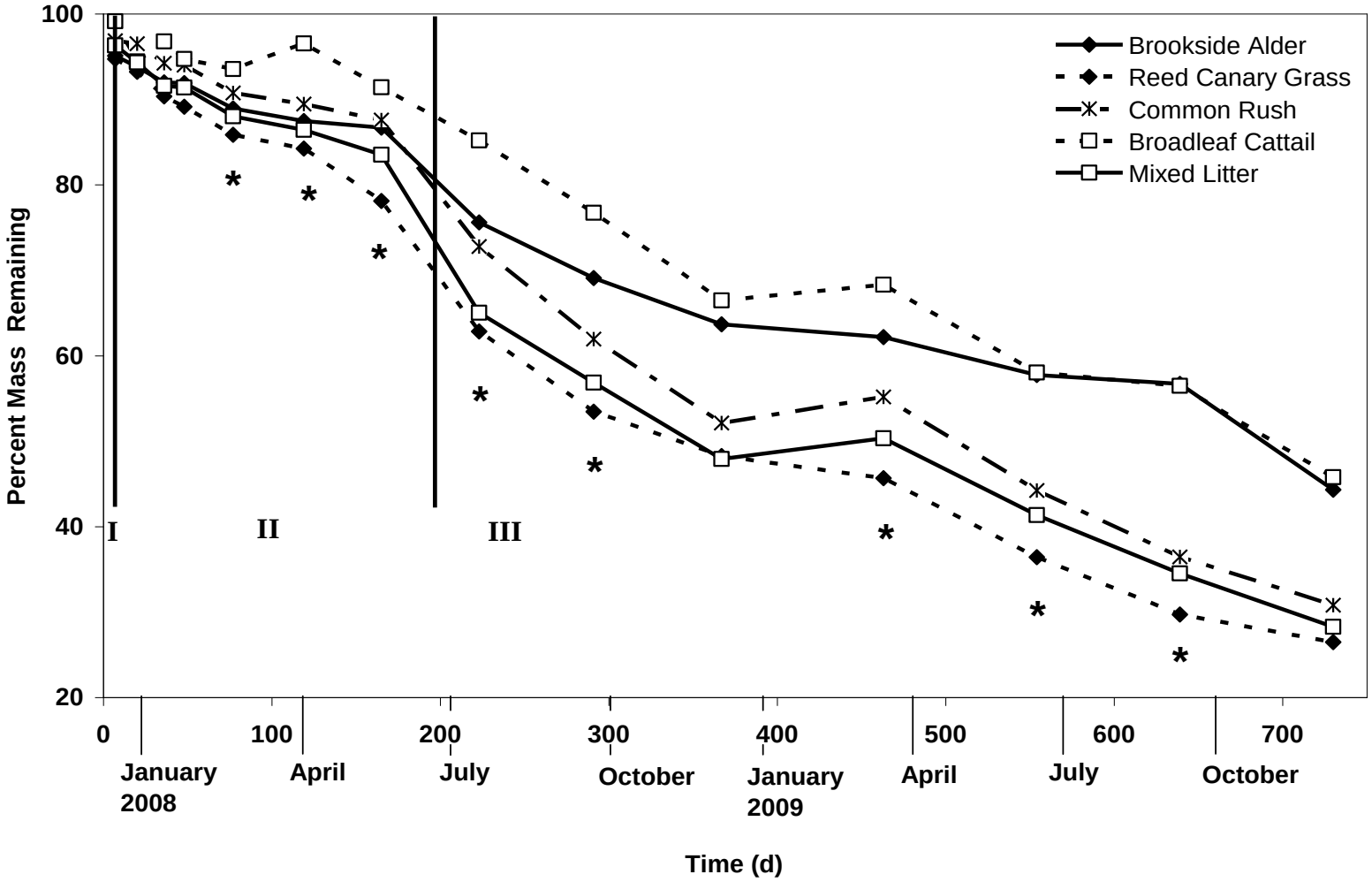

Figure 4. Mean percent ash-free dry mass remaining for five litter types in three mitigated and three reference wetlands in the Allegheny Mountain region of West Virginia, December 2007 through December 2009. An "*" denotes a collection date where at least two litter types are significantly different. The transitions between the first (I), second (II), and third (III) stages of decomposition are identified by vertical lines. The first stage is characterized by the rapid leaching of nutrients, the second phase is characterized by the colonization of the litter surfaces by microbial organisms and breakdown of soft tissues, and the third phase is mechanical fragmentation of remaining material by invertebrates and environmental processes.

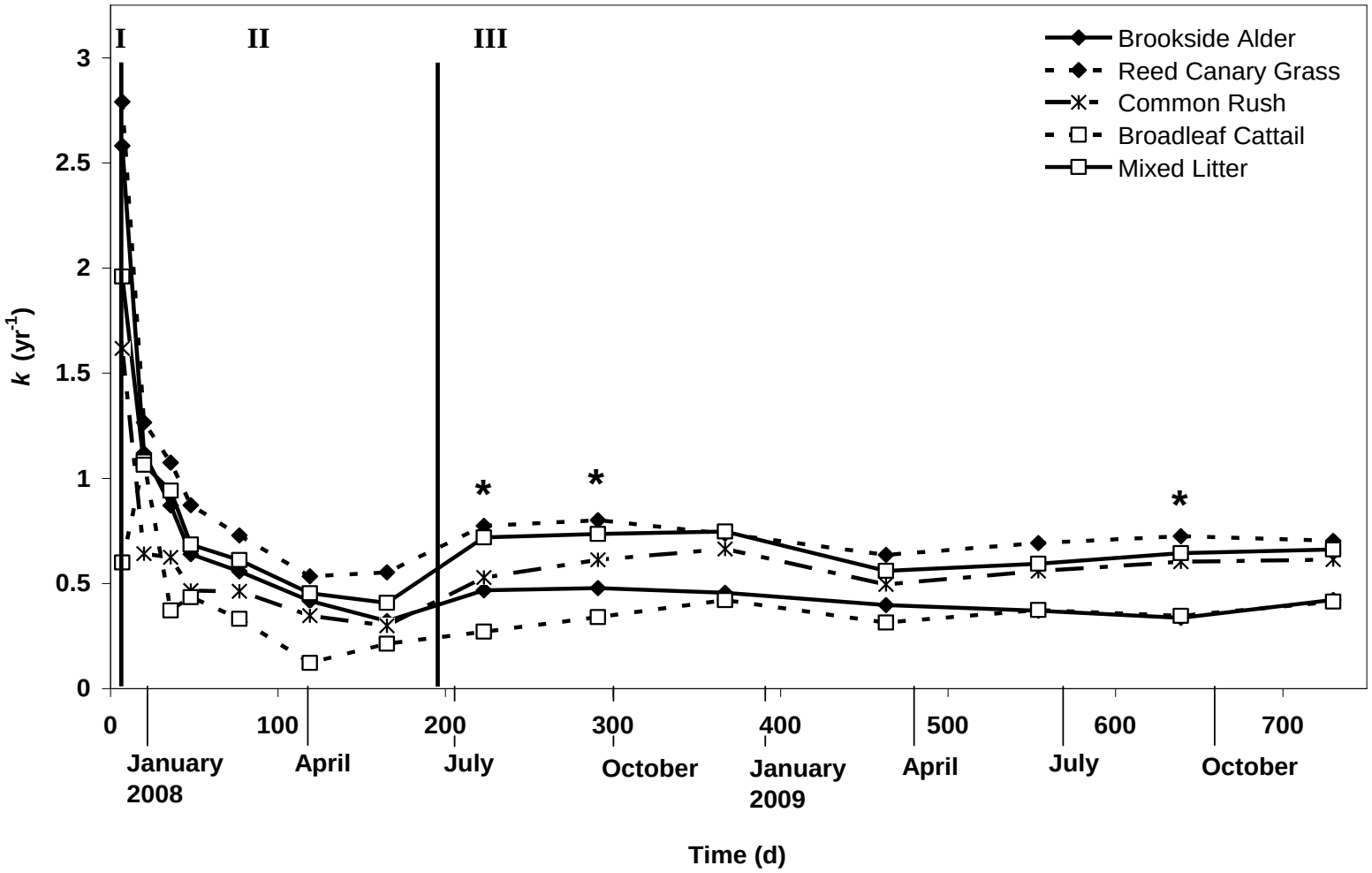

Figure 5. Mean decomposition rate constants *k* (yr $^{-1}$) for three mitigated and three reference wetlands in the Allegheny Mountain region of West Virginia, December 2007 through December 2009. An "*" denotes a collection date where at least two litter types are significantly different. The transitions between the first (I), second (II), and third (III) stages of decomposition are identified by vertical lines. The first stage is characterized by the rapid leaching of nutrients, the second phase is characterized by the colonization of the litter surfaces by microbial organisms and breakdown of soft tissues, and the third phase is mechanical fragmentation of remaining material by invertebrates and environmental processes.

CHAPTER 3

Litter Decomposition in Created and Reference Wetlands in West Virginia, USA

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Wetlands

ABSTRACT

Wetland mitigation has created a net gain in wetland acreage in recent years; however, it is less clear that wetland function is being replaced. Litter decomposition in wetlands is linked to numerous wetland functions, making it a useful metric to assess wetland function. We measured plant litter decomposition rates over 12 months, beginning in November 2008, in 8 created and 8 reference wetlands located in the Allegheny Mountains of West Virginia,. Broadleaf cattail (*Typha latifolia* L.) litter bags were placed in each wetland and collected at 3 month intervals. Decomposition rate constant and percent mass remaining were not statistically different between created and reference wetlands. Age of created wetland was uncorrelated with decomposition rate constant. Our study indicates that created wetlands had similar function, with regards to decomposition, as reference wetlands. This type of study could be implemented into wetland mitigation permitting to address functional replacement.

INTRODUCTION

Wetland functions include floodwater storage, groundwater recharge, biological productivity, biogeochemical cycling and storage, wildlife and community habitat, sediment trapping, and water purification (Richardson 1994; Smith et al. 1995). However, these functions have not always been recognized and valued. Between the 1780s and 1980s 42 million ha (53%) of wetlands were lost in the contiguous United States (Dahl 1990). In 1988, the National Wetlands Policy Forum brought to the forefront the continued loss of wetlands and recommended a policy of "no net loss" of wetlands (Mitsch and Gosselink 2007). This recommendation was adopted by the administration of President George H. W. Bush. Section 401 and 404 of the Clean Water Act (CWA) helped control the loss of wetlands by granting regulatory control of most wetlands to the U.S. Army Corps of Engineers (USACOE) and the U.S. Environmental Protection Agency (USEPA). Permits and mitigation are now required for the dredging or filling of wetlands and a Memorandum of Agreement between the USEPA and Department of the Army, signed in 1990, clarified that wetland function must be replaced in addition to lost acreage (USEPA 1990).

As a result of this legislation, wetland acreage increased by 77,630 ha between 1998 and 2004 (Dahl 2006). Though increases in acreage is a positive trend, two concerns remain, the first being whether correct acreage is being created and reported. Robb (2002) inventoried 345 permitted mitigation projects in Indiana and found that 71% of palustrine forested wetlands and 78% of wet meadow wetlands failed to meet the acreage requirements of their permit. Morgan and Roberts (2003) found that 72% of 50 mitigation projects in Tennessee had less acreage than stipulated. To ensure this criterion is met requires relatively straightforward site visits that involve delineating the wetland boundary to ensure proper acreage.

The second concern is whether wetland function is being replaced. According to Dahl (2006) open water and depressional wetlands were the most frequently created types of wetlands contributing to the net gain in acreage. However, 364,540 ha (4.9%) of freshwater shrub wetlands were among the original wetlands lost. Estuarine vegetated wetlands decreased by 13,100 ha from 1998 to 2004, while estuarine non-vegetated wetlands had a net gain of 1,620 ha. This trend of replacing one wetland type with another emphasizes why it is important to perform functional assessments of mitigated wetlands to ensure that the shift in type allows adequate replacement of lost functions. Previous studies suggest that overall success is mixed. Landscape placement of mitigated wetlands does not always match that of lost wetlands and affects wetland type and function (Bedford 1996; Hoeltje and Cole 2009). Minkin and Ladd (2003) studied 60 mitigated sites to determine if they successfully met their permit objectives and found that 40 (67%) of the wetlands met the criteria of their permits, but that only 10 mitigated sites (17%) were adequate functional replacements for the impacted wetlands. Race and Fonseca (1996) surveyed mitigation projects nationwide and found that the success rate of permit-linked mitigation projects was low overall.

In response to Dahl (2006) and other findings, the USACOE and USEPA issued updated regulations in 2008 that required measurable, enforceable ecological performance standards and regular monitoring of mitigated wetlands (USDOD and USEPA 2008). For functional performance to be fully assessed, each function needs to be addressed; however, not all wetland functions have received equal attention. Vegetative communities (Galatowitsch and van der Valk 1996; Seabloom and van der Valk 2003; Balcombe et al. 2005a; Spieles 2005) and habitat use by wildlife (Williams and Zedler 1999; Snell-Rood and Cristol 2003; Stanczak and Keiper 2004; Balcombe et al. 2005b) have been extensively studied in mitigated wetlands, but other

important functions such as sediment retention, biogeochemical cycling and storage, hydrologic flux and storage, and groundwater recharge have received less focus. Organic matter decomposition has also been largely overlooked, but has gained attention in recent years. Decomposition is linked to many additional wetland functions, making it a useful tool for assessing the evolution of overall ecosystem function (Spieles and Mora 2007). Organic matter accumulation, export, and nutrient cycling are all examples of processes connected to decomposition. Decomposition supports major flows of energy that occur along detrital pathways making it an important driving force in nutrient cycling (Brinson et al. 1981; Webster and Benfield 1986).

Few studies have compared decomposition rates in mitigated wetlands with natural wetlands, but the few that have often find differing results. Atkinson and Cairns (2001) and Fennessy et al. (2008) found that decomposition occurs more slowly in mitigated wetlands compared to reference wetlands, while Taylor and Middleton (2004) and Crawford et al. (2007) found the opposite to be true. Spieles and Mora (2007) found no trend between decomposition rate and wetland age at 3 created wetlands in Ohio. Only Álvares and Bécares (2006) found similar decomposition rates of *Typha latifolia* at a created wetland in Spain as compared to rates reported in the literature. With so few studies and so much variance between results, it is difficult to generalize trends between mitigated and natural wetlands. To determine if created wetlands in West Virginia were functioning similarly to reference sites, with respect to decomposition, we designed an experiment to measure decomposition rates in 8 of each wetland type at sites in West Virginia, USA.

MATERIALS AND METHODS

Study Area

This study was conducted in West Virginia, which is located in the mid-Appalachian region of the U.S. In the Allegheny Mountain ecoregion (Bailey 1983), where most of the study sites were located (Figure 1), mountain ridges can reach between 1,200 and 1,375 m in elevation. The Allegheny Mountains are located in the center of West Virginia and continue north through Maryland into central Pennsylvania. Two of the study sites were located in the Allegheny Plateau ecoregion, which is an unglaciated region to the west of the Allegheny Mountains. Most of the ridges in this part of the state are 450 m or less in elevation.

Eight created wetlands were evaluated in this study: Leading Creek, Sugar Creek, Hazelton, Elk Run, Virginia Electric and Power Company (VECO), Upper Deckers Creek Wildlife Management Area (WMA), Pedlar WMA, and Enoch Branch (Appendix C). All created wetlands were constructed except for Elk Run, which was a combination of created and restored wetland. Pedlar WMA and Enoch Branch were located in the Western Hill region, while all other wetlands were located in the Allegheny Mountain region. One wetland (Leading Creek) was predominantly palustrine scrub-shrub, 2 wetlands (Upper Deckers Creek WMA, Elk Run) were predominantly palustrine unconsolidated bottom and aquatic bed, and the other 5 wetlands were predominantly palustrine emergent persistent (Cowardin et al. 1979). However, all wetlands had some combinations of scrub-shrub, emergent, and aquatic bed. Almost all created wetlands had some level of disturbance on their edge in the form of roads with moderate to heavy traffic, houses, grazing, or cultivated land. Created wetlands ranged in age from 2 to 40 years ($\bar{x}$ = 15.1, S.E. = 4.5), in elevation from 335 to 1,020 m ($\bar{x}$ = 615, S.E. = 75), and in size from 0.1 to 17.0 ha ($\bar{x}$ = 5.9, S.E. = 1.9).

Eight reference wetlands were chosen to compare with the created wetlands: Meadowville, Upper Deckers Creek, Kanes Creek, Bruceton Mills, Indian Creek, Thomas Airfield, Glade Run, and Muddlety. Reference wetlands were chosen based on their proximity to mitigated sites (to minimize differences in climatic events); similarity in elevation, size, and wetland classification; and their relative degree of disturbance. Muddlety and Indian Creek were located in the Western Hill region, while all other wetlands were located in the Allegheny Mountain region. Three reference wetlands (Meadowville, Upper Deckers Creek, Kanes Creek) were classified as palustrine scrub-shrub, 2 (Thomas Airfield, Glade Run) were beaver (*Castor canadensis*) impoundments that were predominantly palustrine aquatic bed, and the other 3 were predominantly palustrine emergent persistent. However, all wetlands had some combination of emergent, scrub-shrub, and aquatic bed. Many of the wetlands had some amount of disturbance adjacent to them in the form of roads with light to heavy traffic, tree plantations, railroad tracks converted to a trail, grazing, or cultivated land. Reference wetlands ranged in elevation from 275 to 965 m ($\bar{x}$ = 596, S.E. = 84) and in size from 0.7 to 11.7 ha ($\bar{x}$ = 5.0, S.E. = 1.6).

Experimental Design

Decomposition rates were measured using the litter bag method (Benfield 1996). Broadleaf cattail (*Typha latifolia* L.) was chosen as the litter type because it is ubiquitous in most wetlands. Many species of wetland vegetation have a standing dead period, during which some fungal colonization and decomposition can occur before it falls to the ground (Kuehn et al. 1999). To help ensure similar vegetation conditions, broadleaf cattail leaves and stems were clipped and collected as they senesced in September 2008 (Davis and van der Valk 1978; Hill 1985; Marsh et al. 2000; Bedford 2005). To minimize differences in litter quality, all broadleaf cattail was collected from only one area in the Meadowville reference wetland. Leaves and

stems were air-dried for a minimum of 10 days before being weighed and bagged (Taylor and Middleton 2004).

Litter bags were constructed from 1.27 mm vinyl-coated fiberglass window mesh and were filled with 20 g of broadleaf cattail (Benfield 1996). The litter bags had external dimensions of 20 x 20 cm and were constructed with one folded side and 3 heat-sealed sides. To reinforce the melted sides, bags were stapled shut at 5-cm intervals with stainless steel staples (Deghi et al. 1980). A small sealed plastic bag containing a plastic tag with a unique identification code was placed in each litter bag, along with the litter, to allow final masses to be matched up with initial masses (Davis and van der Valk 1978; Vargo et al. 1998).

In each wetland, 5 stakes were placed 3 m apart in approximately 30 cm of water between October 31 and November 15, 2008. A total of 28 bags were then attached to the stakes (3 stakes with 6 bags and 2 stakes with 5 bags) with 0.5 m long thick nylon line (Battle and Golladay 2001; Anderson and Smith 2002). The litter bags were dunked to completely wet the surface and minimize any hydrophobic effect the mesh might have contributed and then allowed to float or sink. Twenty litter bags were collected when litter bags were first placed in the field to establish correction factors for initial masses due to incomplete drying and handling (Benfield 1996). Six replicates were then retrieved every 3 months over the course of a year. Unfortunately, loss of litter bags was greater than expected at some wetlands (Leading Creek, Glade Run, Upper Deckers WMA) due to currents during flooding and wildlife damage and resulted in fewer bags being collected (Appendix D). Additionally, thick ice hindered collection at Upper Deckers Creek, allowing only 5 litter bags to be collected after 3 months.

When bags were collected, they were gently brought to the surface if submerged, then excess sediment and plant material were removed from the outside of the litter bag before they

were placed in plastic bags and transported back to the lab on ice (Benfield 1996). Once back at the lab, any additional debris adhering to the outside of the bags was removed before it was opened. Litter was carefully removed from the interior of the bag and sediment was rinsed off. The litter was then oven-dried (65° C) for 1 week until a constant mass was reached. The mass was recorded and the litter was ground to powder in a 2-mm mesh Wiley Mill (Thomas Scientific Wiley Cutting Mill model ED-5; Philadelphia, Pennsylvania). Three subsamples of 250 mg of powder were placed in an aluminum pan and ashed at 550^{o} C for 30 minutes. Once a sample cooled, it was weighed and the proportion of mass remaining was subtracted from the original mass to determine the ash-free dry mass (AFDM). The AFDM was used during analysis to minimize error from sedimentation.

Data Analysis

Litter decomposition was the dependent variable and was analyzed using 2 different models. The first model was the percent mass remaining. The second model was the exponential decay model, which expresses the decomposition rate as constant k (yr^{-1}): $y_t / y_o = e^{-kt}$, where y_t is the AFDM at time t (yr) and y_o is the initial AFDM (Olson 1963; Brock et al. 1985). Analysis of variance (ANOVA) assumptions were tested using PROC UNIVARIATE (SAS® v9.1.3) and both proportion of mass remaining and decomposition rate were found to be normally distributed according to the Shapiro-Wilks test. All analyses were conducted using ANOVA in PROC MIXED (SAS® v9.1.3), with wetland defined as a random effect. Wetland type (n=2), collection date (n=4) and their interaction was tested. Since wetlands were the experimental unit, replicate bags from a wetland were averaged for each collection date. A series of models were run using differing covariance structures to determine which had the best fit, then the model with the lowest AIC value was chosen. One way

comparisons were performed using Tukey's least-square means. Tests were considered significant at $P < 0.05$. The relation between age and decomposition rate was examined using linear and polynomial regression with repeated measures (PROC MIXED in SAS® v9.1.3). Linear, quadratic, cubic, and quartic models were compared and the cubic regression was chosen based on the largest R^2.

RESULTS

Overall decomposition rates were similar between created (% mass remaining: $\bar{x}$ =56.0%, SE = 2.79; *k*: 0.526 yr^{-1}, SE = 0.042) and reference (% mass remaining: $\bar{x}$ =54.6%, SE = 2.67; *k*: 0.517 yr^{-1}, SE = 0.040) wetlands (Figure 2, 3) for both percent of mass remaining ($F_{1,14} = 0.01$; $p = 0.941$) and decomposition rate constants *k* ($F_{1,14} = 0.01$; $p = 0.939$) (Appendix E). The lowest *k* was measured at 6 months and had a mean of 0.429 yr^{-1}, while the highest *k* was measured at 12 months and had a mean of 0.608 yr^{-1} (Figure 3). No significant trend was found between wetland age and decomposition rate constant ($F_{4,3} = 0.98$, $p = 0.528$). The oldest wetland, Upper Deckers Creek WMA (40 years), had the largest mean *k* ($\bar{x}$ = 0.839 yr^{-1}, SE = 0.087) and the second oldest wetland, Elk Run (27 years), had the smallest mean *k* ($\bar{x}$ = 0.240 yr^{-1}, SE = 0.075). A cubic model best fit ($R^2 = 0.263$) the breakdown rates (Figure 4).

DISCUSSION

Our study found decomposition rates to be similar between created and reference wetlands, which agrees with Álvares and Bécares (2006). Most studies comparing decomposition in created and reference wetlands have found differing rates between wetland types (Atkinson and Cairns 2001; Taylor and Middleton 2004; Spieles and Mora 2007; Fennessy et al. 2008). Site conditions, such as environmental (temperature, hydrology, and water pH;

Gingerich 2010: Chapter 4) and biotic (taxonomic groups and functional feeding groups; Gingerich 2010: Chapter 5) variables better explain differences in decomposition rate than wetland type.

The plot of age and decomposition rate suggested that *k* has a nonlinear relation with wetland age (Figure 4). A medium decomposition rate is observed for younger wetlands, then drops with Elk Run (age = 27 yr) having the slowest rate, and finally rises with Upper Deckers Creek WMA (age = 40 yr) having the fastest rate. This is possibly explained by two hypotheses. First, it is possible that wetland succession and decomposition rate do not trend towards natural conditions. Second, if wetlands are trending towards natural conditions it is possible that transitional phases have slower decomposition rates than the final natural phase. Past studies have suggested that 10 to 25 years are needed for created wetland functions to match natural systems (Mitsch and Wilson 1996; Simenstad and Thom 1996; Craft et al. 1999; Gutrich and Hitzhusen 2004). Therefore, in the first 25 years, it is likely that functions such as sediment retention, hydrology, and availability of certain nutrients shifted as upland soils converted to hydric soils and hydrophytes established themselves. A second hypothesis is that a lack of shading in young, poorly-vegetated wetlands led to higher temperatures, which have been found to increase decomposition rate (Brinson 1977; Middleton et al. 1992; Álvarez and Bécares 2006; Gingerich 2010: Chapter 4). As vegetation grew, soil and water temperatures decreased with increased shading, leading to slower decomposition rates in older wetlands. As overall wetland function increases with age, breakdown rate might again increase until it matches natural systems. Because environmental conditions were not measured, we can not specifically determine what conditions might be driving decomposition at these wetlands; however,

hydrology has been shown to be associated with litter decomposition rates (Gingerich 2010: Chapter 4) and may partially account for variance among wetlands.

The 3 phases of decomposition ([1] leaching, [2] microbial colonization and breakdown, and [3] mechanical fragmentation by invertebrates) (Godshalk and Wetzel 1978; Brinson et al. 1981; Gingerich 2010: Chapter 5) may explain the decline in *k* between 3 and 6 months (i.e., breakdown of soft tissues is completed). The decomposition rate then increased after 6 months as the remaining litter was colonized and mechanically fragmented by invertebrates.

Broadleaf cattail has been studied extensively due to its global distribution, high visibility, and ubiquitous distribution in wetland systems. Our *k* values for broadleaf cattail ranged from 0.069-1.092 yr^{-1}, which has a minimum that is lower than rates reported in other studies but generally overlaps with previously reported values (Table 1). When litter bags were first placed in wetlands, 20 litter bags were dried and ashed to calculate a correction factor for initial leaf masses to account for handling loss and convert to ash-free dry masses. The correction factor was calculated as 0.74 and all initial masses were multiplied by this correction factor. The fact that the correction factor was ¾ the initial mass indicates that the material was not dry when it was weighed and bagged. If material was drier on average than the subset used to create the correction, the large correction factor could lead to under-estimated decomposition rates. Likewise, if material was air dried to a constant mass, but was not dried under heat and retained moisture without a correction factor, decomposition rates would be over-estimated. Most studies do not address their correction factor, which indicates how dry initial leaf material was and lends insight into a possible source of error.

For wetland mitigation to be considered fully successful, created wetland function will need to be measured in the future, and that should include decomposition. A study, such as the

one outlined in this publication, requires relatively little work to implement, with the majority of labor being required at initiation when litter bags are created. Any litter type could be used, but cattail is especially abundant, easy to collect, and well documented. However, a few points should be kept in mind when implementing a similar study. The first is that collection location and study species should be chosen based on what species are already present at the study sites. Care should be taken when putting out vegetative material because there is always the possibility of unintended seed being transferred in the litter bag and introducing undesirable species. Secondly, material should be allowed to dry completely by weighing it throughout the drying process until its mass ceases to change. Incomplete drying is a potential source of error when calculating decomposition. A correction factor should also be calculated and used in analysis. Third, make sure to install more litter bags in the field than are needed for the study to allow for losses due to unforeseen events such as high flows during flooding, the loss of stakes, wildlife interference, and loss of material due to litterbag weathering. Finally, decomposition proceeds over the course of seasons and years and diverging trends could potentially emerge after longer periods of time. To address this, study durations should be a minimum of one year, preferably longer.

Conclusion

Wetland function, in regards to decomposition rate, was similar between created and mitigated wetlands in West Virginia. Additionally, created wetland age did not have a linear relation with decomposition rate, suggesting that wetlands are either not trending towards natural conditions or that transitional successional stages have slower decomposition rates than the initial and final phases. Finally, for wetland mitigation to be fully satisfied, wetland function

needs to be addressed during permitting. Decomposition is easily measured by the litter bag technique and can provide a useful means of assessing wetland function.

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Table 1. A comparison of *Typha latifolia* decomposition rate constants (% mass remaining and k [yr^{-1}]) in the literature with this study.

	Mesh Size (mm)	**Study Period (d)**	**% Mass Remaining**	**Decomposition rate constant *k* (yr^{-1})**
Our Study	1.27	365	created wetlands: 56.0%	0.526
			reference wetlands: 54.6%	0.517
Álvarez and Bécares 2006	1	90	extrapolated by	winter: 0.730
			author to 31%	summer: 1.570
Atkinson and Cairns 2001	-	365	2-yr-old wetland: 80%	-
			20-yr-old wetland: 72%	
Findlay et al. 1990	-	365	-	0.31
Kittle et al. 1995	1.5	155	36-46%	-
Middleton 1994	1	190	-	winter: 1.27
				summer: 1.40
Poi de Neiff et al. 2006	2	125	-	1.46
Spieles and Mora 2007	1.6	360	4-yr-old wetland: 21.4%	1.540
			12-yr-old wetland: 61.1%	0.493
			155-yr-old wetland: 33.1%	1.107
Taylor and Middleton 2004	1	150	-	coal slurry pond: 0.986
				natural pond: 0.767
Thormann and Bayley 1997	1	365	36%	-
Vargo et al. 1998	1.5	158	30.3-59%	0.621 - 0.767

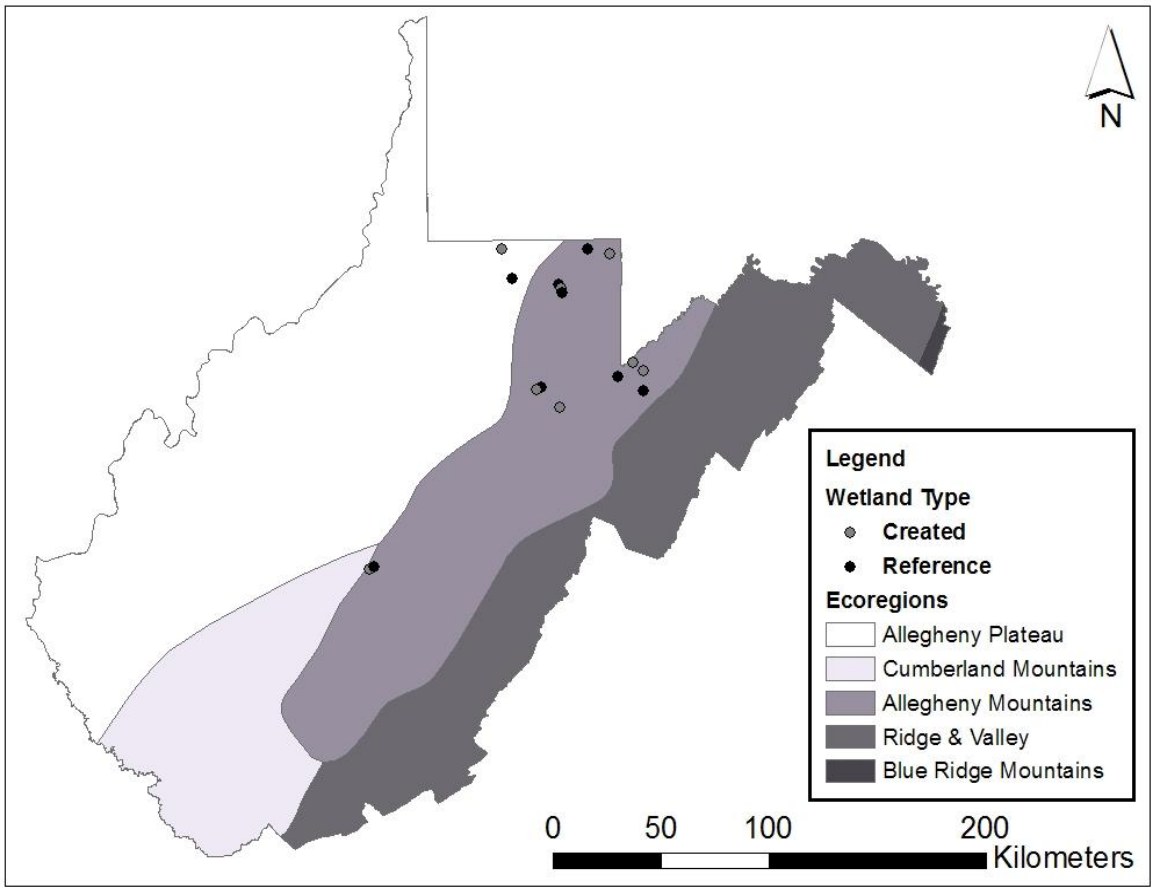

Figure 1. Sixteen study sites, comprised of 8 created and 8 reference wetlands located primarily in the Allegheny Mountain ecoregion of West Virginia, 2007-2009.

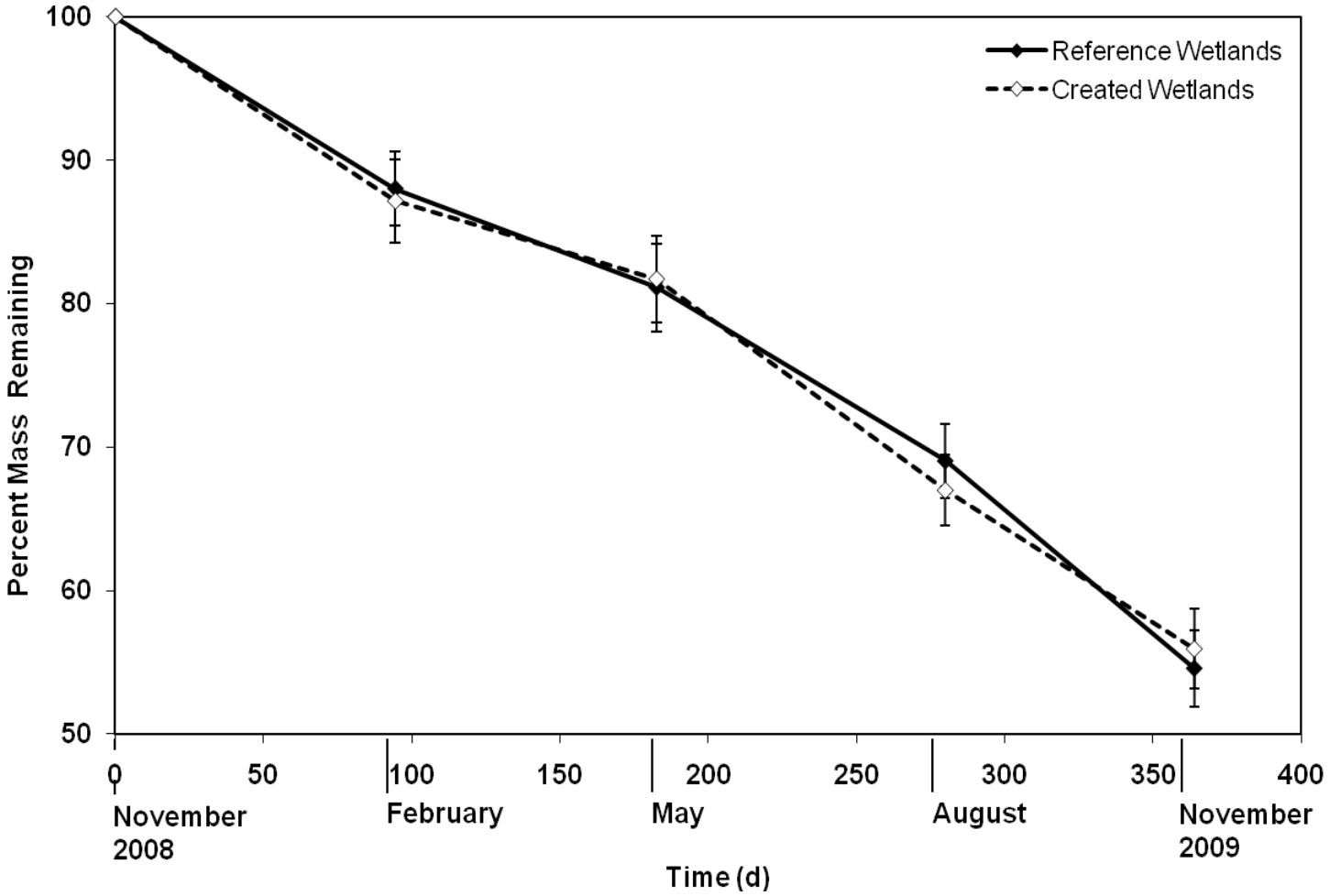

Figure 2. Mean (± S.E.) percent ash-free dry mass remaining for 8 created and 8 reference wetlands in West Virginia, USA, November 2008 through November 2009.

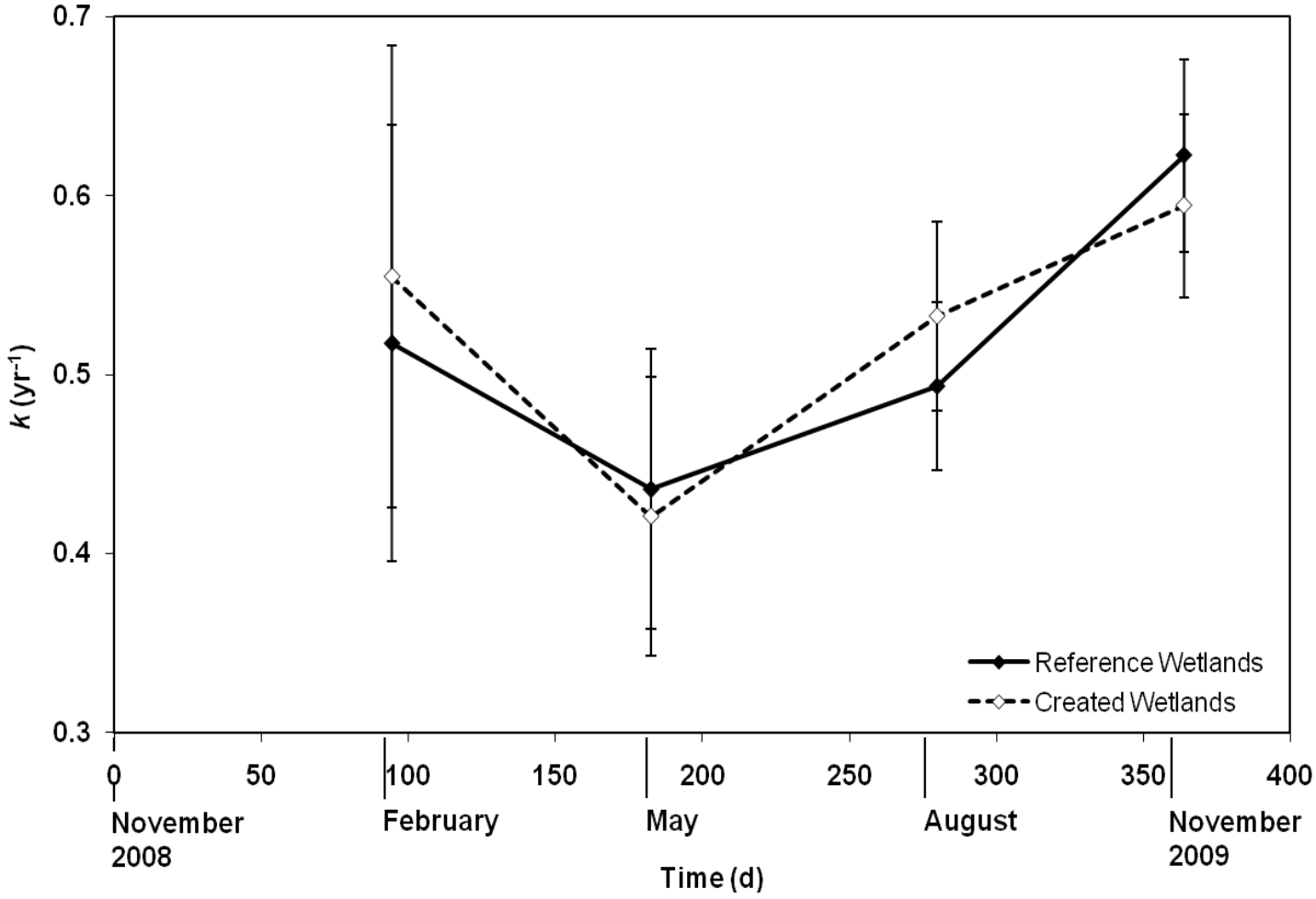

Figure 3. Mean (± S.E.) decomposition rate constants *k* (yr $^{-1}$) for 8 created and 8 reference wetlands in West Virginia, USA, November 2008 through November 2009.

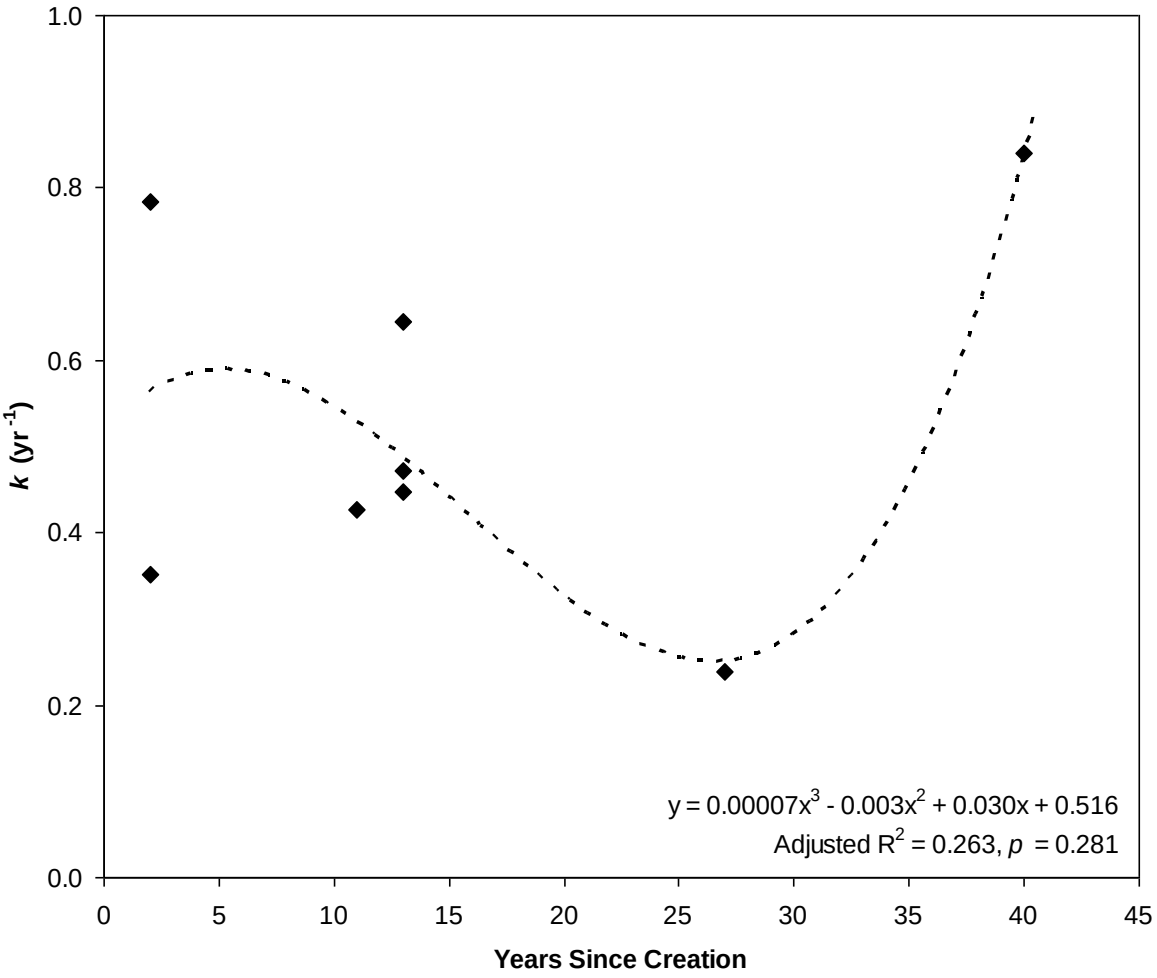

Figure 4. Decomposition rate constant k (yr^{-1}) as a function of wetland age for 8 created wetlands in West Virginia, USA, November 2008 through November 2009. A polynomial regression ($k = 0.00007*years^3 – 0.0034 * years^2 + 0.0297 * years + 0.5164$; Adjusted $R^2 = 0.263$; $p = 0.281$) had the best fit.

CHAPTER 4

Influence of environment on litter decomposition in wetlands in West Virginia, USA

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ABSTRACT

Wetland plant litter decomposition is a component of numerous wetland functions and is therefore a useful means of assessing overall wetland function; however, factors influencing decomposition are not well understood. Environmental conditions influence decomposition differently depending on the litter species and mix of environmental conditions present. To look at environmental controls of decomposition, we measured plant litter decomposition rates in 6 wetlands located in West Virginia, USA. Four common wetland litter species were used to determine decomposition rates: broadleaf cattail (*Typha latifolia* L.), common rush (*Juncus effusus* L.), brookside alder (*Alnus serrulata* (Ait.)Willd.), and reed canary grass (*Phalaris arundinacea* L.). A fifth litter type was created from a mix of common rush, brookside alder, and reed canary grass. Litter bags were collected over 2 years, from December 2007 to December 2009, and environmental variables near litter bags were measured every 2 wk. Nine environmental model parameters and 1 study parameter were then used to construct and test the ability of 22 *a priori* models to predict the decomposition rate of each litter type. The environmental variables that most influenced, and therefore best predicted, decomposition rate varied among litter types. Brookside alder decomposition rate was best predicted by soil temperature (ST), water pH (WPH), and the number of transitions between flooded and exposed conditions (FET); reed canary grass decomposition rate was best predicted by air temperature (AT), WPH, and ST; common rush decomposition rates were best predicted by AT and FET; broadleaf cattail decomposition rate was best predicted by hydroperiod (HP) and FET; and the mixed litter decomposition rate was best predicted by AT and WPH. Overall, AT, ST, and WPH were directly related to decomposition rate, while HP was inversely related. The FET was directly related to decomposition rates of common rush and broadleaf cattail and inversely

related to the decomposition rate of brookside alder. Understanding the environmental factors that direct litter decomposition rate, and through it influence wetland function, allows for the establishment of more complete mitigation and functional assessment criteria, leading to better functional replacement.

1. Introduction

The ability of mitigated wetlands to replace the ecosystem functions of lost natural wetlands has been widely studied and debated in recent years (Mitsch and Wilson, 1996; Zedler and Callaway, 1999; Gutrich and Hitzhusen, 2004; Hoeltje and Cole, 2009). Litter decomposition has been put forth as a useful way of assessing wetland function and quantifying possible differences between mitigated and reference wetland function (Atkinson and Cairns, 2001; Spieles and Mora, 2007; Fennessy et al., 2008). Wetland litter decomposition is linked to many other wetland processes and is therefore an important component of wetland function (Richardson, 1994; Spieles and Mora, 2007). Litter decomposition influences the physical and chemical properties of wetland soils (Mitsch and Gosselink, 2007), nutrient availability and cycling (Prentki et al., 1978; Facelli and Pickett, 1991), primary productivity (Brinson et al., 1981), litter/organic matter accumulation (Gambrell and Patrick Jr., 1978; Xiong and Nilsson, 1997), and seed germination (Xiong and Nilsson, 1997; Taylor and Middleton, 2004). Mitsch and Gosselink (2007) suggested that a common feature of wetland development is a shift from a detritus-poor to a detritus-based system over time.

Organic matter decomposition in wetlands exerts influence at the ecosystem level by supporting major flows of energy that occur along detrital pathways (Brinson et al., 1981; Webster and Benfield, 1986). Organic matter collecting in wetlands during the growing season or deposited during bankfull discharge events of nearby streams is broken down into coarse and

fine particulate organic matter (CPOM and FPOM respectively) and dissolved nutrients that are then released back into streams during later flooding events. These are important riparian wetland exports because they provide a nutrient source for aquatic organisms downstream (Richardson, 1994; Mitsch and Gosselink, 2007). Additionally, waste organics and pollutants are deposited and decomposed in wetlands, which leads to improved water quality (Walbridge, 1993; Mitsch and Gosselink, 2007).

Decomposition can have effects on a global scale. Decomposition of organic matter is an important component in nutrient cycles and is the only process enabling the massive recycling of chemical elements on the scale of whole ecosystems (Richardson, 1994; Björn and Laskowski, 2006). Slow decomposition rates in wetlands lead to organic matter accumulation and CO_2 sequestration (Richardson, 1994). Decomposition is therefore an indicator of organic matter storage potential in wetlands and influences global climate by sequestering carbon, which influences the rate at which CO_2 returns to the atmosphere and balances the atmospheric CO_2 pool (Richardson, 1994; Björn and Laskowski, 2006). This is especially important in wetlands compared to terrestrial systems because, although less than 4% of the earth's surface is covered in wetlands, hydric soils contain about one-third of all organic matter stored in the world's soils (Dodds, 2002). Hence, understanding decomposition in wetlands has important implications for predicting and modeling global climate change.

Decomposition is driven by 3 categories of variables: biotic (microorganisms and invertebrates that break down litter), chemical (physical and nutrient composition of the litter), and physical (environmental conditions where the litter occurs) (Aerts and de Caluwe, 1997). Physical variables exert additional control on decomposition by influencing the biotic communities that are present and their levels of activity (Meentemeyer, 1978; Rejmánková and

Houdková, 2006; Inkley et al., 2008). Hydroperiod and temperature are the 2 environmental variables most often credited as best predicting decomposition rate. Temperature is directly related to decomposition rate (Morris and Lajtha, 1986; Middleton et al., 1992; Álvarez and Bécares, 2006). The role of hydrology is less constant across wetlands, but many studies suggest that wet-dry cycles influence litter decomposition rate (Atkinson and Cairns, 2001; Battle and Golladay, 2001; Anderson and Smith, 2002). Water chemistry (Davis, 1991; Verhoeven and Arts, 1992; Qualls and Richardson, 2000), water pH (Day Jr., 1987; Kittle et al., 1995; Taylor and Middleton, 2004), sedimentation (Vargo et al., 1998; Atkinson and Cairns, 2001), dissolved O_2 (Schipper and Reddy, 1995), and soil moisture (Battle and Golladay, 2007) can all influence plant litter decomposition rates.

Despite the importance of decomposition, the role of physico-chemical variables is not well understood, in part because it is highly variable among locations. Therefore, we evaluated the influence of 9 environmental parameters and 1 study parameter (no. of days litter is in a wetland) on plant litter decomposition in mitigated and reference wetlands in West Virginia. We created 22 *a priori* models based on the 10 parameters to assess the decomposition of broadleaf cattail (*Typha latifolia* L.), common rush (*Juncus effusus* L.), brookside alder (*Alnus serrulata* (Ait.)Willd.), reed canary grass (*Phalaris arundinacea* L.), and a mixed litter. Specifically, our objective was to determine which environmental parameters best predict litter decomposition rate.

2. Materials and methods

2.1. Study Area

Leaf decomposition rates were measured at 3 mitigated and 3 reference wetlands located in the Allegheny Mountain ecoregion (Bailey 1983) of West Virginia, USA (Figure 1; Table 1).

The Allegheny Mountains are part of the Appalachian Mountain Range and form a distinct region in the eastern United States (Fenneman, 1938). The 3 mitigated wetlands were constructed by the West Virginia Division of Highways (WVDOH) to compensate for wetland losses associated with the Corridor H and Mon-Fayette Expressway system projects. The 3 reference wetlands were chosen based on their proximity to mitigated sites; similarity in elevation, size, wetland classification, and vegetative types; and their relative degree of disturbance. The Upper Deckers Creek wetland is an oxbow wetland, the Bruceton Mills wetland is the remnant of a beaver (*Castor canadensis*) impoundment, and the Meadowville wetland is a floodplain wetland. In general, excluding the Upper Deckers Creek oxbow wetland, the mitigated wetlands had more open water and ponded areas than the reference sites, and the reference sites tended to have more scrub-shrub areas than the mitigated sites. Leading Creek is the only mitigated site with a large portion of scrub-shrub and young forest. All wetlands had some level of disturbance on their edge in the form of roads, grazing, or cultivated land.

2.2. Decomposition (Litterbag) Procedures

We studied decomposition using the litter bag method (Benfield, 1996). We chose 4 litter types (i.e., broadleaf cattail, common rush, brookside alder, and reed canary grass) based on common dominant species at mitigated and reference sites in West Virginia (Balcombe et al., 2005; Veselka IV, 2008) and collected them in September and October of 2007. Litter mixes can have non-additive decomposition rates compared to single species (Gartner and Cardon, 2004), so a fifth litter type was created with a mixture (3:2:1) of reed canary grass, common rush, and brookside alder to mimic ratios present in the wetlands (Balcombe et al., 2005).

Many species of wetland vegetation have a standing dead period, during which some fungal colonization and decomposition occur before it falls to the ground (Kuehn et al., 1999).

To help ensure similar vegetative conditions, reed canary grass, common rush, and broadleaf cattail leaves and stems were clipped and collected as they senesced, but while still standing (Marsh et al., 2000; Bedford, 2005). Brookside alder leaves were collected with a STIHL model SH 85 D Shredder Vacuum/Blower (STIHL Incorporated, Virginia Beach, VI) reversed to suck leaves into the tube and then dumped in a basket. Brookside alder leaves that were not intact and any material other than alder leaves were discarded. To minimize differences in litter quality, each species was collected from only one area in a single wetland (Aerts and de Caluwe, 1997; Baker et al., 2001; Fennessy et al., 2008). All litter was air-dried for a minimum of 1 wk before being weighed and bagged.

We constructed 20 × 20 cm litter bags from 1.27 mm vinyl-coated fiberglass window mesh (Benfield, 1996). The litter bags were constructed with one folded side and 3 sides heat sealed and reinforced with stainless steel staples at 5-cm intervals (Deghi et al., 1980). A small sealed plastic bag containing a plastic tag with a unique identification code was placed in each litter bag, to allow final masses to be matched up with initial masses (Davis and van der Valk, 1978; Vargo et al., 1998). For the single species litter bags with broadleaf cattail, common rush, and reed canary grass, 20 g of litter was placed in each bag. For brookside alder, 20 g would have required the litter to be crushed, so only 12 g of litter was used. The mixed litter samples also had 20 g (brookside alder [3.3 g], common rush [6.7 g], and reed canary grass [10 g]).

Nine transects were established, using stratified sampling (Taylor and Middleton 2004), to represent aerial proportions of different environmental conditions, as represented by major vegetation communities, within each wetland. Ten wooden stakes were installed at 7.5 m intervals along each transect and one type of each litter bag, 5 bags total, was attached to the base of each stake with 0.5 m lengths of thick nylon line (Battle and Golladay, 2001; Anderson and

Smith, 2002). Litter bags were placed flat on bare ground or on top of any existing litter to mimic natural litter deposition. If the stake was in standing water the litter bag was first dunked to completely wet the surface and minimize any hydrophobic effect the mesh might have contributed and then allowed to float or sink.

This study was a subset of a larger study (Gingerich, 2010: Chapter 1), with 90 of each type of litter bag (9 transects of 10 stakes with 5 litter bags attached to a stake), 450 total litter bags, in each wetland and 2,700 total litter bags included in the study. Six replicates of each litter type were retrieved the same day the bags were placed in the field to calculate the loss of mass due to handling (Benfield, 1996). For this study, 4 replicates were then retrieved on 8 different dates: 168 d (24 wk), 224 d (32 wk), 294 d (42 wk), 364 d (52 wk), 455 (65 wk), 546 d (78 wk), 637 d (91 wk), and 728 d (104 wk). We sampled the 4 replicates by collecting all litter bags from 4 randomly chosen stakes in each wetland, for a total of 960 bags (192 of each litter type from 192 stakes) being collected.

Litter bags were transported back to the lab on ice, cleared of external material, and opened. Litter was carefully removed from the interior of the bag and sediment was rinsed off. We oven-dried (65° C) leaf litter for about 1 wk until a constant mass was reached (Morris and Lajtha, 1986; Lockaby et al., 1996), recorded mass, and ground the litter to a powder in a 2-mm mesh Thomas Wiley Mill (Thomas Scientific, Swedesboro, NJ). Three subsamples of the ground litter were then incinerated to calculate ash-free dry mass (AFDM).

2.3. Environmental Measurements

We measured environmental variables within 1 m of each stake every 2 wk. Air temperature was measured at every stake. If a stake was inundated we measured water temperature (°C) with an AquaCal® ClineFinder (Catalina Technologies, Inc., Tuscon, AZ),

water depth (cm), and water pH with a YSI® Model 63 pH & Conductivity Meter (YSI, Inc., Yellow Springs, OH). If a stake was exposed we measured soil temperature (°C) and soil moisture. Soil moisture was measured on a scale of 0 (dry) to 10 (saturated) with a Soil Moisture Meter (Lincoln Irrigation, Inc., Lincoln, NE). Two HOBO pendant temperature loggers (Onset Computer Corp., Pocasset, MA) were placed on opposite ends of each wetland to record hourly air temperatures throughout the study.

2.4. Calculation of Model Variables

We used an exponential decay rate to model leaf litter decomposition and calculate decomposition rate:

$$y_t / y_o = e^{-kt} \quad (1)$$

where k is the instantaneous decomposition rate constant (yr^{-1}), y_t is the AFDM at time t (yr), and y_o is the initial AFDM (Olson, 1963; Brock et al., 1985).

No significant difference was found among litter decomposition rates in mitigated and reference wetlands (Gingerich, 2010: Chapter 2) for any of the litter types, therefore all data were pooled and analyzed together. Nine environmental parameters (air temperature [AT], water temperature [WT], soil temperature [ST], water depth [WD], sum fluctuation of water depth [SF], hydroperiod [HP], flood and exposed transitions [FET], water pH [WPH], and soil moisture [SM]) were calculated from the 6 environmental measurements recorded in wetlands and included in analysis along with one model parameter (number of days litter was in the wetland [ND]). Environmental measurements were averaged across sampling dates to obtain a mean value for each stake. SF was calculated as the average observed change in WD per day ($cm\ d^{-1}$):

$$\Sigma\ ((|WD_{m+1} - WD_m|) \div (m_{+1} - m)) \quad (2)$$

where WD_m is the water depth on measurement date m and WD_{m+1} is the water depth on the next measurement date m_{+1}. HP was calculated from water depth measurements as number of days litter bags were flooded divided by total days litter bags were in the wetland. When 2 consecutive measurement dates were flooded or exposed, all days between were considered flooded or exposed, respectively. When there was a transition between flooded and exposed, the number of days between the measurement dates were divided by 2, with half considered flooded and half considered exposed. The number of observed transitions between flooded and exposed conditions was divided by total number of days litter bags were in the wetland to obtain FET. All environmental variables were based on static points in time and limited by the 2-wk measurement period. Changes that potentially occurred between measurement points were not reflected in the data.

To ensure the same population of litter bags were used in all analyses, any stake location missing one or more litter bags was excluded from analysis. Additionally, to ensure that environmental conditions were present long enough to influence decomposition, ≥10% of measurement dates needed to have a measurement obtained for a given parameter for it to be averaged and included in analysis. If one parameter at a stake was not obtained at ≥10% of the measurement dates, the stake and all litter bags associated with it were excluded from analysis. Of the initial 192 stakes we collected, litter bags from only 96 stakes (50%) met the above criteria and were included in analysis.

Normality was checked using the Shapiro-Wilk test (shapiro.test {stats}) in Program R (version 2.10.1) and parameters were transformed to more closely approximate normality. FET and *k* for the mixed litter type were square root transformed. WPH, SF, *k* for brookside alder, and *k* for reed canary grass were natural log transformed. WD was natural log (x+1)

transformed. ST was inverse square root ([1/-(sqrt x)] + 1) transformed. Correlations were checked visually using a scatterplot matrix (pairs {graphics}) and with the Pearson's correlation (cor {stats}) in Program R. No variables were highly correlated (-0.75 > r > 0.75), so all were included in analysis.

2.5. Model Selection

We used Chamberlin's (1931) multiple working hypothesis approach and developed 22 *a priori* linear mixed effects models to predict decomposition rate constant (*k*). Ten of the models were single parameter models (e.g., *k* = AT). The remaining 12 models were based on the literature and included:

1. Decomposition rate is best predicted by temperature (Morris and Lajtha, 1986; Middleton et al., 1992; Álvarez and Bécares, 2006).

   k = AT + WT + ST

2. Decomposition rate is best predicted by exposed conditions (Battle and Golladay, 2007).

   k = AT + ST + SM

   k = AT + ST + SM + WPH

   k = ST + SM

3. Decomposition rate is best predicted by temperature and hydrology (Brinson, 1977; Middleton et al., 1992).

   k = AT + FET

   k = AT + FET + HP

4. Decomposition rate is best predicted by inundated conditions (van der Valk et al., 1991; Neckles and Neill, 1994; Atkinson and Cairns, 2001).

k = HP + FET

k = WD + HP + SF

k = WT + WD + WPH + HP + FET + SF

5. Decomposition rate is best predicted by temperature and pH (Day Jr., 1987; Kittle et al., 1995; Taylor and Middleton, 2004).

k = AT + WPH

k = WT + WPH

6. Decomposition rate is best predicted by the global model, excluding ND.

k = AT + WT + ST + WD + HP + FET + SF + WPH + SM

We used Akaike's Information Criterion for small sample sizes (AIC_c) to compare competing models because the ratio of observations (n = 96) to parameters (n = 10) was < 40 (Burnham and Anderson, 2002). AIC_c is a measure of goodness of fit, with a small value indicating a better model fit, and penalizes models with more parameters (law of parsimony). Models were tested with a linear mixed effects (lme {nlme}) model in Program R, with wetlands treated as a random effect (i.e., factors not deliberately arranged by the experimenters, but which were sampled from a population of possible samples). Models were ranked by AIC_c, with the best model having the smallest AIC_c value (Burnham and Anderson, 2002). We then calculated AIC_c differences ($\Delta_i = AIC_{c\ lowest} - AIC_{ci}$) and Akaike weights ($w_i$) for the i^{th} model in comparison. The larger the Δ_i and smaller the w_i, the less likely it is that the model is the best approximating model given the data. Following Burnham and Anderson (2002), models with $\Delta_i < 2$ have substantial support as the best approximating model. Models with $2 < \Delta_i < 8$ have considerably less support and models $\Delta_i > 8$ have essentially no support. When model selection

was uncertain because multiple models had $\Delta_i < 2$, we averaged the predicted response variables across those models (Burnham and Anderson, 2002).

3. Results

3.1. Decomposition Rates and Environmental Measurements

Litter decomposition rates varied among litter types (Table 2, Appendix L; Gingerich, 2010: Chapter 2), with reed canary grass having the fastest and the mixed litter having the second fastest mean, minimum, and maximum decomposition rates. Broadleaf cattail had the slowest mean, minimum and maximum decomposition rates.

Temperature varied depending on where it was recorded; mean WT was similar (1.1x) to mean AT, but mean ST was nearly double (1.7x) mean AT (Table 3, Appendix M & N). ST also had the highest mean maximum, but WT had the highest mean minimum.

3.2. Brookside Alder

The best model (Table 4; Appendix O) to predict brookside alder decomposition was the {ST} model; however, the Δ_i was low enough and w_i was high enough for the second {FET} and third {WPH} best models that all 3 received substantial support. Therefore, model averaging was applied to all 3 to obtain a final model (Table 5):

$$k = -1.78 + 0.74\times ST - 0.38\times FET + 0.21\times WPH \quad (3)$$

In light of the *a priori* models that were run, a set of *a posteriori* models were run based on the parameters in the models with substantial Akaike support that were not considered with the *a priori* models: Three of the models were found to have lower AIC_c scores than the best *a priori* models:

$$k = -2.41 + 1.48\times ST - 0.34\times FET + 1.06\times WPH \ (\Delta_i = -1.71) \quad (4)$$

k = -2.46 + 1.57×ST + 1.07×WPH (Δ_i = -1.08) (5)

k = -0.47 + 1.38×ST – 0.47×FET (Δ_i = -0.70) (6)

3.3. Reed Canary Grass

The best model predicting reed canary grass decomposition rate (Table 4; Appendix P) was the {AT + WPH} model; however, the second best model {ST} had a Δ_i = 1.81 and a w_i = 0.21 and therefore also was given substantial support. All other models had $\Delta_i > 2$. We averaged the top 2 models and obtained a final model:

k = -2.91 + 0.04×AT + 0.43×ST + 1.06×WPH (7)

We ran a set of *a posteriori* models and came up with 4 models that had lower Δ_i than our best model:

k = -2.26 + 1.67×ST + 1.08×FET + 1.19×WPH (Δ_i = -2.72) (8)

k = -4.13 + 0.06×AT + 1.60×FET + 1.65×WPH (Δ_i = -2.56) (9)

k = -3.88 + 0.06×AT + 0.42×ST + 1.68×FET + 1.61×WPH (Δ_i = -2.11) (10)

k = -2.13 + 1.42×ST + 1.17×WPH (Δ_i = -1.72) (11)

Three of the 4 *a posteriori* models have $\Delta_i < -2$. This lends them substantial Akaike support for being better than our *a priori* best {AT + WPH} model. Though the *a posteriori* models lend support to the parameters in our averaged *a priori* model, when we ran the parameters from our averaged model it had a $\Delta_i = 3.40$. The top 3 *a posteriori* models also include FET, which is not included in our *a priori* top models and therefore is not in our averaged model. The top model from our *a posteriori* models has the same parameters as the averaged model for the brookside alder litter. Based on w_i, the {ST + FET + WPH} model is 6.0 times more likely to be the best explanation of decomposition rate than our averaged {AT + ST + WPH} model.

3.4. Common rush

The {AT + FET} model best predicted common rush decomposition rate (Table 4; Appendix Q); however, the second best model {AT} had a $\Delta_i = 0.49$ and therefore was also given substantial support. When the 2 models were averaged we obtained:

$$k = 0.10 + 0.05 \times AT + 0.42 \times FET \quad (12)$$

We ran 2 additional *a posteriori* models, but both had $\Delta_i > 2$ and therefore did not have much support compared to our top *a priori* models.

3.5. Broadleaf Cattail

The {FET} model best predicted decomposition rate (Table 4; Appendix R); however, the second best model {HP} had a $\Delta_i = 0.32$ and the third best model {HP + FET} had a $\Delta_i = 0.77$, therefore they also were given substantial support. When the 3 models were averaged we obtained:

$$k = 0.33 - 0.11 \times HP + 0.51 \times FET \quad (13)$$

Based on the results of the *a priori* models we ran 3 *a posteriori* models, but the models had $\Delta_i > 2$ and therefore did not have much support compared to our top *a priori* models.

3.6. Mixed Litter

Only one *a priori* model received substantial Akaike support (Table 4; Appendix S):

$$k = -0.88 + 0.03 \times AT + 0.77 \times WPH \quad (14)$$

Two *a posteriori* models were run, but only one had $\Delta_i < 2$:

$$k = -1.15 + 0.04 \times AT + 0.81 \times FET + 0.84 \times WPH \quad (\Delta_i = -2.60) \quad (15)$$

Based on w_i, the *a posteriori* {AT + FET + WPH} model is 3.7 times more likely to be the best explanation of decomposition rate compared to the *a priori* {AT + WPH} model.

4. Discussion

4.1. Brookside Alder

The brookside alder model suggests that both inundated and exposed conditions, and the number of times these conditions alternate, influence decomposition rate of brookside alder. It is important to note that ST and WPH were directly related with decomposition rate, while FET was inversely related. This agrees with other studies that have shown temperature to increase decomposition rate (Morris and Lajtha, 1986; Middleton et al., 1992; Álvarez and Bécares, 2006). It is also interesting to note that ST predicted brookside alder decomposition rate better than AT, stressing the importance of microhabitat conditions over landscape conditions.

The direct WPH relation makes sense because wetlands tend to be acidic and low WPH inhibits decomposition (Day Jr., 1987; Kittle et al., 1995; Taylor and Middleton, 2004). The inverse relation of FET with decomposition conflicts with some past studies that indicate alternating wetting and drying (Battle and Golladay, 2001; Anderson and Smith, 2002; Guo et al., 2008) are generally directly correlated with decomposition rate. It is possible that exposed conditions decreased decomposition by allowing the litter (van der Valk et al., 1991) and soil (Battle and Golladay, 2007) to desiccate, which also would have made conditions less hospitable to invertebrates and microbial organisms. It also is possible that there was more FET than is ideal for decomposition. Lockaby et al. (1996) found that a single, relatively brief inundation period had the greatest positive influence on decomposition rate. Every time conditions change from flooded to exposed or vice versa, invertebrate and microbial communities change. Frequent changes may then decrease decomposition by hindering biological forces that contribute to litter processing.

4.2. Reed Canary Grass

Our models suggest that temperature when litter is exposed (air and soil), and WPH when litter is flooded, are the most important parameters driving decomposition. Decomposition rate had a direct relation with soil temperature and water pH. This agrees with Hough and Cole (2009), who found soil pH to influence reed canary grass decomposition rate. The model also shows a direct relation among decomposition and AT, which agrees with the literature. Unlike any of the other litter types, reed canary grass decomposition rate is best predicted by both ST and AT, suggesting it is strongly influenced by both rapidly fluctuating air temperatures and the more stable soil temperatures. *A posteriori* models suggest that FET is important for reed canary grass as well and supports FET as being an important component among litter types.

4.3. Common Rush

Unlike the models for brookside alder and reed canary grass, ST was not included in the top models for common rush. Common rush has a less dense leaf structure than brookside alder or reed canary grass, with leaves containing arenchyma tissue. It is possible that the structure of the leaves retained moisture better, making them less prone to high ST and drying during exposed periods. Despite several studies (Carpenter et al., 1983; Kittle et al., 1995) indicating common rush decomposition rates to be impeded by low pH, WPH was not included in our top models. We believe that WPH did not vary enough among stakes to significantly influence common rush decomposition rate.

In contrast to brookside alder, FET is directly related to common rush decomposition rate, which suggests that more transition events between flooded and exposed conditions increases decomposition rate and agrees with past studies. It is possible that terrestrial and aquatic communities provide different roles and condition the litter differently. When leaf litter

transitions from flooded to exposed and back, the communities of organisms work in tandem to decompose the litter. More transitions allow each community of organisms more opportunities to access the litter. This tandem processing may be more important for common rush than brookside alder, causing transitions to directly influence common rush decomposition rates. In contrast, brookside alder may only be processed quickly by aquatic or terrestrial communities, but not both. Changes between flooded and exposed conditions would therefore slow the decomposition rate of brookside alder.

4.4. Broadleaf Cattail

The averaged model for broadleaf cattail decomposition rate was similar to the common rush model with regards to FET being directly related to decomposition rate. Broadleaf cattail, like common rush, has arenchyma tissue and may decompose similarly. The top models for broadleaf cattail decomposition rate also did not include WPH, which is only true of it and common rush. However, unlike the models for the other species, the broadleaf cattail model was the only one that did not have a temperature parameter. This contradicts previous cattail studies that found temperature influenced decomposition rate (Morris and Lajtha, 1986; Álvarez and Bécares, 2006).

It also was the only model to include HP, with a negative value implying that longer flooding periods led to lower decomposition rates. This agreed with Atkinson and Cairns (2001) who used broadleaf cattail in their decomposition study and found that slower decomposition rates were associated with longer hydroperiods. They suggested that longer hydroperiods created anaerobic conditions that slowed microbial efficiency. Intermittent flooding may lead to higher decomposition rates for cattail than permanently flooded conditions (van der Valk et al., 1991). However, others have found that more rapid decomposition occurs when litter is flooded

(Middleton et al., 1992). Our study suggests that more frequent changes between flooded and exposed conditions, along with shorter periods of flooding, led to the fastest broadleaf cattail decomposition rates.

4.5. Mixed Litter

Because the mixed litter is comprised of brookside alder, reed canary grass, and common rush, it is not surprising that the model parameters would be a combination of those found in the other 3 species. Both AT and WPH are included in 2 of the averaged, single species models and are directly related with decomposition rate. Interestingly, ST is not included in the model, despite being included for both the reed canary grass and brookside alder models. The lack of ST in the model may suggest that common rush is having a significant influence on the mixed litter's decomposition, even though it is only 1/3 of the leaf litter by mass. The *a posteriori* model containing {AT + FET + WPH} estimates a positive value for {FET}, which is similar to common rush but dissimilar to brookside alder and also supports the hypothesis that common rush is more strongly influencing the parameters effecting the mixed litter than the other two species. If common rush is indeed retaining moisture longer than the other 2 species, it is possible that it is influencing their decomposition rates.

4.6 Management Implications and Conclusions

It is important that compensatory mitigation projects create conditions that will lead to ecological functions similar to those lost. Faster decomposition rates allow for less carbon sequestration and organic matter being released back into adjacent streams; however, slower decomposition rates lead to slower nutrient cycling, which can reduce primary productivity and cause impacts up the food chain. Therefore, rates similar to natural systems are most ideal.

Establishing natural estimates of litter decomposition in wetlands also could allow decomposition to be incorporated into wetland assessments and used to judge landscape functional trends at the state and regional levels. In 2011, the EPA plans to conduct a National Wetland Condition Assessment (USEPA, 2009), and the inclusion of litter decomposition could establish regional norms for decomposition, allowing better understanding and assessment of wetland function.

We found that 5 parameters, air and soil temperature, water pH, hydroperiod, and the number of transitions between flooded and exposed, were in the top models for our 5 litter types. Air temperature was directly related with the decomposition rate of reed canary grass, common rush, and the mixed litter; soil temperature was directly related to decomposition rates of brookside alder and reed canary grass. Water pH was directly related to decomposition rates of brookside alder, reed canary grass, and the mixed litter. Hydroperiod was inversely related to broadleaf cattail decomposition rate. The number of transitions between flooded and exposed conditions was inversely related to brookside alder decomposition rate, but directly related to broadleaf cattail and common rush decomposition rates. Water temperature, water depth, the sum fluctuation of the water depth, soil moisture, and the number of days litter was in the wetland were excluded from top models and were not as strongly associated with decomposition rates as parameters in the averaged models. Also, our mixed litter suggested that common rush may influence the decomposition of reed canary grass and brookside alder.

Environmental conditions driving wetland functions need to be considered when planning wetland creation projects and addressed in criteria to judge wetland functional success. Because different mixes of environmental forces influence decomposition of different litter types, it is important that heterogeneity is incorporated into wetland creation projects. Varying hydrology

and water depths influence decomposition directly, but also lead to varying vegetation communities, which can influence air and soil temperature. Hydrology can be determined, in part, by considering landscape placement (i.e., floodplain, depression, impounded headwater stream) of mitigation projects to match the lost natural wetlands (Hoeltje and Cole, 2007). We know of no simplistic way to influence water pH through wetland construction, but similar to hydrology, landscape placement can partly determine water pH. In West Virginia, where acid mine drainage (AMD) from coal mining acidifies streams and is a large problem, flooding of AMD streams into adjacent wetlands can retard litter decomposition rate (Kittle et al., 1995), thereby impeding natural wetland functions. Therefore, areas receiving AMD should be avoided for mitigation projects unless the mitigation is designed specifically to address AMD issues. Considerations of environmental variables will help ensure similar conditions to those lost and help create a wetland with similar litter decomposition rates and overall function.

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Table 1. List of 3 mitigated and 3 reference wetland study sites in West Virginia, including site name, county, closest town, year constructed, size (ha), elevation (m above sea level), wetland classifications, and dominant vegetative species, 2007-2009.

Site name	County and Closest Town	Year Created	Size (ha)	Elevation (m)	Wetland Classifications[a] at Site	Dominant Vegetative Species
Mitigated Sites						
Leading Creek	Montrose, Randolph Co.	1995	17.0	600	UB, AB, EP, **SS**[b], F	hop sedge (*Carex lupulina* Muhl. ex Willd.), common rush, woodland rush (*J. subcaudatus* var. *subcaudatus* (Engelm.) Coville&Blake), smartweed (*Polygonum hydropiperoides* Michx; *P. persicaria* L.), rice cutgrass (*Leersia oryzoides* (L.)Sw.), brookside alder
Sugar Creek	Meadowville, Barbour Co.	1995	11.0	490	AB, **EP**, SS	reed canary grass, wool grass (*Scirpus cyperinus* (L.)Kunth), woodland rush, American burreed (*Sparganium americanum* Nutt.), brookside alder
Hazelton	Hazelton, Preston Co.	2006	2.7	560	UB, AB, **EP**	broadleaf cattail, common rush, white clover (*Trifolium repens* L.), red clover (*T. pretense* L.), beggar-tick (*Bidens* sp.)
Reference Sites						
Meadowville	Meadowville,. Barbour Co	N/A	11.7	480	AB, EP, **SS**, F	broadleaf cattail, tussock sedge (*Carex stricta* Lam.), rice cutgrass, brookside alder
Upper Deckers Creek	Masontown, Preston Co.	N/A	2.1	515	UB, AB, **SS**, F	cowlily (*Nuphar lutea ssp. advena* (L.)Sm.(Ait.)), buttonbush (*Cephalanthus occidentalis* L.), brookside alder
Bruceton Mills	Bruceton Mills, Preston Co.	N/A	1.4	515	**EP**, SS	reed canary grass, rice cut grass, broadleaf cattail, brookside alder

[a] palustrine: unconsolidated bottom = UB, aquatic bed = AB, emergent persistent = EP, scrub-shrub = SS, forested = F (Cowardin et al. 1979)
[b] bold text indicates dominant classifications

Table 2. Mean, standard error (S.E.), minimum, and maximum results for decomposition of 5 litter types, expressed as decomposition rate constant *k* (yr^{-1}), in 3 mitigated and 3 reference wetlands in West Virginia, 2007 to 2009.

Litter Type	Mean	S.E.	Min	Max
Brookside Alder	0.432	0.016	0.159	1.074
Reed Canary Grass	0.718	0.019	0.399	1.513
Common Rush	0.571	0.016	0.109	1.026
Broadleaf Cattail	0.358	0.016	0.000	0.882
Mixed Litter[a]	0.649	0.017	0.262	1.164

[a] Mixed litter bags contained 3.3 g brookside alder, 6.6 g common rush, and 10.0 g of reed canary grass

Table 3. Mean, standard error (S.E.), and analysis of variance (ANOVA) results for 9 environmental parameters measured in 3 mitigated and 3 reference wetlands in West Virginia, December 2007 to December 2009. Averages were obtained by taking the mean of environmental measurements obtained at 96 stakes included in modeling of decomposition rate. Analysis of variance results compare environmental parameters among mitigated and reference wetlands (α = 0.05).

	Mitigated		Reference		Overall		F value	P value
	Mean	S.E.	Mean	S.E.	Mean	S.E.	(d.f. = 1,4)	
Air Temperature[a]	7.61	0.20	7.01	0.20	7.29	0.15	0.626	0.473
Water Temperature	9.01	0.29	8.39	0.30	8.72	0.22	0.546	0.501
Soil Temperature	14.45	0.67	11.88	0.42	12.67	0.37	5.470	0.079
Water Depth[b]	6.29	0.63	4.80	0.59	5.44	0.46	0.959	0.383
Hydroperiod[c]	0.46	0.02	0.45	0.03	0.45	0.02	0.042	0.847
No. of transitions between flooded and exposed[d]	0.019	0.001	0.021	0.001	0.020	0.001	0.035	0.862
Sum fluctuations[e]	0.42	0.04	0.38	0.04	0.39	0.03	0.066	0.811
Water pH	6.24	0.07	6.32	0.03	6.25	0.03	0.010	0.925
Soil Moisture[f]	7.35	0.22	8.90	0.10	8.19	0.14	2.338	0.201

[a] °C

[b] cm

[c] proportion of days

[d] no. of transitions / days

[e] cm / day

[f] 0 dry – 10 saturated

Table 4. *A priori* models predicting litter decomposition rate with substantial Akaike support. Ranking is based on Akaike's Information Criterion for small sample sizes (AIC_c), with smaller values indicating a better model fit. Air temperature (AT), soil temperature (ST), hydroperiod (HP), the number of transitions between flooded and exposed (FET), and water pH (WPH) were all found to have substantial support for at least one of the litter types.

Model structure	**AIC_c**	**K[a]**	**Δ_i[b]**	**w_i[c]**
Brookside Alder				
k = -2.00 + 1.50×ST	75.99	4	0.00	0.37
k = -0.74 - 1.29×FET	77.04	4	1.05	0.22
k = -2.74 + 0.98×WPH	77.72	4	1.73	0.16
Reed Canary Grass				
k = -3.59 + 0.05×AT + 1.53×WPH	3.38	5	0.00	0.52
k = -1.38 + 1.39×ST	4.97	4	1.59	0.24
Common Rush				
k = 0.04 + 0.06×AT + 0.77×FET	-92.32	5	0.00	0.45
k = 0.18 + 0.05×AT	-92.05	4	0.27	0.39
Broadleaf Cattail				
k = 0.22 + 0.94×FET	-87.22	4	0.00	0.31
k = 0.44 - 0.20×HP	-86.89	4	0.32	0.26
k = 0.36 - 0.17×HP + 0.52×FET	-86.23	5	0.99	0.19
Mixed Litter				
k = -0.88 + 0.03×AT + 0.77×WPH	-171.05	5	0.00	0.98

[a] K = number of parameters, including intercept and error
[b] $\Delta_i = AIC_{c\ lowest} - AIC_{ci}$ for the i^{th} model in comparison
[c] w_i = Akaike weights

Table 5. Parameter estimates, standard errors (SE), and 95% confidence intervals for averaged models[a] predicting decomposition rate constant k (yr^{-1}) of each litter type.

				95% CI	
Model	**Parameter[b]**	**Estimate**	**SE**	**Lower**	**Upper**
Brookside Alder	Intercept	-1.78	5.48	-12.47	8.90
	WPH	0.21	0.27	-0.32	0.74
	FET	-0.38	2.23	-4.73	3.97
	ST	0.74	0.82	-0.86	2.35
Reed Canary Grass	Intercept	-2.91	3.69	-10.10	4.27
	AT	0.04	0.00	0.04	0.04
	WPH	1.06	0.15	0.77	1.35
	ST	0.43	0.49	-0.52	1.37
Common Rush	Intercept	0.10	0.00	0.10	0.10
	AT	0.05	0.00	0.05	0.05
	FET	0.42	0.12	0.18	0.65
Broadleaf Cattail	Intercept	0.33	0.00	0.33	0.33
	HP	-0.11	0.00	-0.11	-0.11
	FET	0.51	0.18	0.16	0.86
Mixed Litter	Intercept	-0.88	0.37	-1.60	-0.16
	AT	0.03	0.01	0.02	0.04
	WPH	0.77	0.19	0.40	1.15

[a] Models were averaged for brookside alder, reed canary grass, common rush, and broadleaf cattail because more than one model predicting litter decomposition rate had substantial Akaike support.

[b] AT = air temperature, ST = soil temperature, HP = hydroperiod, FET = number of transitions between flooded and exposed, and WPH = water pH

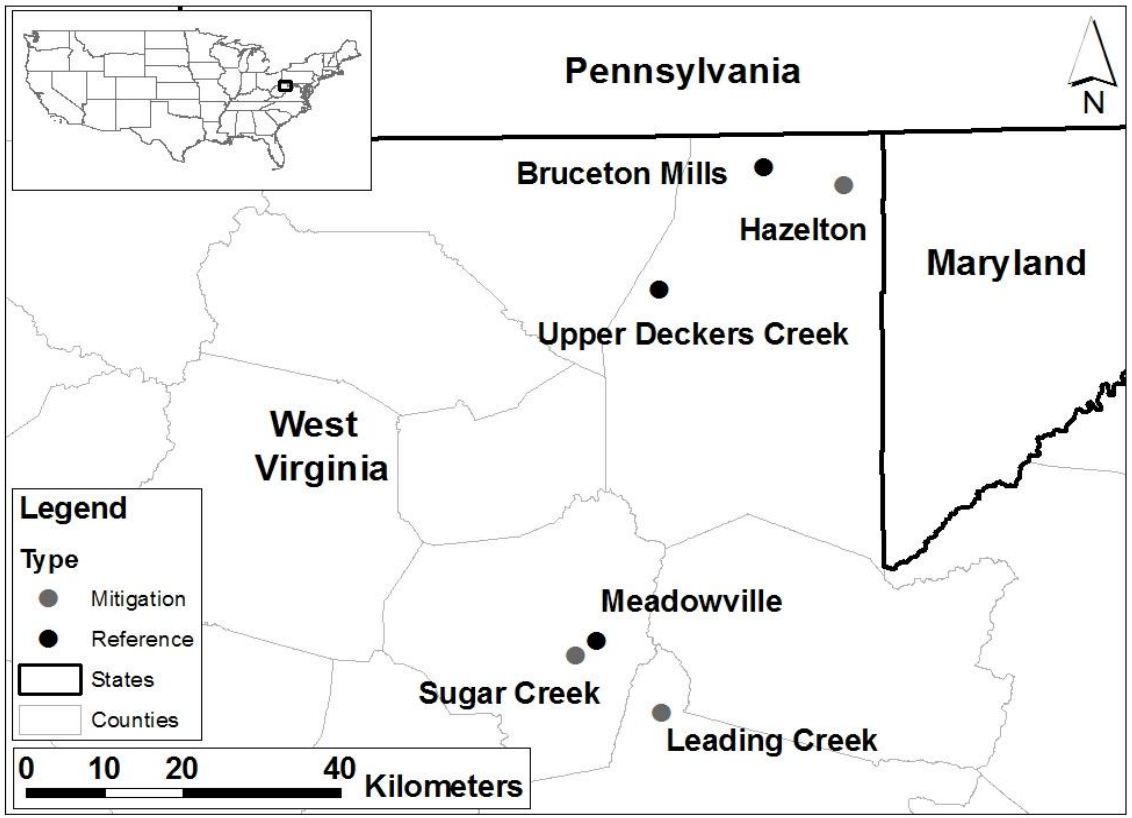

Figure 1. Six study sites, comprised of 3 mitigated and 3 reference wetlands, in the Allegheny Mountain region of West Virginia, USA, 2007-2009.

CHAPTER 5

Biological Influences on Litter Decomposition in Mid-Atlantic Highland, USA Wetlands

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Summary

1. Wetland plant litter decomposition influences many wetland processes, and is itself driven by a complex web of interacting parameters. Invertebrates and microbes make up one portion of that web by processing organic material; however, their role is poorly understood.

2. To explore invertebrate and fungal influence on plant litter decomposition rate, we measured the decomposition of litter in three mitigated and three reference wetlands in the Mid-Atlantic Highlands of West Virginia, USA.

3. Litter decomposition rates and most invertebrate metrics were not statistically different among mitigated and reference wetlands; only oligochaetes (worms) and the functional feeding group (FFG) collector/gatherers had numbers that were statistically higher in mitigated wetlands.

4. Invertebrate metrics were able to explain 24.9 (FFG) to 30.9% (taxonomic groups) of variance in decomposition during the early phases (< 224 days) and 14.9 (FFG) to 21.4% (taxonomic groups) of the variance in the later phase (≥ 224 days) of litter decomposition. Shredders, collector/gatherers, and omnivores were more strongly associated with early phases of decomposition, while oligochaetes and omnivores were most strongly associated with trends in decomposition during the later phase.

5. Fungal biomass, as measured by ergosterol concentration, was similar among wetlands types, but was significantly higher in early phases of litter decomposition than the later phase.

6. *Synthesis*. Decomposition influences many aspects of wetland function, making the variables that determine decomposition rates important to understand. These results show that decomposition rates are similar between mitigated and reference wetlands, and that invertebrate community composition influences decomposition. Understanding these interactions is crucial to being able to assess and mitigate for lost wetland function.

Introduction

To understand functions provided by wetlands, it is important to understand the web of interacting forces that drive those functions. Litter decomposition is an example of a process that is linked to many other wetland processes, including physical and chemical properties of wetland soils (Mitsch & Gosselink 2007), nutrient availability and cycling (Prentki, Gustafson & Adams 1978; Facelli & Pickett 1991), primary production (Brinson, Lugo & Brown 1981), and litter/organic matter accumulation (Gambrell & Patrick Jr. 1978; Xiong & Nilsson 1997). These processes are then linked with other processes and create a chain of interactions that determine wetland function.

Decomposition is driven by biotic (microorganisms and invertebrates that break down litter), physical (environmental conditions the litter encounters), and chemical (composition of the litter) variables (Aerts & de Caluwe 1997). These three variables interact to drive decomposition through three phases (Godshalk & Wetzel 1978; Brinson, Lugo & Brown 1981). The first phase, rapid loss of mass from leaching, occurs within 48-92 h of inundation, and is largely influenced by physical variables (Webster & Benfield 1986; Nykvist 1962). The second phase of decomposition begins as rapid leaching ends and involves the colonization of litter by microbial organisms which break down soft tissues. The third and final phase of decomposition involves mechanical fragmentation of the litter by physical forces and invertebrates (Hieber & Gessner 2002; Fazi & Rossi 2000; Hutchens Jr. & Wallace 2002).

Biological forces exert influence over two of the three phases. Depending on the time of year and stage of the second phase, bacteria (Howard-Williams & Davies 1978; Robb *et al.* 1979) or fungi (Barlocher & Kendrick 1974; Findlay, Dye & Kuehn 2002; Gessner & Chauvet 1994) can drive decomposition rates. Litter exposed to the air is mostly decomposed by fungi

(Holland & Coleman 1987; Facelli & Pickett 1991) and submerged litter is primarily processed by bacteria; however, fungi also can be important in submerged conditions (Mason 1976; Gessner & Chauvet 1994; Bauer *et al.* 2003). Some studies have attributed as much as 7 to 30% of litter mass loss to microbial activities (Petersen & Cummins 1974; Hieber & Gessner 2002).

Many studies have shown differences in decomposition rates and attributed them to macroinvertebrate and detritivore presence or absence (Mason & Bryant 1975; Coulson & Butterfield 1978; Kemp, Conner & Day 1985; Hutchens Jr. & Wallace 2002; Kirby 1992) and many controlled studies have directly observed decomposition rate increasing with macroinvertebrate density (Cummins *et al.* 1973; Petersen & Cummins 1974; Herbst 1982; Fazi & Rossi 2000). Some previous studies have attributed as much as 29 to 64% of mass loss to invertebrate activity (Merritt & Lawson 1979; Hieber & Gessner 2002). Invertebrates belonging to the functional feeding group (FFG) shredders and detritivores are often credited with contributing the greatest influence (Cuffney & Wallace 1987; Graca 1993; Webster & Benfield 1986).

Mesh litter bags have long been used to assess both decomposition rates and the role of macroinvertebrates on decomposition (Witkamp & Olson 1963; Merritt & Lawson 1979; Stewart & Davies 1989). By using multiple mesh sizes, invertebrates can be excluded from or allowed access to the litter creating a continuum that can be studied. In this study, we used two sizes of mesh litter bags to study the role of invertebrates on decomposition. Specifically, our objectives were to determine to what extent invertebrates contributed to litter decomposition rate in six wetlands in the Mid-Atlantic Highlands, USA. Our second objective was to determine if decomposition rates were correlated with fungal biomass, and, if so, to determine how the

influence of fungal biomass on litter decomposition compared with the influence of invertebrates.

Materials and methods

Study Area

Leaf breakdown rates were measured at three mitigated and three reference wetlands located in the Mid-Atlantic Highlands region of West Virginia, USA (Figure 1). The three mitigated wetlands (Leading Creek, Sugar Creek, Hazelton) were constructed by the West Virginia Division of Highways (WVDOH) to compensate for wetland losses associated with the Corridor H and Mon-Fayette Expressway system projects (Table 1). The three reference wetlands (Meadowville, Upper Deckers Creek, Bruceton Mills) were chosen based on their proximity to mitigated sites (to minimize differences in climatic events); similarity in elevation, size, and wetland classification; and their relative degree of disturbance. All wetlands were associated with streams and received water from overbank flooding, with hillslope runoff and groundwater being additional sources of water. All wetlands had a mixture of flooded and exposed conditions for the majority of the year, with brief periods of deeper flooding, but mitigated wetlands tended to have a higher percentage of open water and ponded areas than reference sites. Reference sites tended to have more scrub-shrub areas than the mitigated sites and Leading Creek, Meadowville, and Upper Deckers Creek had portions of scrub-shrub and young forest. All wetlands had some level of disturbance on their edge in the form of roads, grazing, or cultivated land.

Decomposition (Litterbag) Procedures

We collected (September – October 2007) three litter species (common rush [*Juncus effusus* L.], brookside alder [*Alnus serrulata* (Ait.)Willd.], and reed canary grass [*Phalaris arundinacea* L.]) based on common dominant species at mitigated and reference sites in West Virginia (Balcombe *et al.* 2005a; Veselka IV 2008) and used the litter bag method to compute litter decomposition rates (Benfield 1996). Litter mixes can have non-additive decomposition rates compared to single species (Gartner & Cardon 2004), therefore 20 g of litter was created from a mix of 3:2:1 reed canary grass (10 g), common rush (6.6 g), and brookside alder (3.3 g) in an attempt to mimic ratios present in the wetlands (Balcombe *et al.* 2005a; Veselka IV 2008).

To minimize variability, reed canary grass and common rush leaves and stems were clipped and collected as they senesced, but while still standing (Marsh *et al.* 2000; Bedford 2005). We collected brookside alder leaves with a STIHL model SH 85 D Shredder Vacuum/Blower (STIHL Incorporated, Virginia Beach, VI) reversed to suck leaves into the tube. Brookside alder leaves that were not intact and any material other than alder leaves were discarded. To minimize differences in litter quality, each species was collected from only one area in a single wetland (Baker *et al.* 2001; Fennessy, Rokosch & Mack 2008; Aerts & de Caluwe 1997). We air-dried all litter for a minimum of 1 week before weighing and bagging it.

We constructed 20 × 20 cm litter bags from 1.27 mm (fine) and 2.8 mm (coarse) vinyl-coated fiberglass window mesh (Benfield 1996). Litter bags were constructed with one folded side and three sides heat sealed, and reinforced with stainless steel staples at 5-cm intervals (Deghi, Ewel & Mitsch 1980). Each bag was uniquely marked with a plastic tag (Davis & van der Valk 1978; Vargo, Neely & Kirkwood 1998).

Nine transects were established, using stratified sampling (Taylor and Middleton 2004), to represent aerial proportions of environmental conditions, as determined by major vegetation communities, within each wetland. Ten wooden stakes were installed at 7.5 m intervals along each transect and one fine and one coarse-mesh bag was attached to the base of each stake with 0.5 m lengths of nylon fishing line (Battle & Golladay 2001; Anderson & Smith 2002). Litter bags were placed flat on bare ground or on top of any existing litter to mimic natural litter deposition. If the stake was located in standing water, the litter bag was first dunked to completely inundate the surface and minimize any hydrophobic effect the mesh might contribute and then allowed to float or sink without interference.

In December 2007, ninety of each type of litter bag (180 total) were placed in each wetland for a total of 1,080 litter bags. Extra litter bags (1.5x the collected number) were placed in wetlands to compensate for anticipated litter bag losses from environmental disturbance (e.g., currents during flooding) and destruction from wildlife. Six replicates of each litter type were retrieved the same day the bags were placed in the field to calculate the loss of mass due to handling (Benfield 1996). Four replicates were then retrieved on 14 different dates: at 7 days (1 week), 21 days (3 weeks), 35 days (5 weeks), 49 days (7 weeks), 77 days (11 weeks), 119 days (17 weeks), 168 days (24 weeks), 224 days (32 weeks), 294 days (42 weeks), 364 days (52 weeks), 455 (65 weeks), 546 days (78 weeks), 637 days (91 weeks) and 728 days (104 weeks). We sampled the four replicates by collecting all litter bags from four randomly chosen stakes in each wetland. A total of 686 litter bags were collected.

Litter bags were transported to the lab on ice, cleared of external material, and opened. Litter was rinsed from the interior of the bag into a 500 μm sieve and sediment was rinsed off. Invertebrates were picked from the litter and preserved in 80% ethanol. We oven-dried (65° C)

leaf litter for 7 - 9 days until a constant mass was reached (Morris & Lajtha 1986; Lockaby, Murphy & Somers 1996), recorded mass, and ground the litter to a powder in a 2-mm mesh Thomas Wiley Mill (Thomas Scientific, Swedesboro, NJ). Three subsamples of the ground litter were then incinerated to calculate ash-free dry mass (AFDM), which was used for statistical analysis.

Invertebrates

We identified invertebrates to family, FFG, and tallied individuals (Merrit & Cummins 1996; Bland & Jaques 1978; Chu & Cutkomp 1992; Peckarsky *et al.* 1990; Ubick *et al.* 2005; Stehr 1991; Wolfenbarger *et al.* 2008; Dindal 1990). Some individuals proved problematic to identify to family, therefore leeches (Hirundinea), worms (Oligochaeta), and mites (Acarni) were identified to subclass and slugs (Stylommatophora) were identified to order, but were considered equivalent and included in analysis with families. Taxonomic groups that could not be identified to specific feeding guilds (scrapers, filterers, predators, collector/gatherers, shredders) were identified to the general groups of herbivores, omnivores or predators. Because terrestrial invertebrates have greater diversity and less available information on their FFG, they were often identified as herbivores, omnivores, or predators and made up a larger portion of those groups than aquatic species. Total dry mass of oligochaetes was 2.5x greater than the next taxonomic group, therefore they were separated out into their own group for FFG analysis. Total biomass and detritivore metrics were calculated both with and without the inclusion of oligochaetes. Richness was expressed as the number of taxonomic groups/litter bag. Biomass (mg/litter bag) was obtained by oven-drying samples at 55 °C for ≥48 h to a constant mass (0.0001 g) and using an analytic scale (Balcombe *et al.* 2005b).

Ergosterol

Fungal biomass was estimated by the extraction and quantification of ergosterol from ground litter (Kuehn *et al.* 2000; Newell, Arsuffi & Fallon 1988) using a modified form of the cold ethanol procedure described in Richardson and Logendra (1997). We mixed 0.2 g of ground litter and 1 mL of absolute ethanol in 2-mL, screw-cap microcentrifuge tubes (Fisher Scientific, Pittsburgh, PA) in a FastPrep FP120 (Q-biogene, Irvine,CA) with agitation at 6.0 m/s for 30 s. Ergosterol was then extracted for 30 min by rotating, end-over-end at 15 rpm, on a Glas-Col (Terre Haute, IN) mini-rotator. Samples were centrifuged for 10 min at 10,000 rpm in a VSB-14 microcentrifuge (Shelton Scientific, Shelton, CT) before the supernatant was removed and filtered, through a 0.22-µm nylon filter microcentrifuge tube (Costar, Corning, NY), by centrifugation for 2 min at 10,000 rpm.

Ergosterol was analyzed by high-performance liquid chromatography (HPLC) on a 150 mm × 4.6 mm Phenomenex Prodigy 5-µm ODS3 reverse phase C18 column (Phenomenex, Torrance, CA). HPLC conditions were described previously (Panaccione & Coyle 2005) and consisted of a model 600 pump controller with an in-line degasser, a model 717plus autosampler, and a model 2487 absorbance detector (all from Waters Corp., Milford, MA). Samples were eluted isocratically with 100% methanol at a flow rate of 1.0 mL min^{-1}, and peaks were monitored at 280 nm. Ergosterol eluted at ~9.0 min and was quantitated by the external standard method using a pure compound (UV absorption in MeOH, λ_{max} = 282 with shoulders at 269 and 293) obtained from a commercial source (MP Biomedicals, Solon, OH). The presence of ergosterol was confirmed by comparison of HPLC retention times and UV absorption between the unknown peak and pure standard (Appendix T). Ergosterol is expressed as µg ergosterol mg^{-1} dry weight litter.

Data Analysis

We used an exponential decay rate to model leaf litter decomposition and calculate decomposition rate:

$$y_t / y_o = e^{-kt} \quad \text{eqn 1}$$

where k is the instantaneous decomposition rate constant (year $^{-1}$), y_t is the AFDM at time t (years), and y_o is the initial AFDM (Olson 1963; Brock *et al.* 1985).

Normality was checked using the Shapiro-Wilk test (shapiro.test {stats}) in Program R (version 2.10.1) and parameters were transformed to more closely approximate normality. All count data were log transformed, decomposition rate of litter was inverse square root ([1/-(sqrt x)] + 1) transformed, and ergosterol was sqrt transformed. Correlations between invertebrate metrics were checked visually using a scatterplot matrix (pairs {graphics}) and with the Pearson's correlation (cor {stats}) in Program R. Diversity and richness were highly correlated ($r > 0.75$), therefore richness was used because it was better able to predict litter decomposition (lower Akaike Information Criteria value) (Burnham and Anderson, 2002) diversity when tested in a single parameter regression model. Analysis of variance (ANOVA) tested the influence of mesh size (fine, coarse), wetland type (mitigated, reference), collection date, and biomass of invertebrate metrics (collected from litter bags) on decomposition rate using a linear mixed effects (lme {nlme}) model in Program R. Wetlands was treated as a random effect (i.e., factors we did not deliberately arrange, but which were sampled from a population of possible samples) and stakes were experimental units. Regression tree analysis was performed using mvpart {mvpart} in Program R to identify quantitative differences in decomposition rates based on the biomass of taxonomic groups, FFG, and all invertebrate metrics (De'ath & Fabricius 2000).

Regression trees were pruned, based on percent of variance explained, to prevent over-fitting the data.

Results

Decomposition

Decomposition was not statistically different between litter bag mesh sizes (Figure 2) and wetland types (Figure 3). Proportion of mass remaining for fine mesh ($\bar{x}$ = 28.3, S.E. = 1.8) and coarse mesh ($\bar{x}$ = 26.1, S.E. = 1.7) bags were similar ($F_{1,41}$ = 1.05, p = 0.312). Litter decomposition rate constants were rapid initially, likely due to rapid mass loss from leaching. They then continued to slow until 119 to 168 days, after which decomposition rates rose slightly and leveled off to an average rate of 0.69 year $^{-1}$ for the rest of the study period, with only slight fluctuations that were likely due to seasonal effects.

ANOVA indicated a significant interaction between wetland type and mesh size for decomposition rate constant (Table 2); therefore average decomposition rate constants of meshes were tested within each wetland type. For mitigated wetlands, mean k for fine mesh ($\bar{x}$ = 0.69, S.E. = 0.04) and coarse mesh ($\bar{x}$ = 0.78, S.E. = 0.04) bags were not significantly different ($F_{1,315}$ = 3.60, p = 0.059). For reference wetlands, mean k for fine mesh ($\bar{x}$ = 0.87, S.E. = 0.06) and coarse mesh ($\bar{x}$ = 0.77, S.E. = 0.04) bags were again not significant ($F_{1,320}$ = 1.38, p = 0.241). The significant interaction therefore was a product of fine mesh bags having a higher decomposition rate in reference wetlands, but a lower mean rate in mitigated wetlands. Collection date also was significant, indicating that rates changed over time. Because decomposition rate was similar among mesh sizes and wetland types, all litter bags were combined for invertebrate analysis.

Invertebrates

We picked 7,973 individuals from the 642 collected litter bags and identified them to 125 taxonomic groups (120 families, one order, and four subclasses; Appendix U). Oligochaetes (worms), formicids (ants), and stylommatophores (slugs) accounted for 78.7% of the total biomass (9,696 mg dry mass) of invertebrates collected (Table 3). Formicids, chironomids (midge larvae), oligochaetes, and asellids (aquatic pill bugs) accounted for 67.5% of total individuals picked from litter bags. Invertebrates were significantly higher by mass in coarse mesh litter bags than fine mesh bags for nearly all metrics (Table 4). Only mean diversity was higher in fine mesh bags and only shredder, scraper and oligochaete biomasses were similar between coarse and fine mesh bags. Predators were the most abundant FFG, accounting for 72.2% of dry mass. Herbivores were the second most abundant feeders in litter bags, accounting for 13.2% of dry mass. When oligochaetes were included within the grouping of detritivores, it comprised 13.0% by mass; but when oligochaetes were removed only 1.2% of dry mass was detritivores. Collector gatherers were 12.5% of dry mass when oligochaetes were grouped with them, but only 0.75% when oligochaetes were excluded. Only 2.7% of individuals (0.93% by mass) could not be placed in any functional feeding group.

Most invertebrate metrics were similar between mitigated and reference wetlands (Table 4). A total of 4,099 individuals (72.9% by mass) were collected from mitigated wetland bags and 3,874 individuals (27.1% by mass) were collected from reference wetland bags. Differences in mass between wetland types were mostly due to oligochates, with total biomass including oligochaetes, detritivore biomass including oligochaetes, and oligochaetes all being significantly higher in mitigated wetlands. Collector/gatherers also were significantly higher in mitigated

wetlands. Reference wetlands had higher mean richness, diversity, predator biomass, filterer biomass, and omnivore biomass, but none were significantly different.

Biomass for most FFG peaked prior to 224 days, then decreased and leveled off for the remainder of the study (Figure 4); only oligochaetes peaked later, at 546 days. Because of this shift in invertebrate composition, regression tree analysis was run on phases 1 and 2 (early phases, < 224 days) of decomposition separately from phase 3 (late phase, ≥ 224 days). It revealed that in the early phases of decomposition, trends in limnephilids (shredder caddisfly) were most strongly associated with high decomposition rates, but when limnephilids were < 0.15 mg then decomposition was lower and slugs were associated with decomposition (Figure 5, Appendix V). Higher larval dytiscid (predatory beetle) biomass also was associated with higher decomposition rates. In the later phase of decomposition (Figure 6, Appendix W), adult hydrophilids (collector/gatherer beetle) were most strongly associated with higher decomposition rates, followed by oligochaetes.

High collector/gatherer biomass along with high shredder biomass led to the largest decomposition rates during early phases (Figure 7, Appendix X). When collector/gatherer biomass was low, omnivore biomass determined decomposition rates followed by herbivore biomass. In late phase decomposition (Figure 8, Appendix Y), higher rates were associated primarily with oligochaete biomass, followed by omnivores.

When all invertebrate metrics were analyzed together, taxonomic groups were the most strongly associated metric with decomposition rate and the regression tree yielded the same results as taxonomic groups only (Figure 5, Appendix Z). The late phase regression tree, however, was a mix of invertebrate metrics, FFG, and taxa (Figure 9, Appendix AA). Adult hydrophilids were associated with the largest decomposition rates, but when they were < 1.43

mg, oligochaetes were associated with higher decomposition rates. Higher taxonomic richness and total biomass also led to the fastest decomposition rates.

Fungi

Fungi colonized the litter quickly, peaking at 35 days and again with a smaller peak at 77 days (Figure 10). Early phases of decomposition had a mean ergosterol of 0.083 μg mg $^{-1}$ dry litter (S.E. = 0.004), while the late phase of decomposition had a mean ergosterol of 0.052 μg mg^{-1} dry litter (S.E. = 0.004), which was significantly less ($F_{1,312} = 33.62$, $p < 0.001$). Overall mean ergosterol was 0.067 μg mg $^{-1}$ dry litter (S.E. = 0.003), but was not significantly ($F_{1,234} = 1.17$, $p = 0.280$) related to overall decomposition rate. When early and late phase ergosterol and decomposition were tested separately, ergosterol did not significantly predict decomposition for either phase (early: $F_{1,151} = 0.46$, $p = 0.499$; late: $F_{1,154} = 0.154$, $p = 0.695$). Concentrations of ergosterol in leaf litter (Appendix BB) were similar ($F_{1,4} = 0.017$, $p = 0.902$) between mitigated ($\bar{x} = 0.065$, S.E. = 0.004) and reference ($\bar{x} = 0.067$, S.E. = 0.004) wetlands.

Discussion

Litter Decomposition

Litter decomposition in mitigated and reference wetlands was not statistically different, which is supported by results found in several other studies (Álvarez & Bécares 2006; Gingerich 2010: Chapter 2 & 3). Decomposition was not statistically different between two different mesh sizes, suggesting that mesh size and the inclusion or exclusion of invertebrates did not influence decomposition, as has been suggested (Brinson, Lugo & Brown 1981; Stewart & Davies 1989). Litter decomposition rates did change over time before leveling out between 119 and 224 days.

Transitions between phase 2 and phase 3 of decomposition may be marked by the leveling out of decomposition rate and decreased presence of invertebrates and fungi.

Invertebrates

Invertebrates were significantly different between coarse and fine mesh bags for nearly all metrics analyzed; however, decomposition rates were similar, implying that invertebrates did not strongly influence decomposition rates, which is similar to other studies (Mason & Bryant 1975; Coulson & Butterfield 1978). Regression tree analysis revealed trends in invertebrates associated with decomposition. In early phases of decomposition, soft leaf tissue and high fungal colonization attracted many invertebrates to the decomposing litter. Collector/gatherers, shredders and omnivore numbers peaked and high prey numbers attracted predators. As the litter decomposition transitioned from the early phases into the late phase, most invertebrate numbers declined and leveled off, except oligochaetes whose numbers increased. This may be because oligochaetes were able to process the remaining tougher tissues of the litter, or because over time the litter bags were better incorporated into the top soil horizon, allowing oligochaetes better access to the material.

When all metrics were analyzed collectively, taxonomic groups were more strongly associated with trends in decomposing litter than FFG, abundance, richness, or diversity. This suggests that within FFG, certain taxa were more strongly associated with decomposition, and possibly contributed more to decomposition rate, than the group as a whole. As invertebrate numbers declined in late phase decomposition, taxa richness and total biomass became more important, but were still preceded in the regression tree by individual taxa.

Several hypotheses may explain the lack of strong invertebrate associations with decomposition. First, invertebrate communities sampled from litter bags may not adequately

reflect natural community composition (Dobson 1991). All litter bags were collected during the middle of the day, which may have poorly represented invertebrates with diel migrations, such as oligochaetes (Erman 1973) and chironomids (Ola, Irmgard & Anders 2001). Second, predator abundances are likely influencing decomposition through top-down control of decomposers. Predator numbers were extremely high in litter bags and predator taxa were included in regression trees indicating trends strongly associated with decomposition rate. Finally, it is possible that invertebrates did not strongly influence decomposition (Álvarez & Bécares 2006; Hanlon 1982), or influenced decomposition in a way that was not captured by our metrics.

Fungi

Our study confirmed the increased presence of fungi in decomposing litter between 0 and 300 days, but fungal biomass was not a useful predictor of decomposition rate. During early phases of decomposition microbes condition the plant litter, taking advantage of nutrients being released during the breakdown process and facilitating decomposition. Once most nutrients have been leached and soft material has been broken down, decomposition passes into its third phase and the role of microbes diminishes (Godshalk & Wetzel 1978; Brinson, Lugo & Brown 1981). This is supported by the decline and leveling off of ergosterol levels around 300 days. A second increase in fungi occurs between 546 and 639 days, but is likely due to environmental conditions and not the decomposing litter.

This is one of only a few studies comparing fungi in created and reference wetlands, and the only study that has compared fungi in created and reference wetlands using litter decomposition as a basis. Confer and Niering (1992) compared mycorrhizae in roots in created and natural wetlands and found that they were higher in created wetlands, attributing the difference to higher nutrient availability. The fact that ergosterol levels were similar in litter

from mitigated and reference wetlands indicated that fungal biomass involved with decomposition are similar among wetland types and suggests that mitigated wetlands in the Mid-Atlantic Highlands region are functioning similarly to natural wetlands at the microbial level.

Conclusion

Overall, litter decomposition rates were similar among mitigated and reference wetlands and across varying invertebrate communities. Invertebrates were more abundant in coarse mesh bags and were comparable or more abundant in mitigated wetlands. Oligochates and collector/gatherer numbers were higher in mitigated wetlands. Shredders, collector/gatherers, and omnivores were associated with trends in litter decomposition during the early phases, but oligochaetes and omnivores were most strongly associated with decomposition trends in the later phase of decomposition. Because of the importance of individual taxa (oligochaetes, limnephilids, stylommatophores, and dytiscids) future studies should consider identifying taxa to genus. Based on ergosterol levels, fungi colonized the leaf litter quickly, peaking at 35 days, then decline and level off by 300 days. Ergosterol levels were significantly higher in early phases of decomposition than the later phase and were similar among wetlands types. Ergosterol levels were not significant with overall litter decomposition rates.

Invertebrate metrics were able to explain 24.9 to 30.9% of variance in decomposition during the early phases and 14.9 to 21.4% of the variance in the later phase of litter decomposition. These numbers represent substantial portions of a dynamic process that involves many interacting forces and phases, of which invertebrates and fungi comprise only a portion. Though we found low measurable influence of fungi on decomposition, it is likely that their contribution was more significant than our results reflect. Further studies are needed to more fully identify the associations between biological variables and litter decomposition.

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Table 1. List of three mitigated and three reference wetland study sites in West Virginia, including site name, year constructed, size (ha), elevation (m above sea level), and wetland classifications, 2007-2009.

Site name	County and Closest Town	Wetland Type	Year Created	Size (ha)	Elevation (m)	Wetland Classifications† at Site	Dominant Vegetative Species
Leading Creek	Montrose, Randolph, Co.	M	1995	17.0	600	UB, AB, EP, **SS‡**, F	hop sedge (*Carex lupulina* Muhl. ex Willd.), common rush, smartweed (*Polygonum hydropiperoides* Michx; *P. persicaria* L.), rice cutgrass (*Leersia oryzoides (L.)Sw.),* brookside alder
Sugar Creek	Meadowville, Barbour Co.	M	1995	11.0	490	AB, **EP**, SS	reed canary grass, wool grass (*Scirpus cyperinus* (L.)Kunth), woodland rush, American burreed (*Sparganium americanum* Nutt.), brookside alder
Hazelton	Hazelton, Preston Co.	M	2006	2.7	560	UB, AB, **EP**	broadleaf cattail, common rush, white and red clover (*Trifolium repens* L.; *T. pretense* L.), beggar-tick (*Bidens* sp.)
Meadowville	Meadowville, Barbour Co.	R	N/A	11.7	480	AB, EP, **SS**, F	broadleaf cattail, tussock sedge (*Carex stricta* Lam.), rice cutgrass, brookside alder
Upper Deckers Creek	Masontown, Preston Co.	R	N/A	2.1	515	UB, AB, **SS**, F	cowlily (*Nuphar lutea ssp. advena* (L.)Sm.(Ait.)), buttonbush (*Cephalanthus occidentalis* L.), brookside alder
Bruceton Mills	Bruceton Mills, Preston Co.	R	N/A	1.4	515	**EP**, SS	reed canary grass, rice cut grass, cattail brookside alder

† palustrine: unconsolidated bottom = UB, aquatic bed = AB, emergent persistent = EP, scrub-shrub = SS, forested = F (Cowardin *et al.* 1979)

‡ bold text indicates dominant classifications

Table 2. Analysis of variance results for decomposition, expressed as average decomposition rate constant *k* (year $^{-1}$), in six wetlands (three mitigated, three reference) in West Virginia, December 2007 to December 2009. Wetland type (mitigated, reference), mesh size (fine, coarse), date (n=14), and their interactions were all tested. Date and the interaction between type and mesh were significant ($p < 0.05$).

Effect	Num DF	Den DF	F value	*p* value
Type	1	583	0.17	0.680
Mesh	1	583	0.22	0.637
Date	13	583	14.54	**< 0.001***
Type*Mesh	1	583	4.75	**0.030***
Type*Date	13	583	0.9	0.557
Mesh*Date	13	583	0.32	0.990
Type*Mesh*Date	13	583	0.81	0.650

Table 3. Overall means per bag, standard errors (S.E.), and maximums for five invertebrate metrics, seven functional feeding groups (FFG), and the top 20 taxonomic groups by mass (mg dry mass). Minimums were 0 for all metrics.

Invertebrate Metric	Family	Mean (mg)	S.E. (mg)	Max (mg)
Abundance		12.3	2.68	1011
Richness		2.3	0.09	13
Diversity		0.53	0.024	2.3
Biomass (with Oligochaetes)		14.92	1.524	482.9
Biomass (without Oligochaetes)		13.16	1.200	353.5
Detritivores (with Oligochaetes)		1.94	0.954	471.3
Detritivores (without Oligochaetes)		0.18	0.036	11.6
Predators & Parasites		10.78	1.148	353.5
Shredders		0.14	0.042	14.5
Collector/Gatherers		0.11	0.022	7.6
Scrapers		0.02	0.019	12.1
Filterer/Collectors		0.00	0.000	0.3
Herbivores		1.97	0.289	91.3
Omnivores		0.01	0.005	2.7
Oligochaeta (Subclass)		4.51	0.738	235.7
Hymenoptera	Formicidae	1.76	0.954	471.0
Stylommatophora		1.36	0.269	90.6
Isopoda	Asellidae	0.85	0.239	113.5
Veneroida	Sphaeriidae	0.77	0.333	181.8
Diptera	Chironomidae (l)†	0.46	0.224	97.9
Diptera	Tipulidae (l)	0.46	0.100	29.1
Araneae	Pisauridae	0.46	0.095	29.7
Ephemeroptera	Leptophlebiidae	0.44	0.208	114.6
Coleoptera	Hydrophilidae (l)	0.42	0.058	12.4
Basommatophora	Physidae	0.37	0.216	119.4
Decapoda	Cambaridae	0.31	0.306	199.1
Megaloptera	Corydalidae	0.27	0.114	56.8
Basommatophora	Planorbidae	0.24	0.094	35.5
Coleoptera	Carabidae (a)	0.24	0.044	12.2
Basommatophora	Lymnaeidae	0.16	0.068	39.9
Isopoda	Armadillidiidae	0.13	0.047	20.2
Chordeumatida	Conotylidae	0.11	0.037	20.2
Hirudinea (Subclass)		0.11	0.032	11.6
Coleoptera	Dystiscidae (l)	0.10	0.039	18.9

† Indicates adult (a) or larvae (l).

Table 4. Comparisons of means per bag and standard errors (S.E.) using analysis of variance (ANOVA) for five invertebrate metrics, seven functional feeding groups, and oligochaetes, expressed as dry mass (mg), among litter bag mesh sizes and wetland types.

	Fine Mesh		Coarse Mesh				Mitigated Wetlands		Reference Wetlands			
Invertebrate Metric	Mean	S.E.	Mean	S.E.	($F_{1,635}$)	*p* value	Mean	S.E.	Mean	S.E.	($F_{1,635}$)	*p* value
Abundance	5.60	1.3	19.0	5.2	18.86	**< 0.001**	12.7	4.1	11.8	3.5	0.66	0.427
Richness	1.6	0.10	2.9	0.15	55.97	**< 0.001**	1.9	0.12	2.6	0.14	2.26	0.133
Diversity	0.68	0.04	0.38	0.03	47.91	**< 0.001**	0.41	0.03	0.64	0.04	3.33	0.068
Total Mass (without Oligochaeta)	2.95	0.52	17.91	2.55	55.42	**< 0.001**	10.88	1.96	9.94	1.80	0.06	0.803
Total Mass (with Oligochaeta)	6.30	0.95	23.58	2.83	39.8	**< 0.001**	17.83	2.39	12.06	1.90	6.87	**0.009**
Detritivores (without Oligochaeta)	1.85	0.50	7.48	1.36	25.53	**< 0.001**	5.09	1.30	4.22	0.69	0.14	0.708
Detritivores (with Oligochaeta)	5.20	0.93	13.15	1.82	16.84	**< 0.001**	12.03	1.84	6.34	0.93	9.75	**0.002**
Predators	0.85	0.10	4.02	0.42	52.95	**< 0.001**	1.92	0.28	2.94	0.35	1.00	0.320
Shredders	0.01	0.01	0.06	0.02	3.74	0.055	0.05	0.02	0.03	0.01	1.14	0.292
Collector/Gatherers	4.41	0.90	9.16	1.58	5.51	**0.020**	10.45	1.67	3.17	0.70	7.17	**0.008**
Scrapers	0.39	0.20	1.31	0.55	0.75	0.386	0.97	0.53	0.73	0.24	0.01	0.944
Filterers	0.12	0.08	1.43	0.66	3.95	**0.047**	0.73	0.35	0.81	0.57	0.01	0.905
Herbivores	0.16	0.04	0.76	0.16	12.76	**< 0.001**	0.46	0.11	0.45	0.13	0.01	0.933
Omnivores	0.14	0.04	6.14	1.97	25.64	**< 0.001**	3.09	1.29	3.17	1.49	0.03	0.863
Oligochaeta	3.35	0.80	5.67	1.24	2.75	0.101	6.94	1.35	2.12	0.59	11.16	**0.001**

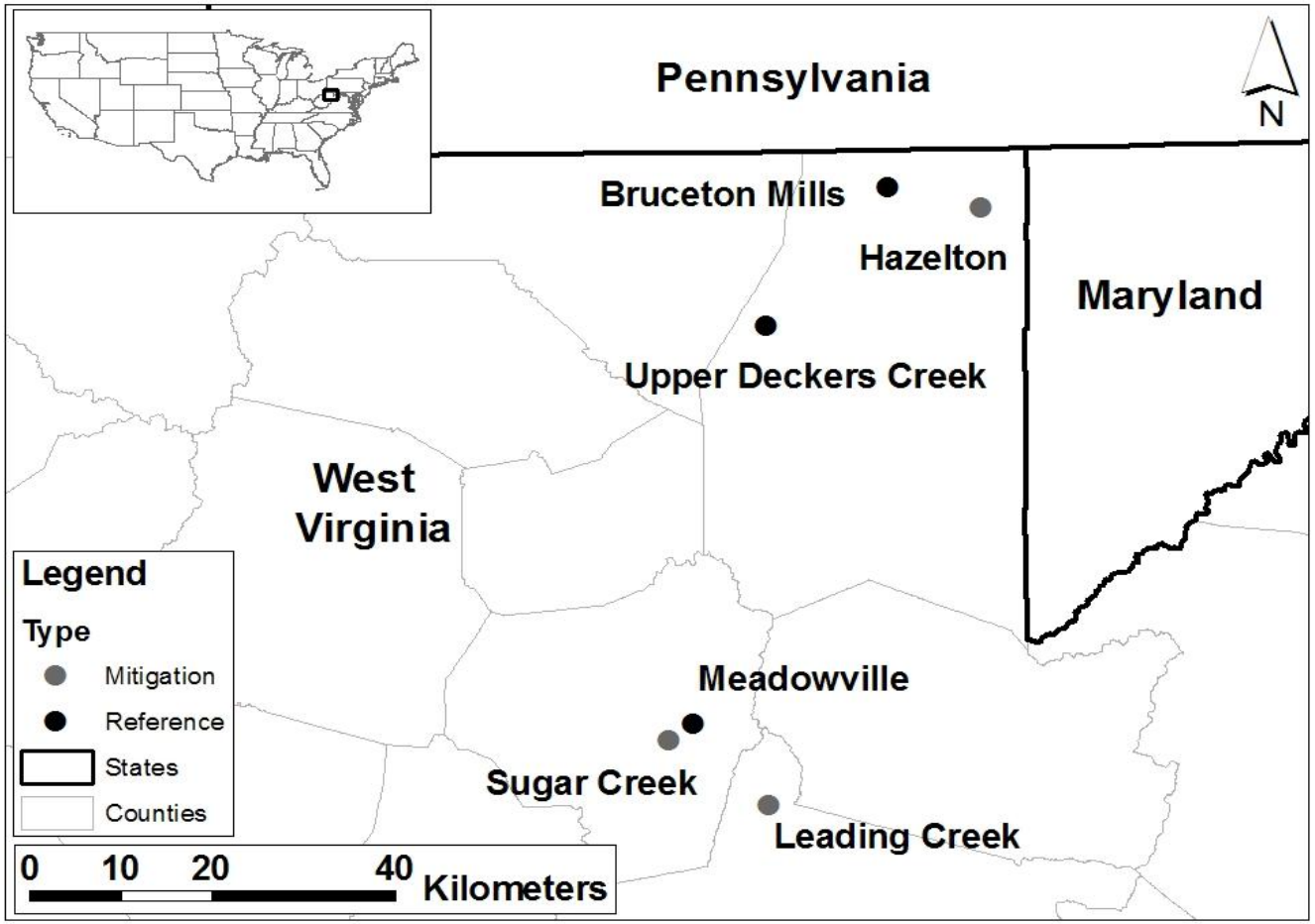


Figure 1. Six study sites, comprised of three mitigated and three reference wetlands, in the Mid-Atlantic Highlands region of West Virginia, USA, 2007-2009.

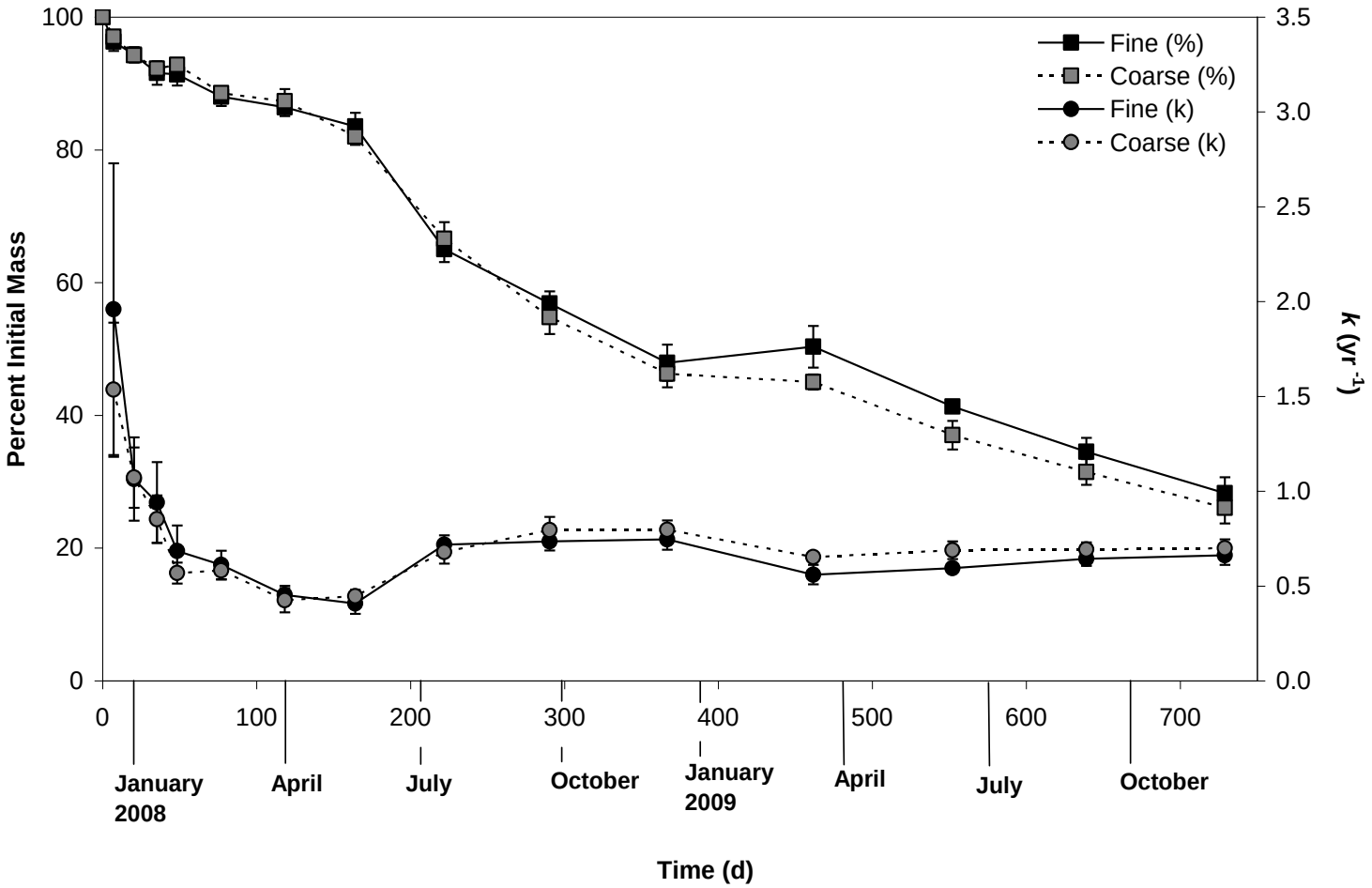


Figure 2. Litter decomposition, expressed as percent initial ash-free dry mass and decomposition rate constant *k* (year $^{-1}$), in litter bags with two mesh sizes (fine [1.27 mm] and coarse [2.8 mm]) over 728 days (December 2007 to December 2009) in three mitigated and three reference wetlands in the Mid-Atlantic Highlands region.

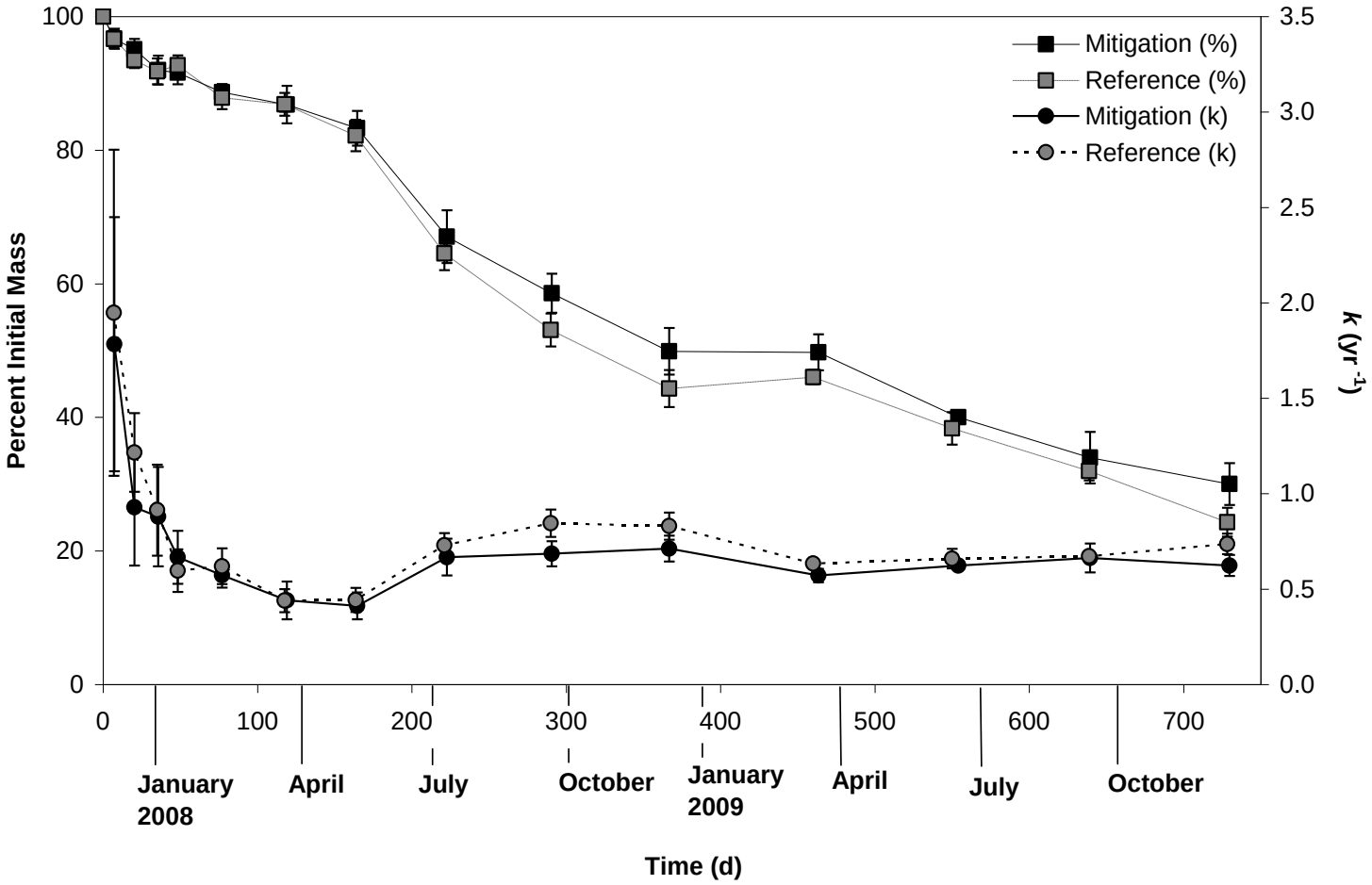


Figure 3. Litter decomposition, expressed as percent initial ash-free dry mass and decomposition rate constant *k* (year $^{-1}$), over 728 days (December 2007 to December 2009) in three mitigated and three reference wetlands in the Mid-Atlantic Highlands region.

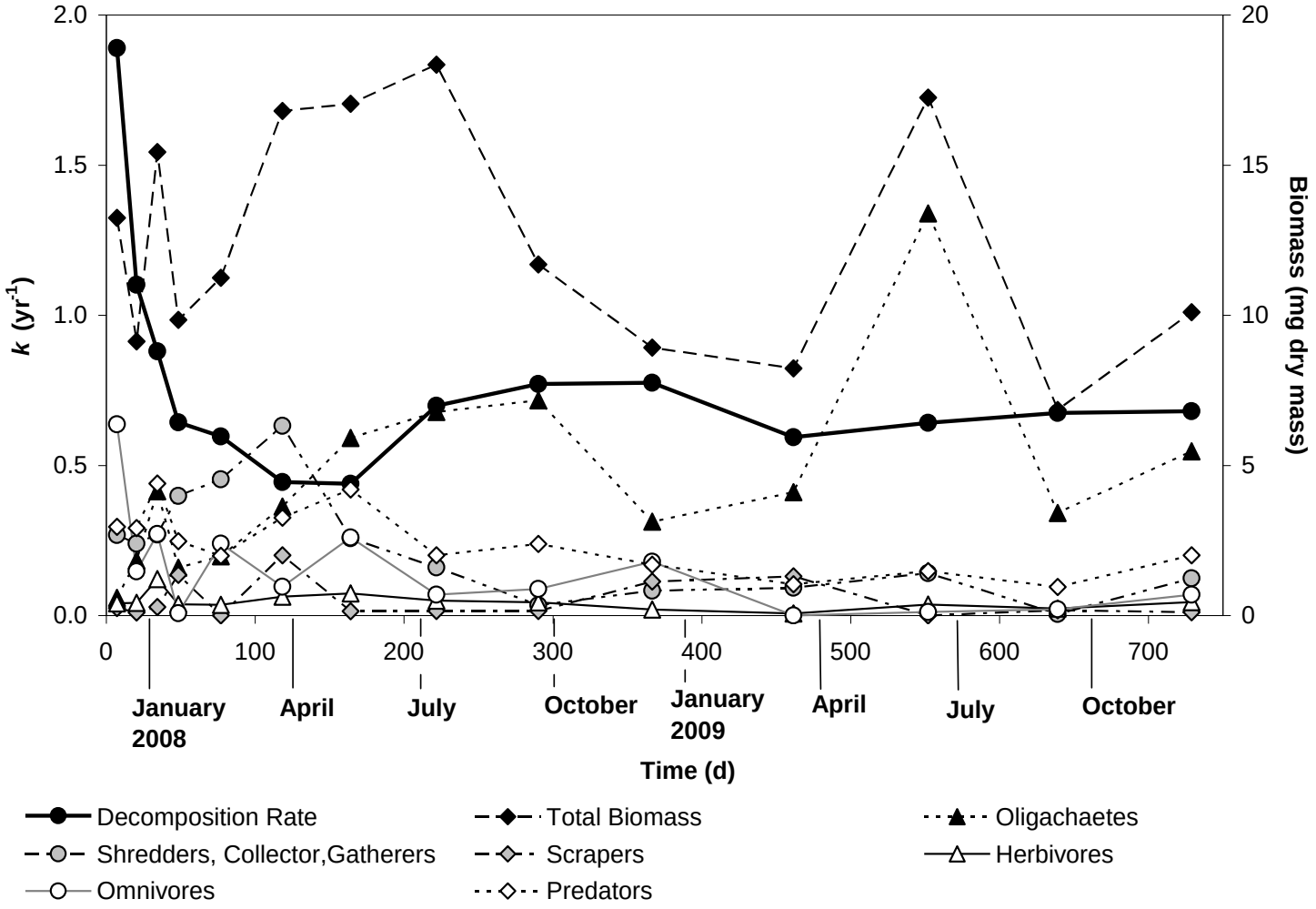
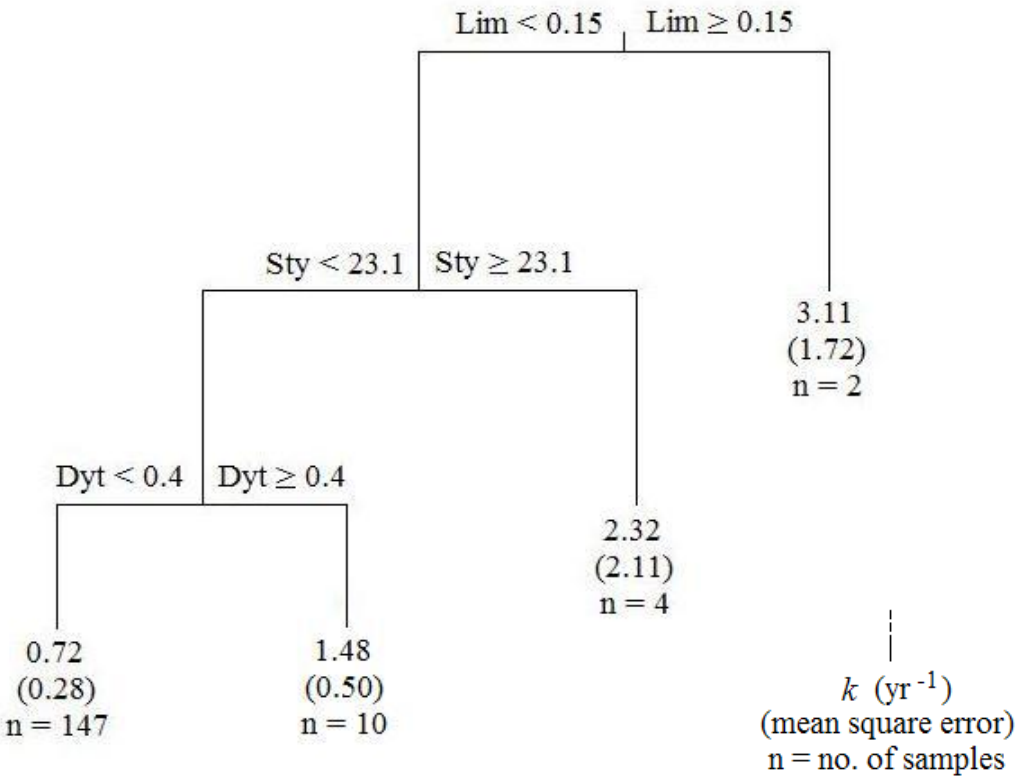
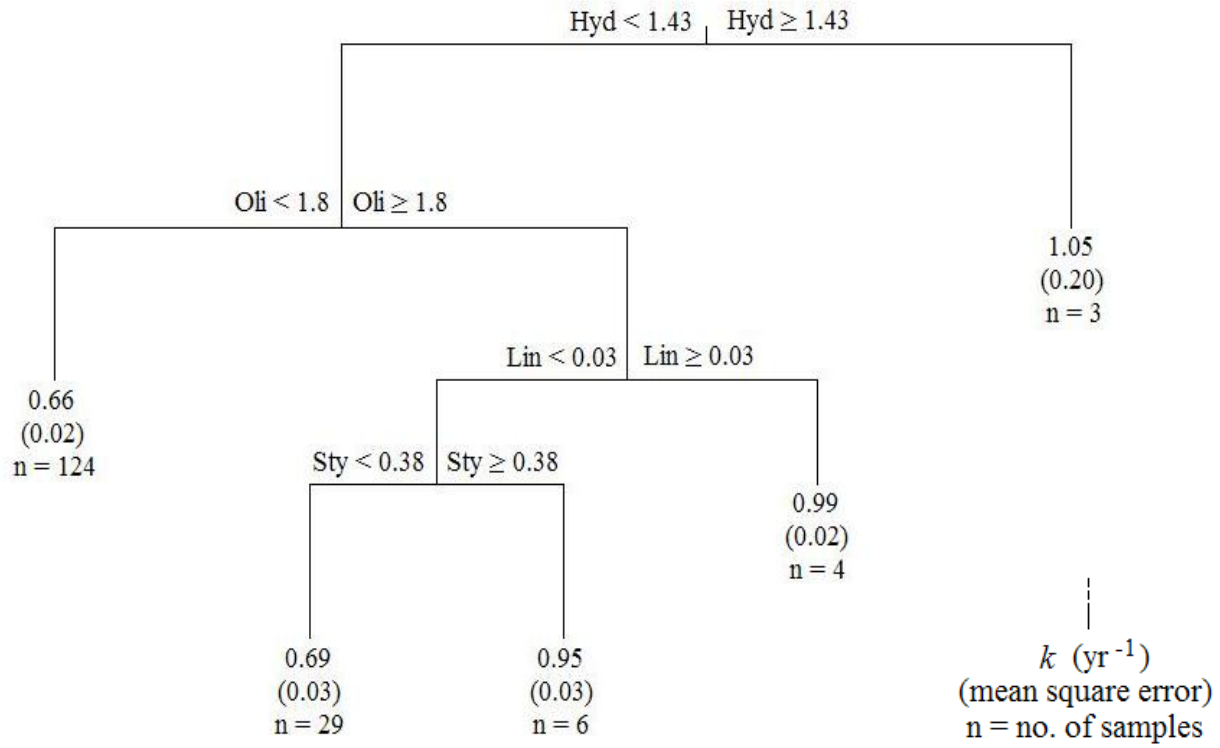


Figure 4. Litter decomposition rate constant k (year^{-1}) and invertebrate functional feeding group biomass (mg dry mass litter) from litter bags collected from three mitigated and three reference wetlands in the Mid-Atlantic Highlands region, December 2007 to December 2009.



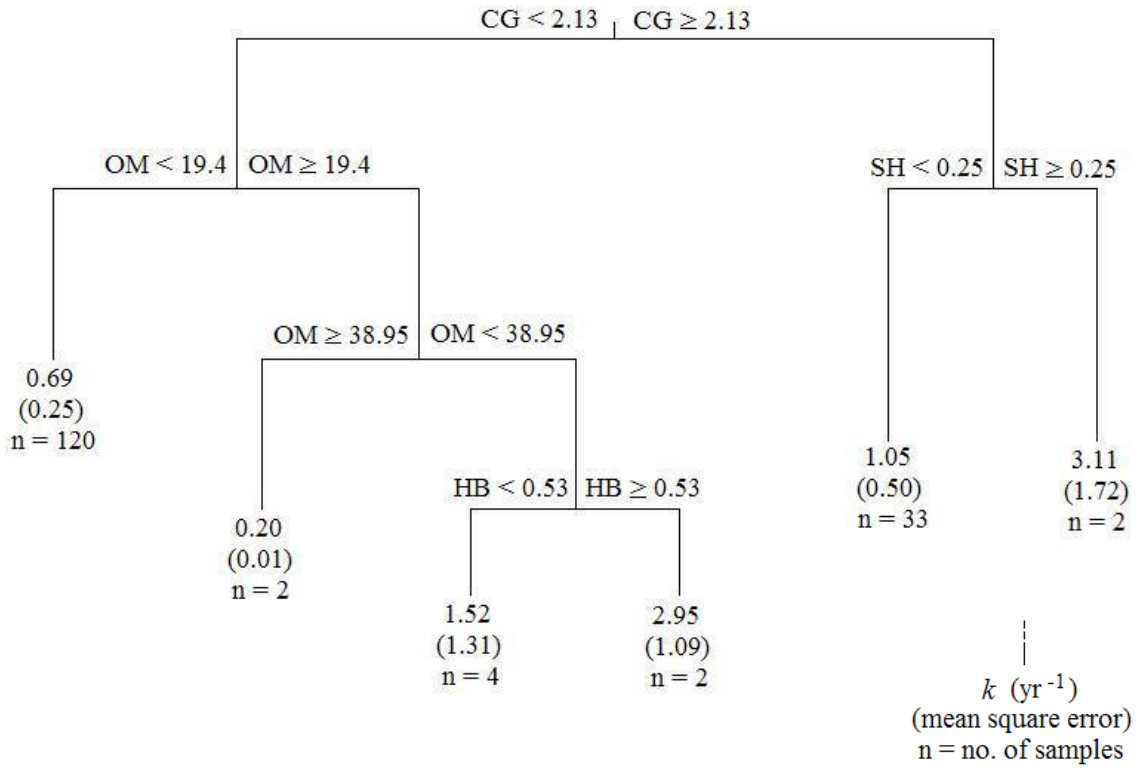
Dyt = Dytiscidae, Coleoptera, larvae (Predator)
Lim = Limnephilidae, Trichoptera (Shredder, filterer)
Sty = Stylommatophora (Order, omnivore, detritivore)

Figure 5. Regression tree analysis to identify invertebrate taxa, by biomass, associated with trends in the early phases (< 224 days) of decomposition. Decomposition was measured over two years in three mitigated and three reference wetlands in the Mid-Atlantic Highlands region, USA, December 2007 to December 2009. Divisions in the regression tree explain 24.9% of variance in decomposition rates.



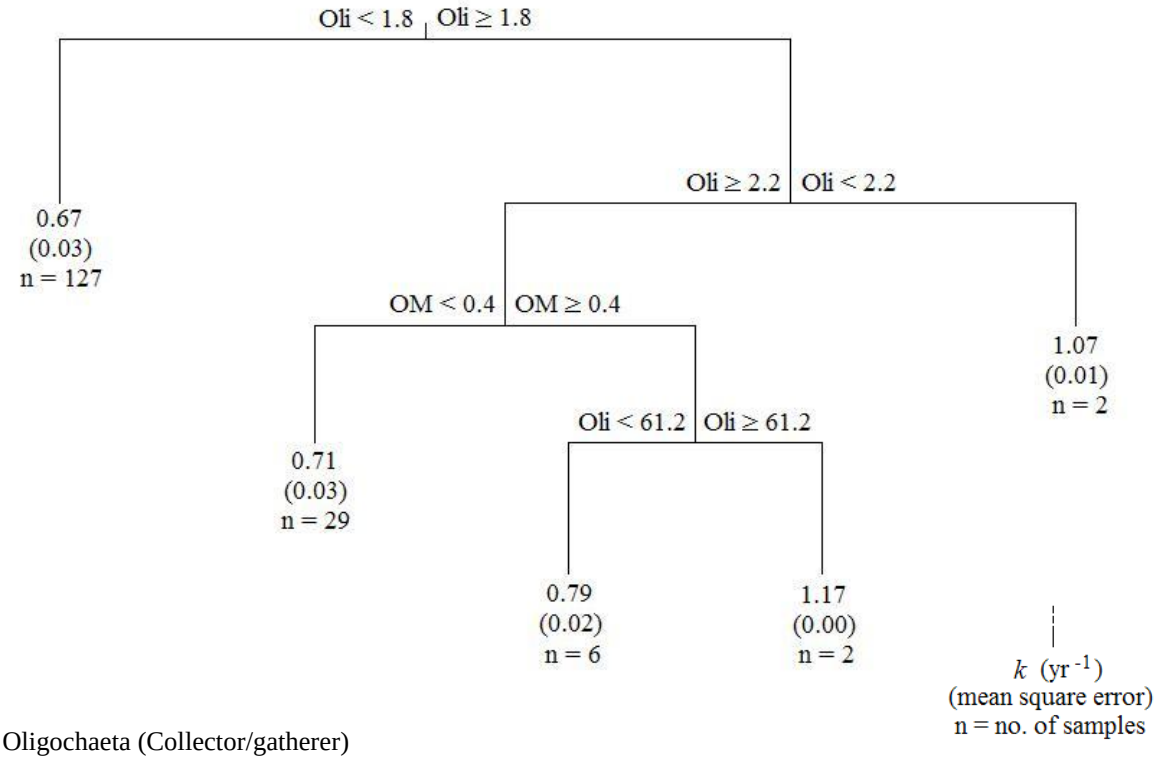
Hyd = Hydrophilidae, Coleoptera, adult (Collector/gatherer)
Lin = Linyphiidae, Araneae (Predator)
Oli = Oligochaeta (Collector/gatherer)
Sty = Stylommatophora (Order, omnivore, detritivore)

Figure 6. Regression tree analysis to identify invertebrate taxa, by biomass, associated with trends in the late phase (≥ 224 days) of decomposition. Decomposition was measured over two years in three mitigated and three reference wetlands in the Mid-Atlantic Highlands region, USA, December 2007 to December 2009. Divisions in the regression tree explain 21.4% of variance in decomposition rates.



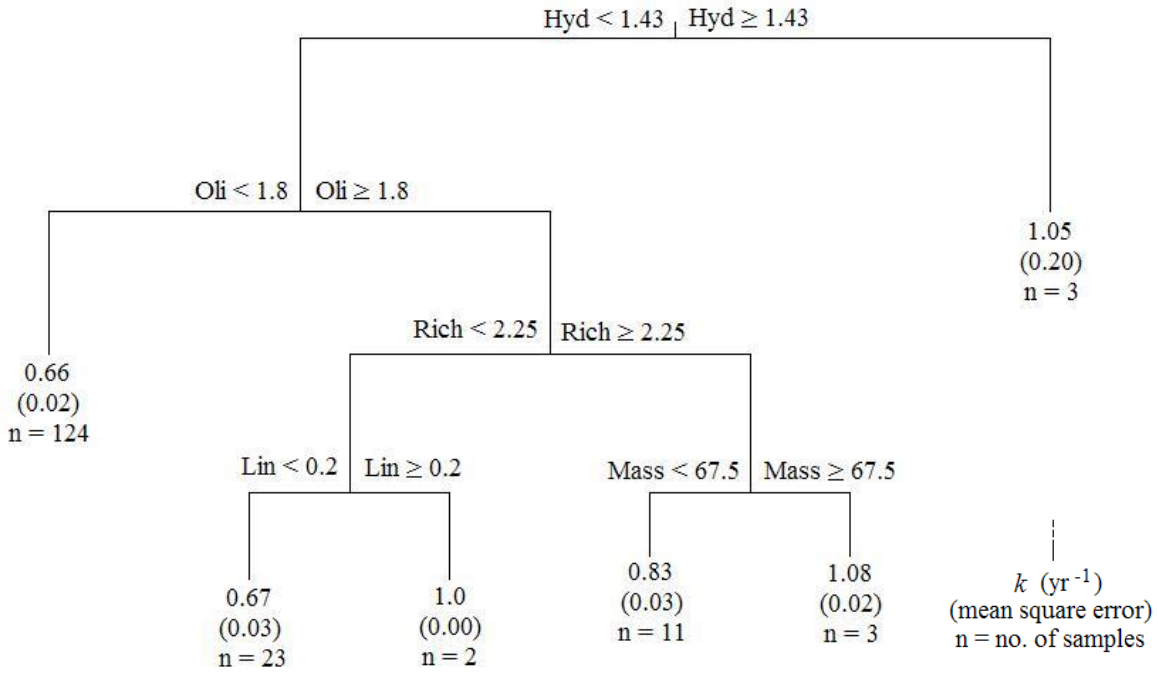
CG = Collector/gatherer
HB = Herbivore
OM = Omnivore
SH = Shredder

Figure 7. Regression tree analysis to identify invertebrate functional feeding groups (FFG), by biomass, associated with trends in the early phases (< 224 days) of decomposition. Decomposition was measured over two years in three mitigated and three reference wetlands in the Mid-Atlantic Highlands region, USA, December 2007 to December 2009. Divisions in the regression tree explain 30.8% of variance in decomposition rates.



Oli = Oligochaeta (Collector/gatherer)
OM = Omnivore

Figure 8. Regression tree analysis to identify invertebrate functional feeding groups (FFG), by biomass, associated with trends in the late phase (≥ 224 days) of decomposition. Decomposition was measured over two years in three mitigated and three reference wetlands in the Mid-Atlantic Highlands region, USA, December 2007 to December 2009. Divisions in the regression tree explain 14.9% of variance in decomposition rates.



Taxonomic Groups (mg dry mass)
Hyd = Hydrophilidae, Coleoptera, adult (Collector/gatherer)
Lin = Linyphiidae, Araneae (Predator)
Oli = Oligochaeta (Collector/gatherer)

Invertebrate Metric
Rich = Richness (no. taxa)
Mass = Total biomass (mg dry mass)

Figure 9. Regression tree analysis to identify invertebrate metrics associated with trends in the late phase (≥ 224 days) of decomposition. Decomposition was measured over two years in three mitigated and three reference wetlands in the Mid-Atlantic Highlands region, USA, December 2007 to December 2009. Divisions in the regression tree explain 20.7% of variance in decomposition rates.

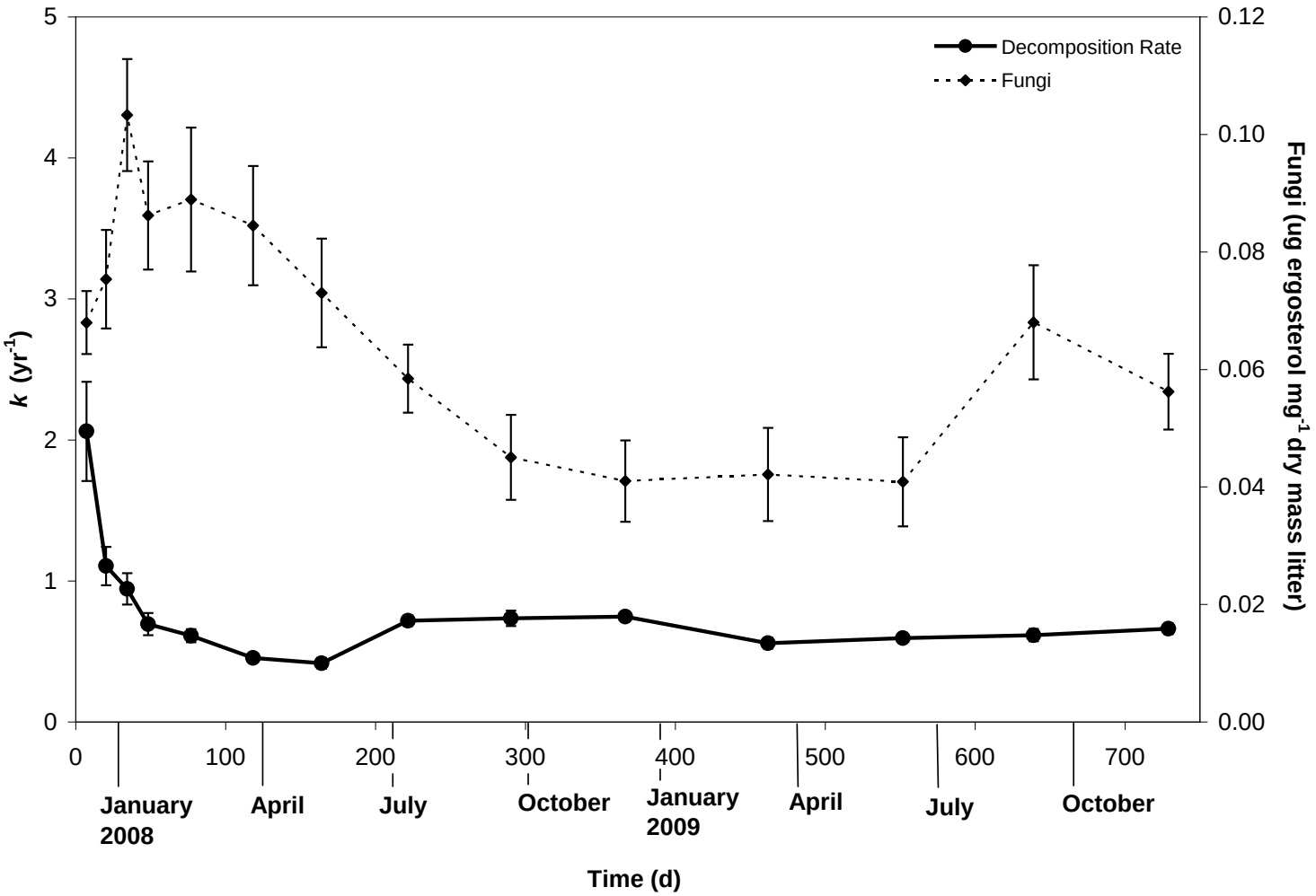


Figure 10. Graph of litter decomposition rate constant *k* (year^{-1}) and fungal biomass (μg ergosterol mg^{-1} dry mass litter) from litter bags collected from three mitigated and three reference wetlands in West Virginia, USA, December 2007 to December 2009.

CHAPTER 6

Review of Hypotheses and Management Implications for Litter Decomposition in Mitigated and Reference Wetlands

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Submitted in the style of:
Wetlands

INTRODUCTION

Wetland mitigation has led to a net gain in wetland acreage in recent years (Dahl 2006); however, it is unclear that wetland function is being adequately replaced (Bedford 1996; Minkin and Ladd 2003; Hoeltje and Cole 2009). Decomposition of plant litter influences many wetland processes and is itself driven by a complex web of interacting forces. This makes plant litter decomposition a useful measure of wetland function and a possible metric for judging functional replacement in compensatory mitigation projects. Litter decomposition is linked to the physical and chemical properties of wetland soils (Mitsch and Gosselink 2007), nutrient availability and cycling (Prentki et al. 1978; Facelli and Pickett 1991), primary productivity (Brinson et al. 1981), litter/organic matter accumulation (Gambrell and Patrick Jr. 1978; Xiong and Nilsson 1997), and seed germination (Xiong and Nilsson 1997; Taylor and Middleton 2004). However, the web of interacting forces that intricately connect decomposition to wetland function also obscures study of individual variables. For decomposition to be used as a metric to judge wetland function, its driving forces must be better understood. To better understand trends in decomposition among mitigated and reference wetlands and the variables influencing them, we conducted a 2-year study of wetland litter decomposition rates in the Allegheny Mountains region (Mid-Atlantic Highlands region) of West Virginia.

OBJECTIVES AND HYPOTHESES

An in-depth study of litter decomposition, using litter bags, was conducted in 3 mitigated and 3 reference wetlands from December 2007 to December 2009 (Gingerich 2010: Chapters 2, 4 & 5). The 8 study objectives and 15 hypotheses for this portion of the study are listed below:

Objective 1: To compare decomposition rates for mitigated versus natural wetlands (Gingerich 2010: Chapter 2).

Hypothesis A: Litter decomposition rate is greater in mitigated wetlands in response to differences in hydrology (longer inundation periods and wetter soil in mitigated wetlands than in reference wetlands).

Objective 2: To determine rates and trends of decomposition for five different litter types: broadleaf cattail (*Typha latifolia* L.), common rush (*Juncus effusus* L.), brookside alder (*Alnus serrulata* (Ait.) Willd.), reed canary grass (*Phalaris arundinacea* L.), and a litter mix of common rush, reed canary grass, and brookside alder (Gingerich 2010: Chapter 2).

Hypothesis B: Litter types have significantly different rates of decomposition.

Hypothesis C: Brookside alder and the mixed litter have significantly faster decomposition rates.

Hypothesis D: Broadleaf cattail has significantly lower rates of decomposition.

Hypothesis E: The order of litter decomposition rates among litters do not vary with wetland type.

Objective 3: To measure the influence of environmental variables on litter decomposition (Gingerich 2010: Chapter 4).

Hypothesis F: Temperature is positively associated with decomposition.

Hypothesis G: Water pH is positively associated with decomposition.

Hypothesis H: Soil moisture is positively associated with decomposition.

Hypothesis I: Longer inundation periods are positively associated with decomposition.

Hypothesis J: More frequent transitions between flooded and exposed conditions are positively associated with decomposition.

Objective 4: To measure the influence of biotic variables (invertebrates and fungi) on litter decomposition (Gingerich 2010: Chapter 5).

Hypothesis K: Invertebrate abundance, diversity, and total biomass are positively associated with decomposition, but to a lesser degree than hydroperiod or temperature.

Hypothesis L: Invertebrate metrics are similar between mitigated and reference wetlands.

Hypothesis M: Fungal biomass has a weak positive association with decomposition.

Hypothesis N: Fungal biomass is greater in reference wetlands.

Objective 5: To model decomposition trends over time (Gingerich 2010: Chapter 2-5).

Hypothesis O: Decomposition rates change over time, corresponding with the 3 phases of decomposition (leaching [rapid], microbial decomposition and conditioning of soft tissues [moderate], and mechanical fragmentation by biotic and environmental forces [slow]).

Objective 6: To investigate the feasibility of using decomposition of known litters as a means of assessing wetland function.

A secondary study measured decomposition rates in a broader range of wetlands (8 mitigated and 8 reference) in West Virginia , USA, from November 2008 to November 2009 (Gingerich 2010: Chapter 3). Objectives and hypotheses for the secondary study are listed below:

Objective 7: To compare decomposition rates for created versus natural wetlands (Gingerich 2010: Chapter 3).

Hypothesis P: Litter decomposition rate is greater in created wetlands.

Objective 8: To determine how decomposition rate changes with created wetland age (Gingerich 2010: Chapter 3).

Hypothesis Q: Younger created wetlands have faster decomposition rates

Hypothesis *R*: Litter decomposition in created wetlands trend towards rates in natural wetlands as created wetlands age.

RESULTS

Comparison of Mitigated and Reference Wetlands

Litter decomposition rates were found to be similar ($p > 0.05$) between created and reference wetlands in the primary study (Gingerich 2010: Chapter 2; mean % mass remaining after 728 d for all litter types: $\bar{x}$ =35.1%, SE = 4.1; *k*: 0.675 yr^{-1}, SE = 0.086) and the secondary study (Gingerich 2010: Chapter 3; % mass remaining after 365 d for broadleaf cattail: $\bar{x}$ =55.3%, SE = 1.9; *k*: 0.522 yr^{-1}, SE = 0.037), which failed to support hypotheses A and P. The similarity in decomposition rates between wetland types can be explained by the fact that nearly all variables measured for mitigated wetlands were similar to reference wetlands. All environmental measurements (Gingerich 2010: Chapter 4) and fungal biomass (Gingerich 2010: Chapter 5) were similar between wetland types, which failed to support hypothesis N, and most invertebrate metrics (Gingerich 2010: Chapter 5) were similar, supporting hypothesis L. Only invertebrate metrics that included oligochaetes (total biomass, detritivore biomass, and oligochaetes biomass) and biomass of the functional feeding group collector/gatherers were significantly higher in mitigated wetlands.

Decomposition rate did not follow a linear trend with wetland age and failed to support hypotheses Q and R. Decomposition rates in young wetlands were moderately fast, but then declined in a 27-year-old wetland before reaching the fastest rate in a 40-year-old wetland. This non-linear progression suggests that mitigation wetlands may not be trending towards a final "natural" state but may instead be more randomly transitioning based on stochastic forces such as environmental conditions.

Comparison of Litter Types

Proportion of mass remaining was significantly different among litter types on 8 of 14 collection dates and decomposition rate was significantly different on 3 of 14 collection dates (Gingerich 2010: Chapter 2), supporting hypothesis B. Reed canary grass had the highest *k* for every collection period, except 364 d, and had the highest mean (0.920 yr^{-1}, SE = 0.153), minimum (0.534 yr^{-1}), and maximum (2.790 yr^{-1}) of all species. The mixed litter had the second highest *k* for 11 of the 14 collection dates, the second highest mean (0.770 $year^{-1}$, SE = 0.102) and minimum (0.407 $year^{-1}$), and the third highest maximum (1.960 yr^{-1}) of all species, supporting hypothesis C. However, brookside alder had a significantly larger proportion of mass remaining on 3 of the 14 collection dates and a significantly lower decomposition rate constant on 1 of the collection dates, which failed to support hypothesis C's prediction for alder. Broadleaf cattail had the lowest *k* for 11 of the 14 collection dates and the lowest mean (0.402 yr^{-1}, SE = 0.060), minimum (0.121 yr^{-1}), and maximum (1.079 yr^{-1}) of all species, supporting hypothesis D. Comparisons of decomposition rates among litter types were not made among wetland types, but within litter types the order of fastest decomposition rate changed over collection dates, which failed to support hypothesis E.

Influence of Environmental Variables on Litter Decomposition

The environmental variables that most influenced, and therefore best predicted, decomposition rate varied among litter types. Brookside alder decomposition rate was best predicted by soil temperature (ST), water pH (WPH), and the number of transitions between flooded and exposed conditions (FET); reed canary grass decomposition rate was best predicted by air temperature (AT), WPH, and ST; common rush decomposition rates were best predicted by AT and FET; broadleaf cattail decomposition rate was best predicted by hydroperiod (HP) and FET; and the mixed litter decomposition rate was best predicted by AT and WPH. AT, ST, and WPH were positively associated with decomposition rate, which supports hypotheses F and G, while HP was negatively associated with decomposition rate, which failed to support hypothesis I. Soil moisture was not included in the top models predicting decomposition rate, disproving hypothesis H. The FET was positively associated with decomposition rates of common rush and broadleaf cattail and negatively associated with the decomposition rate of brookside alder, giving only partial support to hypothesis J.

Influence of Biological Variables on Litter Decomposition Rate

Invertebrate metrics explained 24.9 to 30.9% of variance in decomposition during the early phases (< 224 d) and 14.9 to 21.4% of the variance in the later phase (≥ 224 d) of litter decomposition (Gingerich 2010: Chapter 5). Individual taxa were more strongly associated with trends in decomposition than functional feeding groups or invertebrate metrics (abundance, richness, diversity). Shredders, collector/gatherers, and omnivores were more strongly associated with early phases of decomposition, while oligochaetes and omnivores were most strongly associated with trends in decomposition during the later phase.

Fungal biomass was significantly higher (Gingerich 2010: Chapter 5) in the early phases of decomposition, peaking ($\bar{x}$ = 0.103 μg ergosterol mg $^{-1}$ dry litter, S.E. = 0.010) at 35 days, but then declined and leveled off ($\bar{x}$ = 0.041 μg ergosterol mg $^{-1}$ dry litter, SE = 0.007) around 300 d. Fungal biomass was not significantly related to decomposition rate and failed to support hypothesis M.

It is not possible to judge whether environmental or biological variables had a greater association with decomposition (hypothesis K) because environmental variables were modeled with parametric statistical methods and invertebrates were modeled with non-parametric methods. Based on results for environmental and biological variables, both sets of variables influenced decomposition rates and explained a portion of the variance that was observed.

Trends in Decomposition

A distinct trend emerged (hypothesis O) in decomposition rate that was present regardless of litter type, mesh size, or wetland type (Gingerich 2010: Chapter 2 & 5) and seemed to follow the 3 phases of decomposition (Godshalk and Wetzel 1978; Brinson et al. 1981). The first phase is leaching of soluble nutrients and brings about rapid mass loss. The second phase of decomposition is colonization and conditioning of soft leaf tissues by microbes. The third phase is mechanical fragmentation by environmental forces and invertebrates.

The highest decomposition rates were always measured on the first collection period (7 d), except for broadleaf cattail which peaked on the second collection date (21 d), and were likely due to leaching. Decomposition rates continued to be high on subsequent collection dates but declined rapidly, reaching their lowest levels between 119 and 168 days. Invertebrate biomass for most functional feeding groups peaked and declined before 168 days, but ergosterol concentration peaked and remained high for longer, declining but not leveling off until about

300 d. Between 168 and 224 d, decomposition transitioned from rapidly fluctuating early rates into a steadier late phase of decomposition. This likely signified the transition from the second phase of decomposition, when invertebrate functional feeding groups such as shredders peaked, to the third phase of decomposition when only tougher tissues remained and oligochaete biomass peaked. Though microbial activity is generally associated with the second phase of decomposition, based on this study it appears that microbes are high, peaking during the second phase, but then continue to have elevated numbers into the third (late) phase of decomposition.

Management Implications

Functions within wetland systems are intricately interwoven and therefore when portions of a wetland system are missing or impaired they can cause rippling effects throughout other functions. This study demonstrated the wide range of variables associated with litter decomposition in wetlands and the opportunity decomposition provides to measure wetland function. However, for decomposition to become useful as a metric of wetland assessments, studies need to be performed to determine regional "norms" and allow for a standard to compare results against. The National Wetland Condition Assessment that the US Environmental Protection Agency plans to conduct in 2011 (USEPA 2009) provides a good example of a large-scale study that could incorporate measurements of decomposition rate using a standardized litter (cattail is recommended because of its ubiquitous distribution and relative ease to collect) to identify regional trends. Though litter bag studies can require a significant amount of preparation and processing time for thorough studies, such as the one conducted here, methods could be shortened and standardized to define a number of litter bags to place throughout a wetland and then collect them at the 1 year mark, allowing the litter enough time to pass through early stages of high fluctuation and into a more constant state of decomposition.

This study also illustrates the importance of heterogeneity in wetland mitigation projects. With so many variables linked to wetland function, it is difficult to fully consider and implement a design that best replicates function. Therefore, heterogeneity helps improve the likelihood that the mix of conditions present in a wetland system are able to support a complete array of functions.

In conclusion, litter decomposition should be considered for inclusion in wetland functional assessments as a component of a comprehensive multimetric approach. The national wetland policy of "no net loss" can only be fully achieved once complete functional replacement has been met, and litter decomposition provides a metric to evaluate that goal.

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Appendices

Appendix A. Mean and standard error (S.E.) results for decomposition of five litter types, expressed as percent of ash-free dry mass remaining, in six wetlands in the Allegheny Mountains of West Virginia, December 2007 to December 2009. All 14 collection dates are displayed, with litter types in order of percent mass remaining. Within each collection period, litter type is ordered by their mean percent mass remaining.

Litter	Days	Mean[a]		S.E.
Reed Canary Grass	7	94.74	a	1.17
Brookside Alder	7	95.10	a	1.13
Mixed Litter	7	96.31	a	1.41
Common Rush	7	96.87	a	0.63
Broadleaf Cattail	7	99.12	a	0.88
Reed Canary Grass	21	93.24	a	0.96
Brookside Alder	21	93.80	a	0.65
Mixed Litter	21	94.32	a	1.16
Broadleaf Cattail	21	94.44	a*	1.78
Common Rush	21	96.50	a	0.55
Reed Canary Grass	35	90.34	a	1.24
Mixed Litter	35	91.58	a	1.77
Brookside Alder	35	92.00	a	0.62
Common Rush	35	94.24	a	0.77
Broadleaf Cattail	35	96.77	a	1.93
Reed Canary Grass	49	89.13	a	1.43
Mixed Litter	49	91.38	a	1.69
Brookside Alder	49	91.90	a	0.67
Common Rush	49	94.02	a	0.72
Broadleaf Cattail	49	94.72	a	1.66
Reed Canary Grass	77	85.86	a	1.31
Mixed Litter	77	88.00	a,b	1.39
Brookside Alder	77	88.94	a,b	0.80
Common Rush	77	90.76	a,b	1.01
Broadleaf Cattail	77	93.55	b	1.31
Reed Canary Grass	119	84.23	a	1.51
Mixed Litter	119	86.43	a	1.33
Brookside Alder	119	87.46	a	0.80
Common Rush	119	89.46	a,b	1.29
Broadleaf Cattail	119	96.54	b	2.51
Reed Canary Grass	168	78.12	a	0.41
Mixed Litter	168	83.53	a,b	2.04
Brookside Alder	168	86.68	a,b	1.04
Common Rush	168	87.58	a,b	1.55
Broadleaf Cattail	168	91.41	b*	1.20
Reed Canary Grass	224	62.85	a	1.79
Mixed Litter	224	65.01	a*	1.93
Common Rush	224	72.77	a,b*	1.29
Brookside Alder	224	75.61	a,b	2.03
Broadleaf Cattail	224	85.20	b*	2.03
Reed Canary Grass	294	53.45	a	1.91
Mixed Litter	294	56.84	a,b	1.83
Common Rush	294	61.95	a,b	2.63
Brookside Alder	294	69.08	a,b	3.06
Broadleaf Cattail	294	76.71	b	1.12
Mixed Litter	364	47.92	a	2.72
Reed Canary Grass	364	48.27	a	2.05
Common Rush	364	52.13	a	2.50
Brookside Alder	364	63.67	a	2.66
Broadleaf Cattail	364	66.46	a	3.22
Reed Canary Grass	455	45.67	a	2.11
Mixed Litter	455	50.34	a,b	3.15
Common Rush	455	55.17	a,b	2.28
Brookside Alder	455	62.19	a,b	2.80
Broadleaf Cattail	455	68.30	b	3.22
Reed Canary Grass	546	36.43	a	2.02
Mixed Litter	546	41.33	a,b	0.59
Common Rush	546	44.22	a,b	2.48
Brookside Alder	546	57.74	b	1.21
Broadleaf Cattail	546	58.03	b	2.20
Reed Canary Grass	637	29.72	a	1.84
Mixed Litter	637	34.51	a	2.08
Common Rush	637	36.46	a,b	2.77
Broadleaf Cattail	637	56.48	b	2.84
Brookside Alder	637	56.71	b	3.44
Reed Canary Grass	728	26.48	a	2.09
Mixed Litter	728	28.26	a	2.39
Common Rush	728	30.79	a	2.93
Brookside Alder	728	44.30	a	2.67
Broadleaf Cattail	728	45.80	a	4.79

* Indicates a significant change ($P < 0.05$) from the previous collection.

[a] Means followed by the same lowercase letters are not different ($P > 0.05$) across litter types.

Appendix B. Mean and standard error (S.E.) results for decomposition of five litter types, expressed as k (yr^{-1}), in six wetlands in the Allegheny Mountains of West Virginia, December 2007 to December 2009. All 14 collection dates are displayed, with litter types in order of percent mass remaining. Within each collection period, litter type is ordered by their mean k.

Litter	Days	Mean[a]		S.E.	Litter	Days	Mean		S.E.
Broadleaf Cattail	7	0.599	a	0.466	Broadleaf Cattail	224	0.271	a	0.039
Common Rush	7	1.617	a	0.309	Brookside Alder	224	0.467	a,b	0.045
Mixed Litter	7	1.960	a	0.769	Common Rush	224	0.528	a,b	0.029
Brookside Alder	7	2.581	a	0.595	Mixed Litter	224	0.718	b*	0.049
Reed Canary Grass	7	2.790	a	0.645	Reed Canary Grass	224	0.773	b	0.048
Common Rush	21	0.642	a*	0.100	Broadleaf Cattail	294	0.340	a	0.019
Mixed Litter	21	1.064	a	0.219	Brookside Alder	294	0.477	a,b	0.062
Broadleaf Cattail	21	1.079	a*	0.327	Common Rush	294	0.612	a,b	0.052
Brookside Alder	21	1.118	a	0.149	Mixed Litter	294	0.735	b	0.047
Reed Canary Grass	21	1.265	a	0.185	Reed Canary Grass	294	0.801	b	0.048
Broadleaf Cattail	35	0.371	a	0.203	Broadleaf Cattail	364	0.420	a	0.050
Common Rush	35	0.623	a	0.094	Brookside Alder	364	0.455	a	0.041
Brookside Alder	35	0.870	a	0.083	Common Rush	364	0.663	a	0.052
Mixed Litter	35	0.941	a	0.213	Reed Canary Grass	364	0.736	a	0.041
Reed Canary Grass	35	1.074	a	0.159	Mixed Litter	364	0.746	a	0.055
Broadleaf Cattail	49	0.435	a	0.137	Broadleaf Cattail	455	0.314	a	0.041
Common Rush	49	0.466	a	0.055	Brookside Alder	455	0.397	a	0.041
Brookside Alder	49	0.639	a	0.050	Common Rush	455	0.495	a	0.047
Mixed Litter	49	0.685	a	0.135	Mixed Litter	455	0.560	a	0.051
Reed Canary Grass	49	0.872	a	0.114	Reed Canary Grass	455	0.635	a	0.037
Broadleaf Cattail	77	0.332	a	0.065	Brookside Alder	546	0.370	a	0.014
Common Rush	77	0.462	a	0.053	Broadleaf Cattail	546	0.373	a	0.024
Brookside Alder	77	0.557	a	0.043	Common Rush	546	0.558	a	0.037
Mixed Litter	77	0.611	a	0.075	Mixed Litter	546	0.593	a	0.012
Reed Canary Grass	77	0.728	a	0.072	Reed Canary Grass	546	0.692	a	0.039
Broadleaf Cattail	119	0.121	a	0.080	Brookside Alder	637	0.336	a	0.037
Common Rush	119	0.346	a	0.044	Broadleaf Cattail	637	0.346	a	0.030
Brookside Alder	119	0.417	a	0.028	Common Rush	637	0.602	a,b	0.047
Mixed Litter	119	0.453	a	0.047	Mixed Litter	637	0.644	a,b	0.038
Reed Canary Grass	119	0.534	a	0.054	Reed Canary Grass	637	0.724	b	0.040
Broadleaf Cattail	168	0.213	a	0.029	Broadleaf Cattail	728	0.413	a	0.055
Common Rush	168	0.298	a	0.039	Brookside Alder	728	0.422	a	0.033
Brookside Alder	168	0.321	a	0.028	Common Rush	728	0.613	a	0.051
Mixed Litter	168	0.407	a	0.055	Mixed Litter	728	0.661	a	0.051
Reed Canary Grass	168	0.553	a	0.013	Reed Canary Grass	728	0.702	a	0.056

* Indicates a significant change ($P < 0.05$) from the previous collection.

[a] Means followed by the same lowercase letters are not different ($P > 0.05$) across litter types.

Appendix C. List of 8 created and 8 reference wetland study sites in West Virginia, including site name, year constructed, size (ha), the organization that created the wetland, elevation (m above sea level), Universal Transverse Mercator (UTM) coordinates, basin, and watershed, 2008-2009.

Site Name	Year	Size (ha)	Source	Elev. (m)	UTM Y	UTM X	Basin	Watershed
Created Wetlands								
Leading Creek	1995	17.0	Division of Highways	600	4321563	602550	Tygart Valley	Leading Creek
Sugar Creek	1995	11.0	Division of Highways	490	4328850	591470	Tygart Valley	Laurel Creek
Hazelton	2006	2.7	Division of Highways	560	4390990	625708	Cheat River	Little Sandy Creek
Pedlar WMA	2006	0.1	Division of Natural Resources	335	4393134	575877	Dunkard Creek	Dunkard Creek
Upper Deckers Creek WMA	1968	3.5	Monongahela Soil Conservation District	520	4375719	602837	Monongahela River	Upper Deckers Creek
Elk Run	1981	3.8	Island Creek Coal Co.	830	4341542	636104	North Branch of the Potomac	Elk Run
VEPCO	1995	5.7	Virginia Electric Power Co.	1020	4338218	641309	Cheat River	Blackwater River
Enoch Branch	1997	3.4	Division of Highways	570	4248058	513819	Gauley River	Muddlety Creek
Reference Wetlands								
Meadowville	-	11.7	-	480	4330920	593940	Tygart Valley	Laurel Creek
Upper Deckers Creek	-	2.1	-	515	4377282	602193	Monongahela	Upper Deckers Creek
Bruceton Mills	-	1.4	-	515	4393306	615536	Cheat River	Big Sandy Creek
Indian Creek	-	0.7	-	275	4379544	580789	Monongahela River	Monongahela River
Kanes Creek	-	8.9	-	520	4373209	603528	Monongahela River	Upper Deckers Creek
Thomas Airfield	-	3.5	-	940	4335279	629233	Cheat River	Blackwater River
Glade Run	-	1.7	-	965	4328921	641158	Cheat River	Blackwater River
Muddlety	-	10.4	-	560	4248673	516774	Gauley River	Muddlety Creek

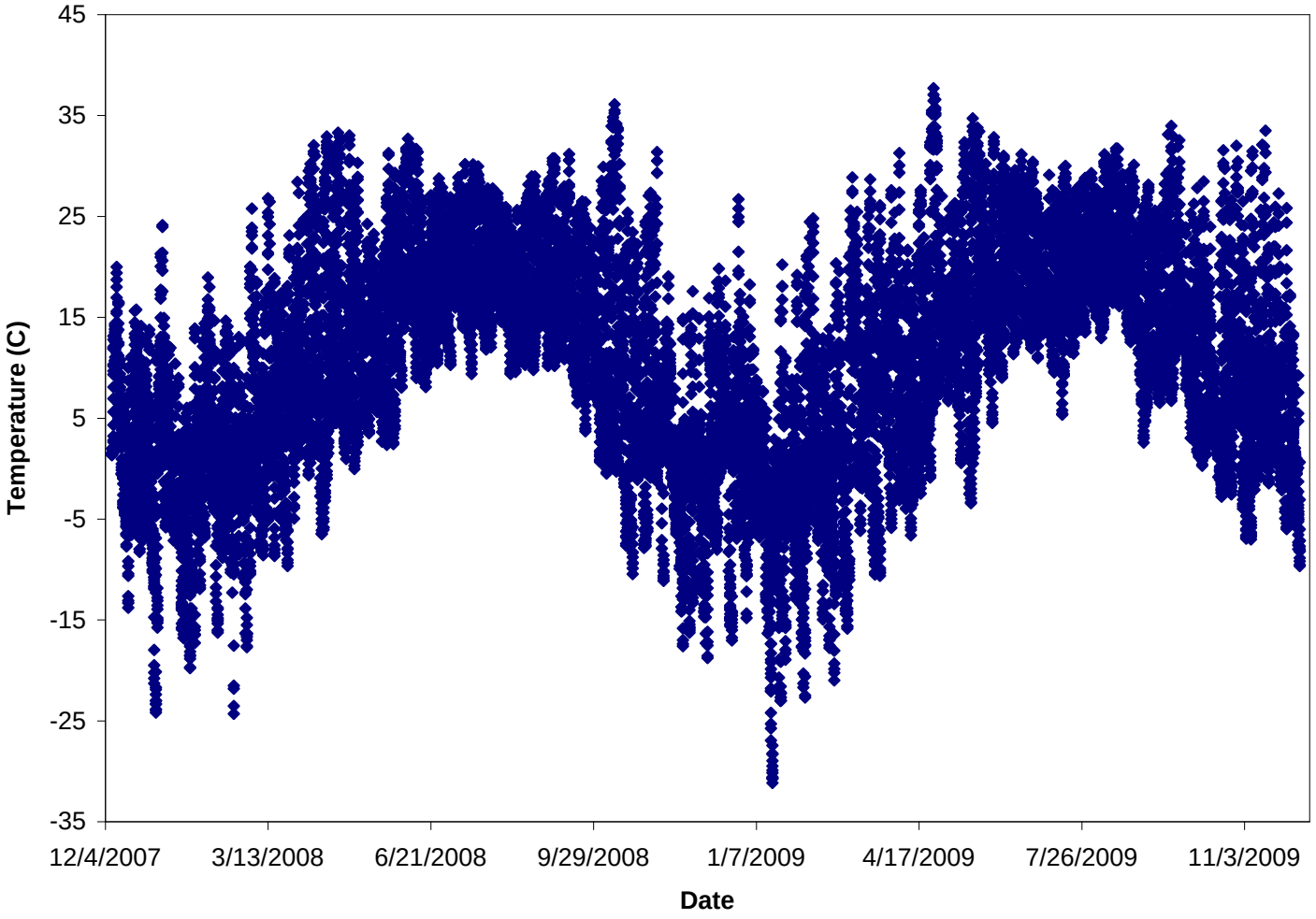
Appendix D. Number of litter bags collected at each wetland for each date. Flooding early in the study at Leading Creek and Glade Run caused losses to be higher than expected and resulted in lower collection numbers at 9 and 12 months. Thick ice at Upper Deckers Creek hindered collection and caused there to be only 5 bags collected at 3 months. Losses at Upper Deckers Creek WMA were high when wildlife destroyed one of the stakes; therefore, only 5 bags were collected at 9 months to ensure a full set at 12 months.

	No. of Bags Collected on Each Collection Date			
Created Wetlands	3 months	6 months	9 months	12 months
Leading Creek	6	6	4	4
Sugar Creek	6	6	6	6
Hazelton	6	6	6	6
Pedlar WMA	6	6	6	6
Upper Deckers Creek WMA	6	6	5	6
Elk Run	6	6	6	6
VEPCO	6	6	6	6
Enoch Branch	6	6	6	6
Reference Wetlands				
Meadowville	6	6	6	6
Upper Deckers Creek	5	6	6	6
Bruceton Mills	6	6	6	6
Indian Creek	6	6	6	6
Kanes Creek	6	6	6	6
Thomas Airfield	6	6	6	6
Glade Run	6	6	4	2
Muddlety	6	6	6	6

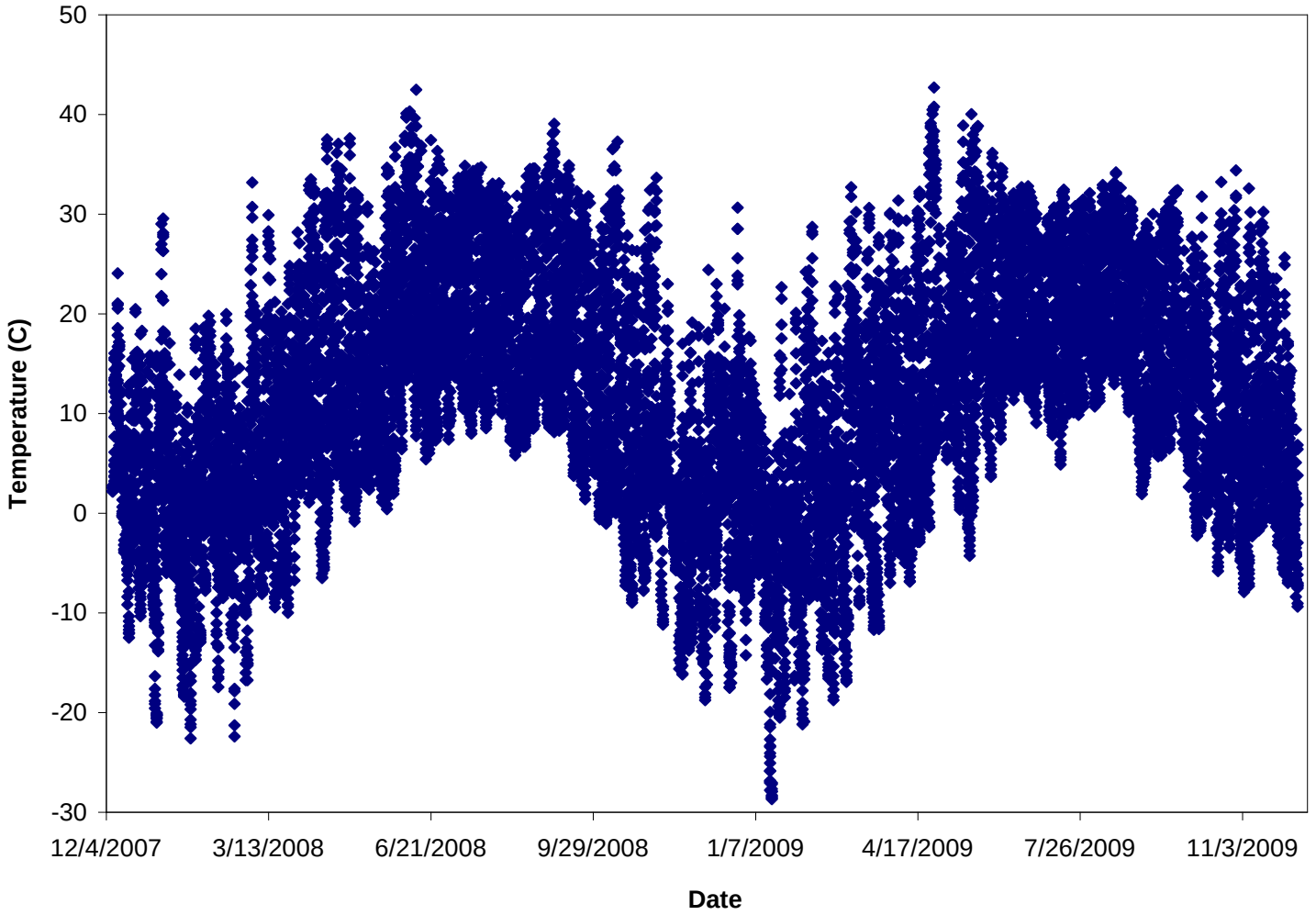
Appendix E. Decomposition rate, presented as mean percent ash-free dry mass remaining and decomposition rate constant *k* (yr^{-1}), for each collection date for 16 wetlands (8 created and 8 reference) in West Virginia, November 2008 to November 2009.

	3 mo		6 mo		9 mo		12 mo	
Created Wetlands	Proportion	Rate	Proportion	Rate	Proportion	Rate	Proportion	Rate
Leading Creek	87.198	0.539	88.598	0.242	71.948	0.429	56.059	0.581
Sugar Creek	90.987	0.369	82.168	0.401	65.890	0.545	56.515	0.574
Hazelton	94.930	0.227	89.662	0.219	70.451	0.458	60.689	0.501
Elk Run	98.426	0.069	92.486	0.157	76.424	0.350	68.892	0.382
VEPCO	78.800	0.838	72.244	0.635	66.586	0.523	56.201	0.582
Enoch Branch	91.424	0.362	83.904	0.360	70.493	0.458	59.157	0.528
Pedlar WMA	79.526	0.942	75.117	0.580	54.476	0.802	44.840	0.811
Upper Deckers WMA	76.057	1.092	69.705	0.773	59.838	0.695	45.359	0.797
Average	87.169	0.555	81.736	0.421	67.013	0.533	55.964	0.594
Reference Wetlands								
Meadowville	90.718	0.397	72.570	0.645	65.204	0.558	54.145	0.629
Upper Deckers Creek	92.035	0.329	93.153	0.146	73.742	0.400	62.740	0.467
Bruceton Mills	93.243	0.281	84.902	0.327	65.728	0.545	57.644	0.552
Thomas Airfield	76.162	1.061	71.678	0.665	63.656	0.589	56.078	0.587
Glade Run	92.927	0.258	88.077	0.248	83.895	0.228	39.541	0.940
Muddlety	86.774	0.576	77.342	0.520	61.110	0.652	49.074	0.719
Indian Creek	95.172	0.206	89.024	0.239	71.025	0.451	54.795	0.611
Kanes Creek	77.232	1.033	72.435	0.700	67.953	0.525	62.635	0.476
Average	88.033	0.518	81.148	0.436	69.039	0.494	54.581	0.623

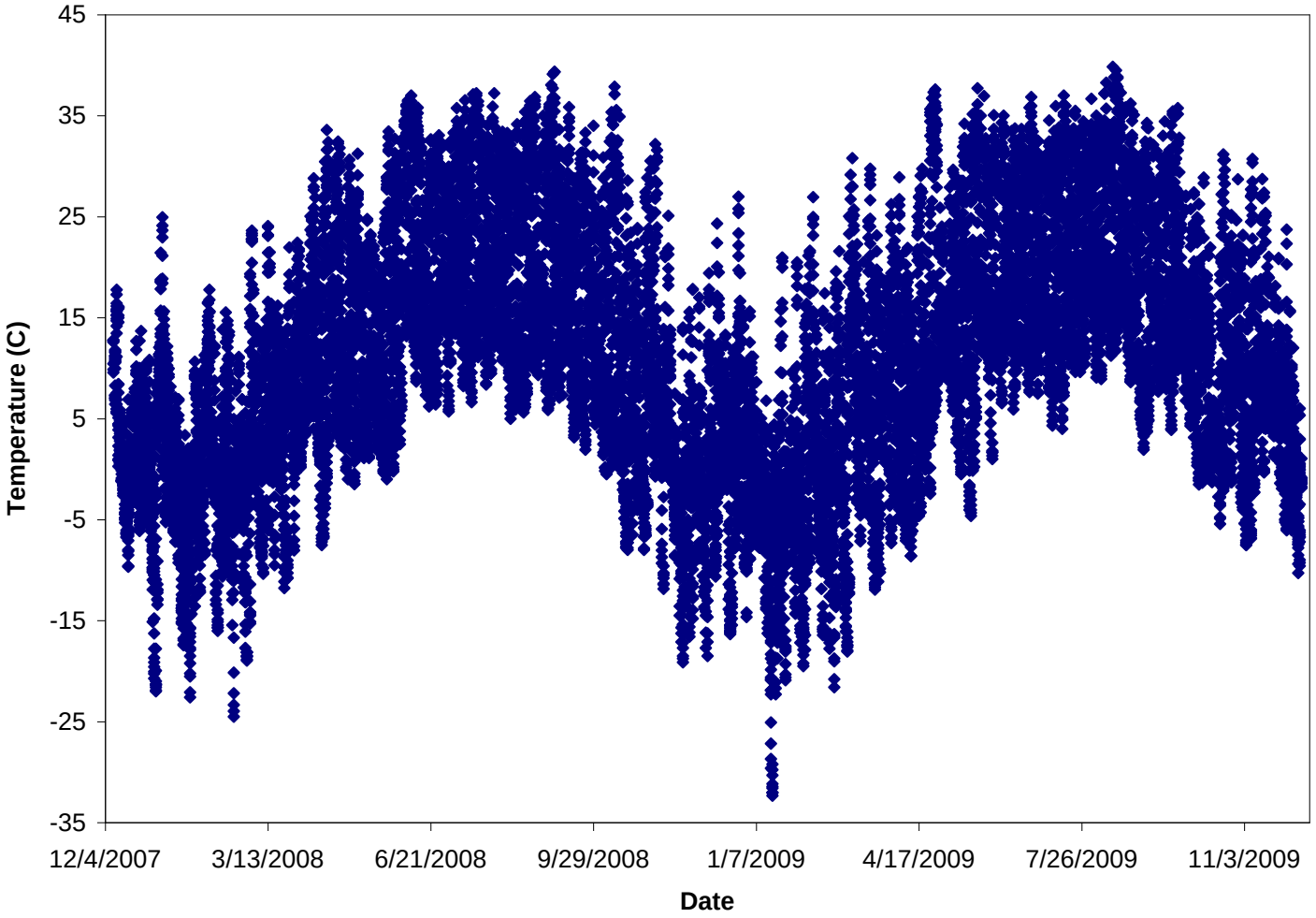
Appendix F. Average air temperature, recorded hourly from December 2007 to December 2009, by two temperature loggers in Leading Creek mitigated wetland.



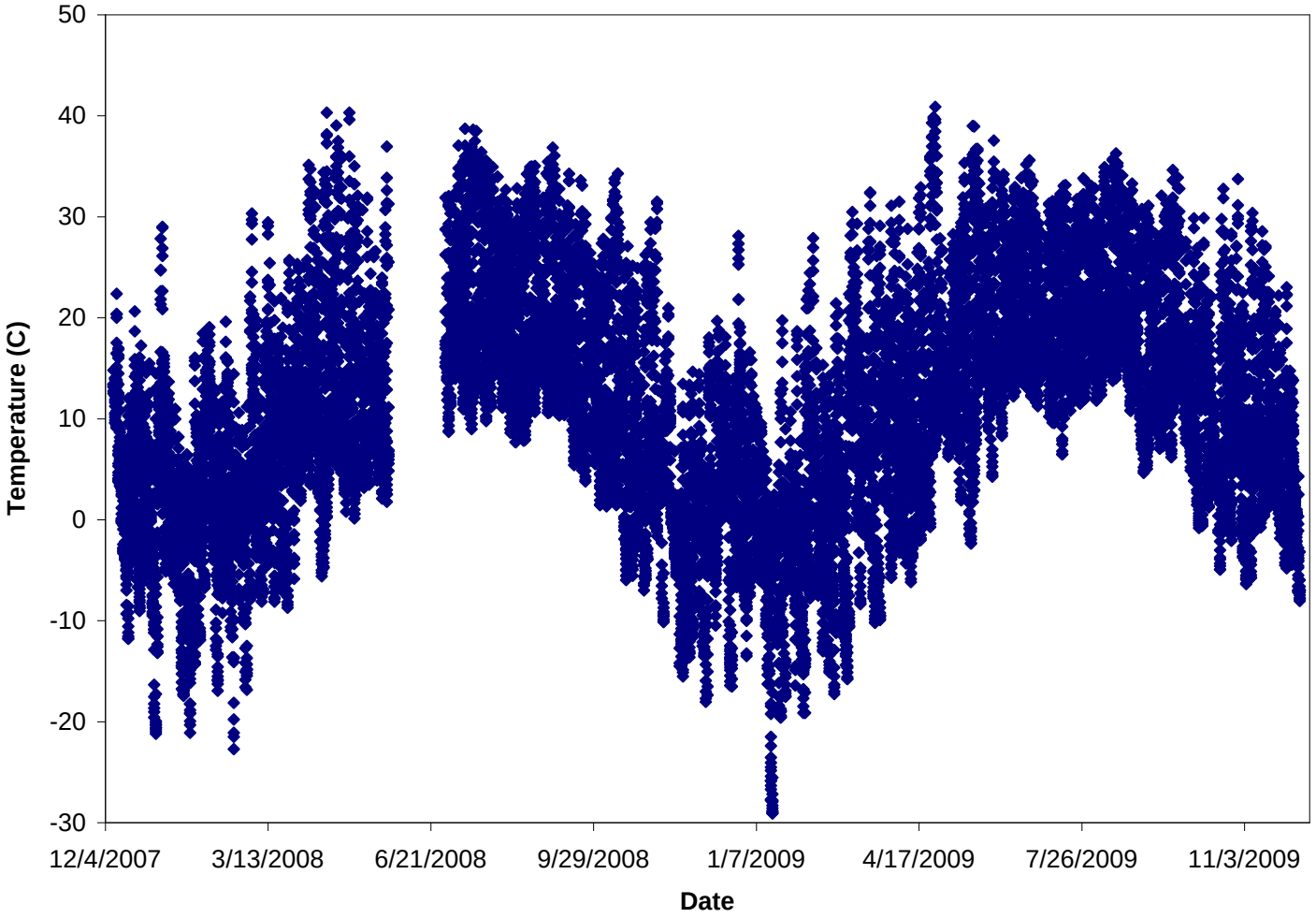
Appendix G. Average air temperature, recorded hourly from December 2007 to December 2009, by two temperature loggers in Sugar Creek mitigated wetland.



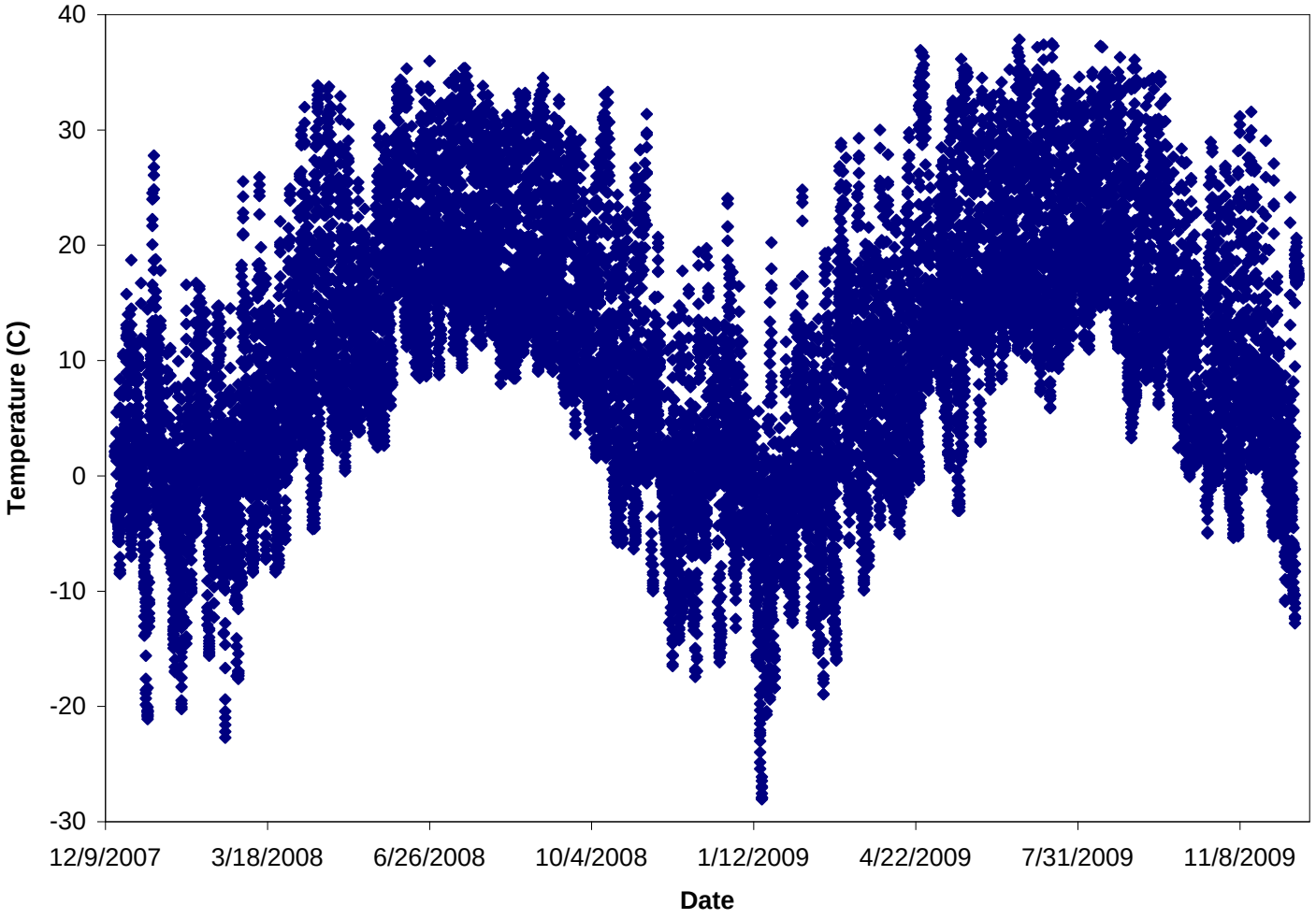
Appendix H. Average air temperature, recorded hourly from December 2007 to December 2009, by two temperature loggers in Hazelton mitigated wetland.



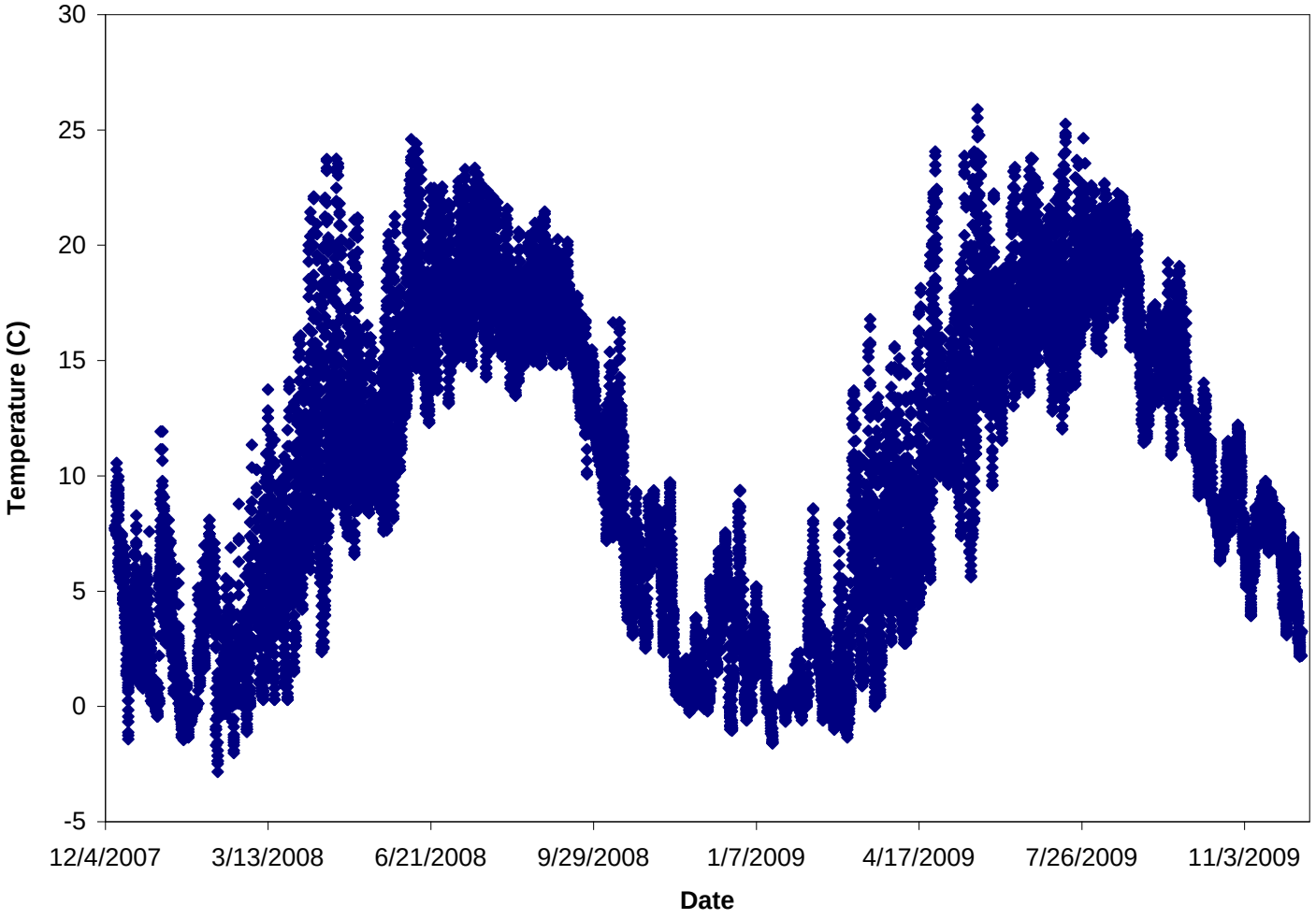
Appendix I. Average air temperature, recorded hourly from December 2007 to December 2009, by two temperature loggers in Meadowville reference wetland.



Appendix J. Average air temperature, recorded hourly from December 2007 to December 2009, by two temperature loggers in Upper Deckers Creek reference wetland.



Appendix K. Average air temperature, recorded hourly from December 2007 to December 2009, by two temperature loggers in Bruceton Mills reference wetland.



Appendix L. Mean, standard error (S.E.), minimum, and maximum results for decomposition of 5 litter types (brookside alder, reed canary grass, common rush, broadleaf cattail, mixed litter), expressed as decomposition rate constant *k* (yr^{-1}), in 3 mitigated and 3 reference wetlands in West Virginia, 2007 to 2009. Number of stakes from each wetland are shown in parentheses below the wetland name.

		Mitigated Wetlands			Reference Wetlands		
Litter Type		Leading Creek (n = 16)	Sugar Creek (n = 20)	Hazelton (n = 8)	Meadowville (n = 16)	Upper Deckers Creek (n = 18)	Bruceton Mills (n = 18)
Brookside Alder	Mean	0.434	0.419	0.282	0.467	0.399	0.517
	SE	0.020	0.031	0.033	0.036	0.030	0.056
	Min	0.252	0.242	0.159	0.255	0.228	0.204
	Max	0.549	0.631	0.466	0.894	0.747	1.074
Reed Canary Grass	Mean	0.758	0.669	0.522	0.786	0.645	0.839
	SE	0.038	0.028	0.034	0.045	0.031	0.057
	Min	0.521	0.458	0.399	0.415	0.400	0.410
	Max	1.014	0.928	0.673	1.082	0.906	1.513
Common Rush	Mean	0.612	0.573	0.390	0.632	0.541	0.590
	SE	0.037	0.029	0.018	0.041	0.032	0.044
	Min	0.367	0.397	0.302	0.424	0.247	0.109
	Max	0.849	0.806	0.462	1.026	0.818	0.937
Broadleaf Cattail	Mean	0.431	0.297	0.262	0.491	0.316	0.326
	SE	0.034	0.031	0.059	0.040	0.026	0.033
	Min	0.250	0.134	-0.008	0.219	0.047	0.102
	Max	0.735	0.603	0.497	0.882	0.589	0.565
Mixed Litter	Mean	0.661	0.612	0.464	0.727	0.609	0.733
	SE	0.035	0.026	0.037	0.048	0.033	0.047
	Min	0.354	0.433	0.262	0.442	0.262	0.421
	Max	0.848	0.769	0.631	1.162	0.836	1.164

Appendix M. Mean, standard error (S.E.), minimum, and maximum for 9 environmental parameters measured in 3 mitigated and 3 reference wetlands in West Virginia, December 2007 to December 2009. Number of stakes from each wetland are shown in parentheses under the wetland name.

		Mitigated Wetlands			Reference Wetlands		
Environmental Parameters[a]		Leading Creek (n = 16)	Sugar Creek (n = 20)	Hazelton (n = 8)	Meadowville (n = 16)	Upper Deckers Creek (n = 18)	Bruceton Mills (n = 18)
AT	Mean	7.869	7.661	6.970	7.851	6.399	7.070
	SE	0.424	0.258	0.355	0.398	0.317	0.376
	Min	3.303	5.498	5.957	4.350	3.083	2.487
	Max	10.759	9.428	8.674	10.084	8.440	9.228
WT	Mean	8.517	9.415	8.899	8.886	6.906	9.417
	SE	0.417	0.454	0.832	0.457	0.370	0.581
	Min	5.080	7.232	4.813	5.970	4.857	5.900
	Max	12.073	13.400	12.341	11.836	11.850	15.717
ST	Mean	14.445	13.394	16.428	13.569	11.839	10.240
	SE	1.172	0.589	2.216	0.841	0.488	0.793
	Min	8.567	8.791	8.710	9.467	7.378	3.986
	Max	27.340	18.388	27.650	19.917	18.117	19.200
WD	Mean	6.936	5.916	5.496	3.282	6.035	3.152
	SE	0.835	1.291	0.601	0.448	0.624	0.439
	Min	1.906	1.000	2.696	0.671	2.091	0.395
	Max	13.625	24.375	7.923	7.047	12.078	6.129
HP	Mean	0.472	0.428	0.506	0.455	0.263	0.558
	SE	0.042	0.039	0.044	0.044	0.037	0.056
	Min	0.251	0.130	0.237	0.162	0.126	0.137
	Max	0.755	0.685	0.616	0.707	0.697	0.854
FET	Mean	0.022	0.016	0.022	0.018	0.023	0.021
	SE	0.002	0.001	0.002	0.002	0.002	0.002
	Min	0.011	0.006	0.014	0.004	0.011	0.009
	Max	0.039	0.029	0.029	0.033	0.040	0.035
SF	Mean	0.513	0.341	0.379	0.156	0.745	0.137
	SE	0.064	0.062	0.063	0.016	0.053	0.011
	Min	0.113	0.097	0.135	0.066	0.309	0.051
	Max	1.096	0.947	0.614	0.273	1.302	0.214

[a] AT- air temperature (°C), WT - water temperature, ST – soil temperature, WD - water depth (cm), HP - hydroperiod (proportion of days), FET - number of transitions between flooded and exposed (# / days), SF – sum fluctuation of water depth (cm / day), WPH - water pH, SM - soil moisture (0 dry - 10 saturated)

Appendix M. Continued.

Environmental Parameters[a]		Mitigated Wetlands			Reference Wetlands		
		Leading Creek (n = 16)	Sugar Creek (n = 20)	Hazelton (n = 8)	Meadowville (n = 16)	Upper Deckers Creek (n = 18)	Bruceton Mills (n = 18)
WPH	Mean	6.176	5.956	6.937	6.271	6.230	6.461
	SE	0.072	0.070	0.129	0.100	0.030	0.022
	Min	5.767	5.400	6.600	5.241	5.900	6.296
	Max	6.700	6.686	7.586	6.700	6.450	6.660
SM	Mean	6.393	7.212	9.312	9.101	8.675	8.782
	SE	0.246	0.287	0.274	0.140	0.196	0.163
	Min	4.765	4.583	7.765	8.136	6.524	7.444
	Max	8.600	9.250	10.000	10.000	9.889	9.750

[a] AT- air temperature (°C), WT - water temperature, ST – soil temperature, WD - water depth (cm), HP - hydroperiod (proportion of days), FET - number of transitions between flooded and exposed (# / days), SF – sum fluctuation of water depth (cm / day), WPH - water pH, SM - soil moisture (0 dry - 10 saturated)

Appendix N. Mean and standard error (S.E.) for 9 environmental parameters measured in 3 mitigated and 3 reference wetlands in West Virginia, December 2007 to December 2009. Averages were obtained by taking the mean of environmental measurements obtained at 90 stakes in each wetland.

	Mitigated		Reference		Overall		F value	P value
	Mean	S.E.	Mean	S.E.	Mean	S.E.	(d.f. = 1,4)	
Air Temperature[a]	10.51	0.25	10.24	0.21	10.37	0.16	0.674	0.458
Water Temperature	8.83	0.85	8.80	1.12	8.82	0.63	0.001	0.982
Soil Temperature	13.04	0.31	11.97	0.61	12.50	0.39	2.469	0.191
Water Depth[b]	4.20	0.36	3.49	1.34	3.85	0.64	0.265	0.634
Hydroperiod[c]	0.28	0.03	0.31	0.08	0.29	0.04	0.073	0.801
No. of transitions between flooded and exposed[d]	0.011	0.001	0.013	0.002	0.012	0.001	0.547	0.501
Sum fluctuations[e]	0.25	0.03	0.25	0.15	0.25	0.07	0.001	0.984
Water pH	6.20	0.24	6.28	0.05	6.24	0.11	0.111	0.756
Soil Moisture[f]	7.73	0.53	8.67	0.26	8.20	0.34	2.487	0.190

[a] °C

[b] cm

[c] proportion of days

[d] no. of transitions / days

[e] cm / day

[f] 0 dry – 10 saturated

Appendix O. Akaike rankings for 23 *a priori* models predicting brookside alder decomposition rate. Soil temperature, number of transitions between flood and exposed, and water pH all had substantial Akaike support based on the data.

Akaike Support for Model	Model structure[a]	K[b]	AIC_c	Δ_i[c]	$£(g_i\|x)$[d]	w_i[e]	w_{lowest} / w_i
Substantial	*k* = -2.00 + 1.50×ST	4	75.99	0.00	1.00	0.37	
	k = -0.74 - 1.29×FET	4	77.04	1.05	0.59	0.22	1.7
	k = -2.74 + 0.98×WPH	4	77.72	1.73	0.42	0.16	2.4
Good	*k* = -3.99 + 0.06×AT + 1.43×WPH	5	79.44	3.45	0.18	0.07	5.6
	k = -0.87 + 0.16×HP - 0.89×FET	5	79.97	3.98	0.14	0.05	7.3
	k = -1.01 + 0.20×HP	4	80.72	4.73	0.09	0.03	11
	k = -1.26 + 0.05×AT - 0.17×FET	5	81.11	5.12	0.08	0.03	13
	k = -1.29 + 0.05×AT	4	81.52	5.53	0.06	0.02	16
	k = -2.07 + 1.46×ST + 0.01×SM	5	82.95	6.96	0.03	0.01	32
	k = -1.045 + 0.07×WD	4	82.90	6.90	0.03	0.01	32
	k = -0.86 + 0.05×SF	4	83.60	7.61	0.02	0.01	45
Poor	*k* = -1.35 + 0.05×AT + 0.12×FET + 0.13×HP	6	84.34	8.35	0.02	0.01	65
	k = -2.89 + 0.02×WT + 0.96×WPH	5	84.61	8.62	0.01	0.00	74
	k = -1.11 + 0.02×WT	4	84.98	8.99	0.01	0.00	89
	k = -1.09 + 0.02×SM	4	84.99	9.00	0.01	0.00	90
	k = -4.15 + 0.05×AT + 0.22×ST + 0.01×SM + 1.40×WPH	7	86.65	10.65	0.00	0.00	206
	k = -1.64 + 0.04×AT + 0.37×ST + 0.02×SM	6	88.54	12.55	0.00	0.00	531
	k = -1.87 + 0.03×AT + 0.02×WT + 0.79×ST	6	89.07	13.08	0.00	0.00	694
	k = -0.85 - 0.07×WD + 0.29×HP + 0.08×SM	6	89.95	13.96	0.00	0.00	1.E+03
	k = -2.34 + 0.02×WT - 0.18×WD + 0.96×WPH + 0.39×HP - 1.34×FET + 0.16×SF	9	95.28	19.28	0.00	0.00	2.E+04
	k = -0.89 - 0.00007×ND	4	95.55	19.55	0.00	0.00	2.E+04
	k = -3.71 + 0.06×AT + 0.01×WT - 0.25×WD + 1.39×WPH + 0.41×HP - 0.44×FET+ 0.21×SF + 0.23×ST + 0.01×SM	12	104.91	28.92	0.00	0.00	2.E+06

[a] AT = air temperature, WT = water temperature, ST = soil temperature, WD = water depth, HP = hydroperiod, FET = no. of transitions between flooded and exposed, SF = sum fluctuation of water depth, WPH = water pH, SM = soil moisture, ND = no. days in the wetland

[b] K = number of parameters, including intercept and error

[c] $\Delta_l = AIC_{c\ lowest} - AIC_{ci}$ for the i^{th} model in comparison

[d] $£(g_i|x)$ = likelihood of a model

[e] w_i = Akaike Weights

Appendix P. Akaike rankings for 23 *a priori* models predicting reed canary grass decomposition rate. Air temperature, soil temperature, and water pH all had substantial Akaike support based on the data.

Akaike Support for Model	Model structure[a]	K[b]	AIC_c	Δ_i[c]	$£(g_i\|x)$[d]	w_i[e]	w_{lowest} / w_i
Substantial	*k* = -3.59 + 0.05×AT + 1.53×WPH	5	3.38	0.00	1.00	0.52	
	k = -1.38 + 1.39×ST	4	4.97	1.59	0.45	0.24	2.2
Good	*k* = -2.47 + 1.13×WPH	4	6.18	2.80	0.25	0.13	4.1
	k = -0.93 + 0.05×AT + 1.21×FET	5	8.96	5.57	0.06	0.03	16
	k = 0.38 + 0.02×FET	4	9.36	5.98	0.05	0.03	20
	k = -0.70 + 0.04×AT	4	10.03	6.64	0.04	0.02	28
Poor	*k* = -3.72 + 0.05×AT + 0.12×ST + 0.02×SM + 1.48×WPH	7	11.71	8.32	0.02	0.01	64
	k = -1.47 + 1.31×ST + 0.02×SM	5	12.19	8.81	0.01	0.01	82
	k = -0.91 + 0.05×AT + 1.13×FET - 0.03×HP	6	13.36	9.97	0.01	0.00	146
	k = -0.38 - 0.003×HP	4	13.35	9.97	0.01	0.00	146
	k = -0.38 - 0.002×HP + 0.02×FET	5	13.70	10.31	0.01	0.00	174
	k = -2.39 - 0.01×WT + 1.15×WPH	5	14.11	10.73	0.00	0.00	214
	k = -0.37 - 0.01×WD	4	15.27	11.88	0.00	0.00	381
	k = -0.61 + 0.03×SM	4	15.46	12.08	0.00	0.00	419
	k = -0.37 + 0.01×SF	4	15.49	12.11	0.00	0.00	426
	k = -0.68 + 0.05×AT - 0.02×WT + 0.18×ST	6	16.99	13.60	0.00	0.00	900
	k = -0.27 - 0.01×WT	4	17.01	13.63	0.00	0.00	9.E+02
	k = -1.12 + 0.04×AT + 0.40×ST + 0.02×SM	6	17.51	14.13	0.00	0.00	1.E+03
	k = -0.19 - 0.11×WD + 0.16×HP + 0.07×SF	6	23.75	20.36	0.00	0.00	3.E+04
	k = -0.35 - 0.00007×ND	4	26.93	23.55	0.00	0.00	1.E+05
	k = -3.64 + 0.07×AT - 0.02×WT - 0.22×WD + 1.66×WPH + 0.22×HP + 0.29×FET + 0.14×SF + 0.22×ST + 0.02×SM	12	28.86	25.48	0.00	0.00	3.E+05
	k = -2.07 - 0.01×WT - 0.14×WD + 1.17×WPH + 0.22×HP - 0.72×FET + 0.09×SF	9	29.03	25.64	0.00	0.00	4.E+05

[a] AT = air temperature, WT = water temperature, ST = soil temperature, WD = water depth, HP = hydroperiod, FET = no. of transitions between flooded and exposed, SF = sum fluctuation of water depth, WPH = water pH, SM = soil moisture, ND = no. days in the wetland

[b] K = number of parameters, including intercept and error

[c] $\Delta_I = AIC_{c\ lowest} - AIC_{ci}$ for the i^{th} model in comparison

[d] $£(g_i|x)$ = likelihood of a model

[e] w_i = Akaike Weights

Appendix Q. Akaike rankings for 23 *a priori* models predicting common rush decomposition rate. Air temperature and number of transitions between flood and exposed had substantial Akaike support based on the data.

Akaike Support for Model		Model structure[a]	K[b]	AIC_c	Δ_i[c]	$£(g_i\|x)$[d]	w_i[e]	w_{lowest} / w_i
	Substantial	k = 0.04 + 0.06×AT + 0.77×FET	5	-92.32	0.00	1.00	0.45	
		k = 0.18 + 0.05×AT	4	-92.05	0.27	0.87	0.39	1.1
	Good	k = 0.04 + 0.05×AT + 0.08×WPH	5	-89.21	3.12	0.21	0.09	4.8
		k = 0.09 + 0.06×AT + 0.59×FET - 0.08×HP	6	-87.89	4.44	0.11	0.05	9.2
		k = -0.41 + 1.36×ST	4	-84.48	7.84	0.02	0.01	50
	Poor	k = 0.04 + 0.05×AT + 0.12×ST + 0.01×SM	6	-81.42	10.91	0.00	0.00	233
		k = 0.13 + 0.05×AT - 0.002×WT + 0.10×ST	6	-79.90	12.43	0.00	0.00	499
		k = -0.07 + 0.05×AT + 0.12×ST + 0.01×SM + 0.06×WPH	7	-78.57	13.75	0.00	0.00	969
		k = -0.43 + 1.35×ST + 0.002×SM	5	-75.76	16.56	0.00	0.00	4.E+03
		k = 0.64 - 0.55×FET	4	-73.62	18.70	0.00	0.00	1.E+04
		k = 1.18 - 0.33×WPH	4	-72.44	19.89	0.00	0.00	2.E+04
		k = 0.57 - 0.01×HP	4	-68.87	23.45	0.00	0.00	1.E+05
		k = 0.67 - 0.04×HP - 0.66×FET	5	-68.64	23.69	0.00	0.00	1.E+05
		k = 0.61 - 0.03×WD	4	-67.62	24.70	0.00	0.00	2.E+05
		k = 0.53 - 0.02×SF	4	-67.22	25.10	0.00	0.00	3.E+05
		k = 0.48 + 0.01×SM	4	-65.80	26.53	0.00	0.00	6.E+05
		k = 0.50 + 0.01×WT	4	-64.84	27.49	0.00	0.00	9.E+05
		k = 1.14 0.01×WT - 0.35×WPH	5	-63.15	29.17	0.00	0.00	2.E+06
		k = -0.41 + 0.04×AT + 0.01×WT - 0.18×WD + 0.06×WPH + 0.04×HP + 0.10×FET + 0.10×SF + 1.09×ST + 0.01×SM	12	-58.14	34.18	0.00	0.00	3.E+07
		k = 0.48 + 0.0002×ND	4	-59.18	33.14	0.00	0.00	2.E+07
		k = 0.62 - 0.05×WD + 0.08×HP + 0.01×SF	6	-56.95	35.37	0.00	0.00	5.E+07
		k = 1.38 + 0.01×WT - 0.10×WD -0.31×WPH + 0.11×HP - 0.80×FET + 0.05×SF	9	-45.50	46.82	0.00	0.00	1.E+10

[a] AT = air temperature, WT = water temperature, ST = soil temperature, WD = water depth, HP = hydroperiod, FET = no. of transitions between flooded and exposed, SF = sum fluctuation of water depth, WPH = water pH, SM = soil moisture, ND = no. days in the wetland

[b] K = number of parameters, including intercept and error

[c] $\Delta_l = AIC_{c\ lowest} - AIC_{ci}$ for the i^{th} model in comparison

[d] $£(g_i|x)$ = likelihood of a model

[e] w_i = Akaike Weights

Appendix R. Akaike rankings for 23 *a priori* models predicting broadleaf cattail decomposition rate. Hydroperiod and number of transitions between flood and exposed had substantial Akaike support based on the data.

Akaike Support for Model	Model structure[a]	K[b]	AIC_c	Δ_i[c]	$£(g_i\|x)$[d]	w_i[e]	w_{lowest} / w_i
Substantial	k = 0.22 + 0.94×FET	4	-87.22	0.00	1.00	0.31	
	k = 0.44 - 0.20×HP	4	-86.89	0.32	0.85	0.26	1.2
	k = 0.36 - 0.17×HP + 0.52×FET	5	-86.23	0.99	0.61	0.19	1.6
Good	k = 0.48 - 0.07×WD	4	-84.83	2.39	0.30	0.09	3.3
	k = 0.59 - 0.32×ST	4	-84.44	2.78	0.25	0.08	4.0
	k = 0.53 - 0.10×WPH	4	-83.42	3.79	0.15	0.05	6.7
	k = 0.33 - 0.02×SF	4	-79.25	7.97	0.02	0.01	54
Poor	k = 0.10 + 0.01×AT + 1.22×FET	5	-79.08	8.13	0.02	0.01	58
	k = 0.22 + 0.01×AT + 0.81×FET - 0.18×HP	6	-78.44	8.77	0.01	0.00	80
	k = 0.46 - 0.01×WT	4	-78.67	8.55	0.01	0.00	72
	k = 0.45 - 0.01×SM	4	-77.88	9.33	0.01	0.00	106
	k = 0.32 + 0.004×AT	4	-76.66	10.56	0.01	0.00	196
	k = 0.63 - 0.28×ST - 0.01×SM	5	-76.07	11.15	0.00	0.00	263
	k = 0.62 - 0.01×WT - 0.08×WPH	5	-75.98	11.24	0.00	0.00	275
	k = 0.57 - 0.09×WD - 0.05×HP + 0.03×SF	6	-75.22	12.00	0.00	0.00	403
	k = 0.46 + 0.004×AT - 0.07×WPH	5	-74.02	13.20	0.00	0.00	735
	k = 1.03 + 0.03×AT - 0.02×WT - 1.02×ST	6	-72.44	14.78	0.00	0.00	2.E+03
	k = 0.29 + 0.0001×ND	4	-70.00	17.22	0.00	0.00	5.E+03
	k = 0.77 + 0.02×AT -0.66×ST - 0.01×SM	6	-68.47	18.75	0.00	0.00	1.E+04
	k = 0.67 + 0.02×AT - 0.68×ST - 0.01×SM + 0.06×WPH	7	-65.77	21.44	0.00	0.00	5.E+04
	k = 0.64 - 0.01×WT - 0.06×WD - 0.05×WPH - 0.07×HP + 0.25×FET + 0.014×SF	9	-62.81	24.40	0.00	0.00	2.E+05
	k = 0.43 + 0.02×AT - 0.01×WT - 0.08×WD + 0.16×WPH + 0.001×HP + 0.52×FET + 0.03×SF - 0.37×ST - 0.01×SM	12	-45.45	41.77	0.00	0.00	1.E+09

[a] AT = air temperature, WT = water temperature, ST = soil temperature, WD = water depth, HP = hydroperiod, FET = no. of transitions between flooded and exposed, SF = sum fluctuation of water depth, WPH = water pH, SM = soil moisture, ND = no. days in the wetland

[b] K = number of parameters, including intercept and error

[c] $\Delta_I = AIC_{c\ lowest} - AIC_{ci}$ for the i^{th} model in comparison

[d] $£(g_i|x)$ = likelihood of a model

[e] w_i = Akaike Weights

Appendix S. Akaike rankings for 23 *a priori* models predicting decomposition rate for the mixed litter (3.3 g brookside alder, 6.6 g common rush, and 10 g reed canary grass). Air temperature and water pH had substantial Akaike support based on the data.

Akaike Support for Model		Model structure[a]	K[b]	AIC_c	Δ_i[c]	$£(g_i\|x)$[d]	w_i[e]	w_{lowest} / w_i
	Substantial	*k* = -0.88 + 0.03×AT + 0.77×WPH	5	-171.05	0.00	1.00	0.98	
	Poor	*k* = 0.47 + 0.03×AT + 0.60×FET	5	-161.29	9.77	0.01	0.01	132
		k = 0.59 + 0.03×AT	4	-161.30	9.76	0.01	0.01	131
		k = -0.85 + 0.03×AT - 0.08×ST - 0.001×SM + 0.79×WPH	7	-158.45	12.60	0.00	0.00	545
		k = 0.27 + 0.72×ST	4	-158.86	12.20	0.00	0.00	446
		k = 0.52 + 0.03×AT + 0.46×FET - 0.06×HP	6	-156.25	14.80	0.00	0.00	2.E+03
		k = -0.15 + 0.51×WPH	4	-155.35	15.71	0.00	0.00	3.E+03
		k = 0.81 - 0.14×FET	4	-151.92	19.14	0.00	0.00	1.E+04
		k = 0.28 + 0.73×ST - 0.001×SM	5	-149.35	21.70	0.00	0.00	5.E+04
		k = 0.54 + 0.03×AT + 0.04×ST 0.003×SM	6	-148.94	22.12	0.00	0.00	6.E+04
		k = 0.80 - 0.03×HP	4	-148.08	22.98	0.00	0.00	1.E+05
		k = 0.59 + 0.03×AT - 0.002×WT + 0.01×ST	6	-147.69	23.36	0.00	0.00	1.E+05
		k = 0.84 - 0.04×HP - 0.23×FET	5	-146.31	24.75	0.00	0.00	2.E+05
		k = 0.80 - 0.01×WD	4	-145.93	25.13	0.00	0.00	3.E+05
		k = 0.80 + 0.01×SF	4	-145.78	25.27	0.00	0.00	3.E+05
		k = -0.16 + 0.002×WT + 0.50×WPH	5	-144.61	26.45	0.00	0.00	6.E+05
		k = 0.76 + 0.004×SM	4	-144.58	26.47	0.00	0.00	6.E+05
		k = 0.77 + 0.003×WT	4	-143.35	27.70	0.00	0.00	1.E+06
		k = -0.88 + 0.04×AT + 0.0001×WT - 0.11×WD + 0.77×WPH + 0.06×HP + 0.19×FET + 0.09×SF + 0.32×ST + 0.001×SM	12	-134.91	36.15	0.00	0.00	7.E+07
		k = 0.77 + 0.00005×ND	4	-134.72	36.33	0.00	0.00	8.E+07
		k = 0.87 - 0.03×WD + 0.01×HP + 0.03×SF	6	-134.12	36.93	0.00	0.00	1.E+08
		k = 0.09 + 0.002×WT - 0.06×WD + 0.49×WPH + 0.05×HP - 0.44×FET + 0.05×SF	9	-123.54	47.51	0.00	0.00	2.E+10

[a] AT = air temperature, WT = water temperature, ST = soil temperature, WD = water depth, HP = hydroperiod, FET = no. of transitions between flooded and exposed, SF = sum fluctuation of water depth, WPH = water pH, SM = soil moisture, ND = no. days in the wetland

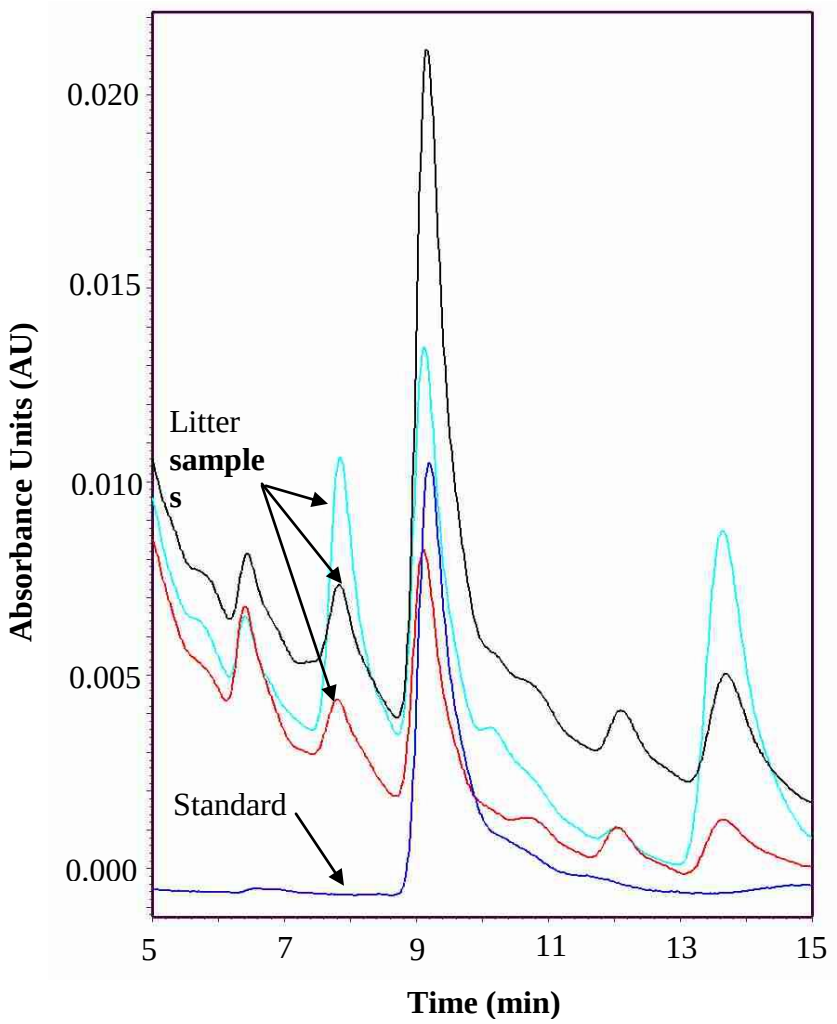
[b] K = number of parameters, including intercept and error

[c] $\Delta_I = AIC_{c\ lowest} - AIC_{ci}$ for the i^{th} model in comparison

[d] $£(g_i|x)$ = likelihood of a model

[e] w_i = Akaike Weights

Appendix T. Sample printout of high-performance liquid chromatography results. Peaks represent chemicals coming off the column at different times. Ergosterol peaks of litter samples are identified by comparison of retention time on the column with the standard and are quantified by comparison of the area under the peak with the area of the standard.



Appendix U. Table of taxonomic groups identified in litter bags collected over 2 years in 3 mitigated and 3 reference wetlands. Total abundance along with total, mean, S.E., and maximum biomass (mg dry mass) are presented for each taxonomic group along with functional feeding guild and if members are detritivores. Adults (a) and larvae (l) are indicated after taxonomic groups where the distinction is unclear.

Subclass	Order	Family	Total Abundance	Total Biomass	Mean Biomass	S.E. of Biomass	Max Biomass	Functional Feeding Group	Detritivore
Oligochaeta			669	2930.00	4.51	0.74	235.7	CG	Y
Pterygota	Hymenoptera	Formicidae	3295	1141.90	1.76	0.95	471.0	OM	
Pulmonata	Stylommatophora		113	886.70	1.36	0.24	113.5	OM	Y
Eumalacostraca	Isopoda	Asellidae	617	550.25	0.85	0.33	181.8	CG	Y
Heterodonta	Veneroida	Sphaeriidae	175	1001.57	0.77	0.27	90.6	FC	N
Pterygota	Diptera	Chironomidae (l)	801	301.80	0.46	0.09	29.7	CG	Y
Pterygota	Diptera	Tipulidae (l)	74	297.20	0.46	0.21	114.6	CG,SH	Y
Micrura	Araneae	Pisauridae	227	296.90	0.46	0.06	12.4	PR	N
Pterygota	Ephemeroptera	Leptophlebiidae	120	284.60	0.44	0.22	119.4	CG	N
Pterygota	Coleoptera	Hydrophilidae (l)	142	272.10	0.42	0.31	199.1	PR	N
Pulmonata	Basommatophora	Physidae	32	485.37	0.37	0.22	97.9	SC	Y
Eumalacostraca	Decapoda	Cambaridae	1	199.10	0.31	0.09	35.5	CG	Y
Pterygota	Megaloptera	Corydalidae	24	176.70	0.27	0.04	12.2	PR	N
Pulmonata	Basommatophora	Planorbidae	59	316.04	0.24	0.10	29.1	SC	Y
Pterygota	Coleoptera	Carabidae (a)	108	155.10	0.24	0.07	39.9	PR	N
Pulmonata	Basommatophora	Lymnaeidae	24	204.16	0.16	0.11	56.8	SC	Y
Eumalacostraca	Isopoda	Armadillidiidae	30	81.10	0.12	0.05	20.2	HB	Y
Helminthomorpha	Chordeumatida	Conotylidae	58	73.30	0.11	0.03	11.6	HB	Y
Hirudinea			69	71.80	0.11	0.04	18.9	PR, PA	N
Pterygota	Coleoptera	Dystiscidae (l)	31	66.50	0.10	0.06	33.6	PR	N
Pterygota	Diptera	Tabanidae (l)	6	64.90	0.10	0.01	3.4	PR	N
Pterygota	Coleoptera	Staphylinidae (a)	114	56.60	0.09	0.04	25.4	PR	N
Pterygota	Lepidoptera	Noctuidae	15	50.40	0.08	0.01	3.1	HB	N
Micrura	Araneae	Lycosidae	35	41.30	0.06	0.03	17.1	PR	N
Orthogastropoda	Neotaenioglossa	Hydrobiidae	10	79.46	0.06	0.04	20.2	SC	Y
Micrura	Araneae	Anyphaenidae	26	39.00	0.06	0.02	6.1	PR	N
Pterygota	Lepidoptera	Arctiidae	4	37.20	0.06	0.03	14.5	HB	N
Micrura	Araneae	Theridiosomatidae	92	35.60	0.05	0.01	7.7	PR	N

PR – Predator CG – Collector/gatherer HB – Herbivore
PA – Parasite SC – Scraper OM – Omnivore
SH – Shredder FC – Filterer/collector

Appendix U. Continued.

Subclass	Order	Family	Total Abundance	Total Biomass	Mean Biomass	S.E. of Biomass	Max Biomass	Functional Feeding Group	Detritivore
Pterygota	Coleoptera	Lampyridae (l)	6	33.90	0.05	0.03	12.1	PR	N
Micrura	Araneae	Linyphiidae	102	32.40	0.05	0.01	6.4	PR	N
Pterygota	Collembola	Isotomidae	176	33.20	0.05	0.02	9.9	CG	Y
Pterygota	Coleoptera	Dystiscidae (a)	15	33.00	0.05	0.02	13.7	PR	N
Pterygota	Coleoptera	Hydrophilidae (a)	30	28.62	0.04	0.01	6.0	CG	N
Pterygota	Odonata	Coenagrionidae	37	27.30	0.04	0.03	15.7	PR	N
Pterygota	Diptera	Ceratopogonidae (l)	56	26.00	0.04	0.03	22.0	PR	N
Pterygota	Coleoptera	Carabidae (l)	29	23.40	0.04	0.01	5.2	PR	N
Pterygota	Collembola	Poduridae	125	18.10	0.03	0.01	4.2	CG	Y
Pterygota	Diptera	Stratiomyidae (l)	10	16.70	0.03	0.01	4.7	CG	Y
Pterygota	Odonata	Libellulidae	4	16.00	0.02	0.02	16.0	PR	N
Pterygota	Diptera	Ptychopteridae (a)	4	15.80	0.02	0.02	11.8		
Pterygota	Hemiptera	Hebridae	55	15.80	0.02	0.01	3.2	PR	N
Pterygota	Diptera	Ephydridae (l)	6	12.70	0.02	0.01	9.3	CG	N
Anamorpha	Lithobiomorpha	Lithobiidae	11	12.50	0.02	0.01	4.2	PR	N
Pterygota	Coleoptera	Gyrinidae (a)	4	12.10	0.02	0.02	12.1	PR	N
Eumalacostraca	Isopoda	Porcellionidae	7	11.10	0.02	0.01	5.7	HB	Y
Pterygota	Coleoptera	Staphylinidae (l)	17	10.80	0.02	0.01	3.7	PR	N
Pterygota	Coleoptera	Cerambycidae (a)	2	7.60	0.01	0.01	2.8	HB	N
Pterygota	Coleoptera	Scirtidae (l)	12	7.60	0.01	0.01	7.6	SC	N
Pterygota	Coleoptera	Curculionidae (a)	9	7.30	0.01	0.01	4.0	SH	N
Micrura	Araneae	Salticidae	8	7.20	0.01	0.01	3.3	PR	N
Pterygota	Hemiptera	Mesoveliidae	2	6.70	0.01	0.01	6.7	PR	N
Pterygota	Hemiptera	Aradidae	22	6.60	0.01	0.00	2.6	HB	N
Pterygota	Coleoptera	Chrysomelidae (a)	6	6.50	0.01	0.01	2.8	SH	N
Micrura	Araneae	Gnaphosidae	3	6.20	0.01	0.01	2.9	PR	N
Pterygota	Ephemeroptera	Caenidae	15	5.90	0.01	0.01	3.6	CG	N
Pterygota	Ephemeroptera	Siphlonuridae	15	5.90	0.01	0.01	5.9	CG	N
Pterygota	Hemiptera	Hydrometridae	4	5.70	0.01	0.01	5.7	PR	N
Dromopoda	Pseudoscorpionida	Neobisiidae	21	5.50	0.01	0.00	0.8	PR	N

PR – Predator CG – Collector/gatherer HB – Herbivore
PA – Parasite SC – Scraper OM – Omnivore
SH – Shredder FC – Filterer/collector

Appendix U. Continued.

Subclass	Order	Family	Total Abundance	Total Biomass	Mean Biomass	S.E. of Biomass	Max Biomass	Functional Feeding Group	Detritivore
Pterygota	Coleoptera	Haliplidae (a)	4	5.50	0.01	0.01	4.7	SH	N
Pterygota	Diptera	Psychodidae (l)	13	4.40	0.01	0.01	4.4	CG	N
Pterygota	Orthoptera	Gryllidae	1	4.40	0.01	0.00	3.1	OM	Y
Pterygota	Coleoptera	Noteridae (a)	2	3.50	0.01	0.00	2.7	PR	N
Pterygota	Plecoptera	Perlodidae	28	3.40	0.01	0.00	2.5	PR	N
Pterygota	Hemiptera	Thyreocoridae	1	3.00	0.00	0.00	3.0	HB	N
Acarni			25	3.00	0.00	0.00	0.8	HB	
Pterygota	Coleoptera	Anthribidae (a)	2	2.90	0.00	0.00	2.6	HB	N
Dromopoda	Opiliones	Sclerosomatidae	3	2.80	0.00	0.00	2.0	PR	N
Pterygota	Ephemeroptera	Ephemerellidae	3	2.80	0.00	0.00	2.0	CG	Y
Pterygota	Hemiptera	Psyllidae	5	2.70	0.00	0.00	1.1	HB	N
Pterygota	Coleoptera	Byrrhidae (a)	4	2.20	0.00	0.00	1.0	HB	N
Pterygota	Hemiptera	Cicadellidae	3	2.20	0.00	0.00	2.1	HB	N
Micrura	Araneae	Mimetidae	2	2.00	0.00	0.00	1.1	PR	N
Pterygota	Plecoptera	Capniidae	1	2.00	0.00	0.00	2.0	SH	Y
Pterygota	Diptera	Sciomyzidae (l)	1	1.90	0.00	0.00	1.9	PR	N
Pterygota	Coleoptera	Coccinellidae (a)	2	1.70	0.00	0.00	1.4	PR	N
Pterygota	Lepidoptera	Hesperiidae	1	1.60	0.00	0.00	1.6	HB	N
Micrura	Araneae	Liocranidae	6	1.50	0.00	0.00	1.1	PR	N
Pterygota	Coleoptera	Endomychidae (a)	2	1.50	0.00	0.00	0.8	HB	N
Pterygota	Hemiptera	Largidae	1	1.50	0.00	0.00	1.5	HB	N
Pterygota	Hemiptera	Pyrrhocoridae	1	1.50	0.00	0.00	1.5	HB	N
Micrura	Araneae	Thomisidae	2	1.40	0.00	0.00	1.0	PR	N
Pterygota	Trichoptera	Limnephilidae	3	1.40	0.00	0.00	0.8	SH	Y
Micrura	Araneae	Philodromidae	2	1.30	0.00	0.00	1.3	PR	N
Pterygota	Coleoptera	Elateridae (a)	1	1.30	0.00	0.00	1.3	HB	N
Pterygota	Diptera	Dolichopodidae (a)	4	1.10	0.00	0.00	0.4	PR	N
Anamorpha	Lithobiomorpha	Henicopidae	1	1.00	0.00	0.00	1.0	PR	N
Pterygota	Diptera	Phoridae (a)	2	1.00	0.00	0.00	0.6	HB	N

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Appendix U. Continued.

Subclass	Order	Family	Total Abundance	Total Biomass	Mean Biomass	S.E. of Biomass	Max Biomass	Functional Feeding Group	Detritivore
Pterygota	Diptera	Tipulidae (a)	2	1.0	0.00	0.00	0.6	PR	N
Pterygota	Plecoptera	Leuctridae	4	0.9	0.00	0.00	0.8	SH	Y
Pterygota	Coleoptera	Cantharidae (a)	1	0.8	0.00	0.00	0.8	PR	N
Pterygota	Coleoptera	Elmidae (a)	1	0.8	0.00	0.00	0.8	CG,SC	N
Pterygota	Diptera	Dolichopodidae (l)	2	0.8	0.00	0.00	0.4	PR	N
Pterygota	Hemiptera	Miridae	1	0.8	0.00	0.00	0.8	OM	N
Pterygota	Plecoptera	Nemouridae	1	0.8	0.00	0.00	0.8	SH	Y
Pterygota	Lepidoptera	Gelechiidae	3	0.8	0.00	0.00	0.6	HB	N
Pterygota	Coleoptera	Pselaphidae (a)	3	0.7	0.00	0.00	0.4	Non-feeding	
Pterygota	Lepidoptera	Pyralidae	3	0.7	0.00	0.00	0.4	HB	N
Pterygota	Hemiptera	Aphididae	4	0.7	0.00	0.00	0.4	HB	N
Pterygota	Plecoptera	Chloroperlidae	1	0.7	0.00	0.00	0.7	PR	N
Pterygota	Diptera	Psychodidae (a)	2	0.6	0.00	0.00	0.5	OM	N
Pterygota	Odonata	Corduliidae	1	0.6	0.00	0.00	0.6	PR	N
Pterygota	Diptera	Ceratopogonidae (a)	2	0.5	0.00	0.00	0.3	PA	N
Pterygota	Diptera	Empididae (a)	1	0.5	0.00	0.00	0.5	PR	N
Pterygota	Hymenoptera	Halictidae	1	0.5	0.00	0.00	0.5	HB	N
Pterygota	Hymenoptera	Platygastridae	1	0.5	0.00	0.00	0.5	PA	N
Pterygota	Lepidoptera	Tortricidae		0.5	0.00	0.00	0.5	HB	N
Pterygota	Coleoptera	Elmidae (l)	1	0.4	0.00	0.00	0.4	CG,SC	N
Pterygota	Collembola	Sminthuridae	4	0.4	0.00	0.00	0.1	CG	Y
Pterygota	Diptera	Milichiidae (a)	1	0.4	0.00	0.00	0.4	PR	N
Pterygota	Hymenoptera	Scelionidae	1	0.4	0.00	0.00	0.4	PA	N
Pterygota	Coleoptera	Bostrichidae (a)	1	0.3	0.00	0.00	0.3	HB	N
Pterygota	Diptera	Sciaridae (a)	2	0.3	0.00	0.00	0.3		
Pterygota	Ephemeroptera	Baetidae	1	0.3	0.00	0.00	0.3	CG	N
Pterygota	Hemiptera	Reduviidae	4	0.3	0.00	0.00	0.3	PR	N
Pterygota	Hemiptera	Tingidae	1	0.3	0.00	0.00	0.3	HB	N
Pterygota	Coleoptera	Rhysodidae (a)	1	0.2	0.00	0.00	0.2	HB	N

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Appendix U. Continued.

Subclass	Order	Family	Total Abundance	Total Biomass	Mean Biomass	S.E. of Biomass	Max Biomass	Functional Feeding Group	Detritivore
Pterygota	Collembola	Hypogastruridae	2	0.2	0.00	0.00	0.1	CG	Y
Pterygota	Diptera	Mycetophilidae (a)	1	0.2	0.00	0.00	0.2		
Pterygota	Trichoptera	Dipseudopsidae	2	0.2	0.00	0.00	0.2	FC	N
Pterygota	Diptera	Chaoboridae (a)	1	0.1	0.00	0.00	0.1		
Pterygota	Diptera	Rhagionidae (a)	1	0.1	0.00	0.00	0.1	PR	N
Pterygota	Diptera	Trichoceridae (a)	1	0.1	0.00	0.00	0.1		
Pterygota	Hemiptera	Pemphigidae	1	0.1	0.00	0.00	0.1	HB	N
Pterygota	Hemiptera	Piesmatidae	1	0.1	0.00	0.00	0.1	HB	N
Pterygota	Hymenoptera	Braconidae	1	0.1	0.00	0.00	0.1	HB,PA	N

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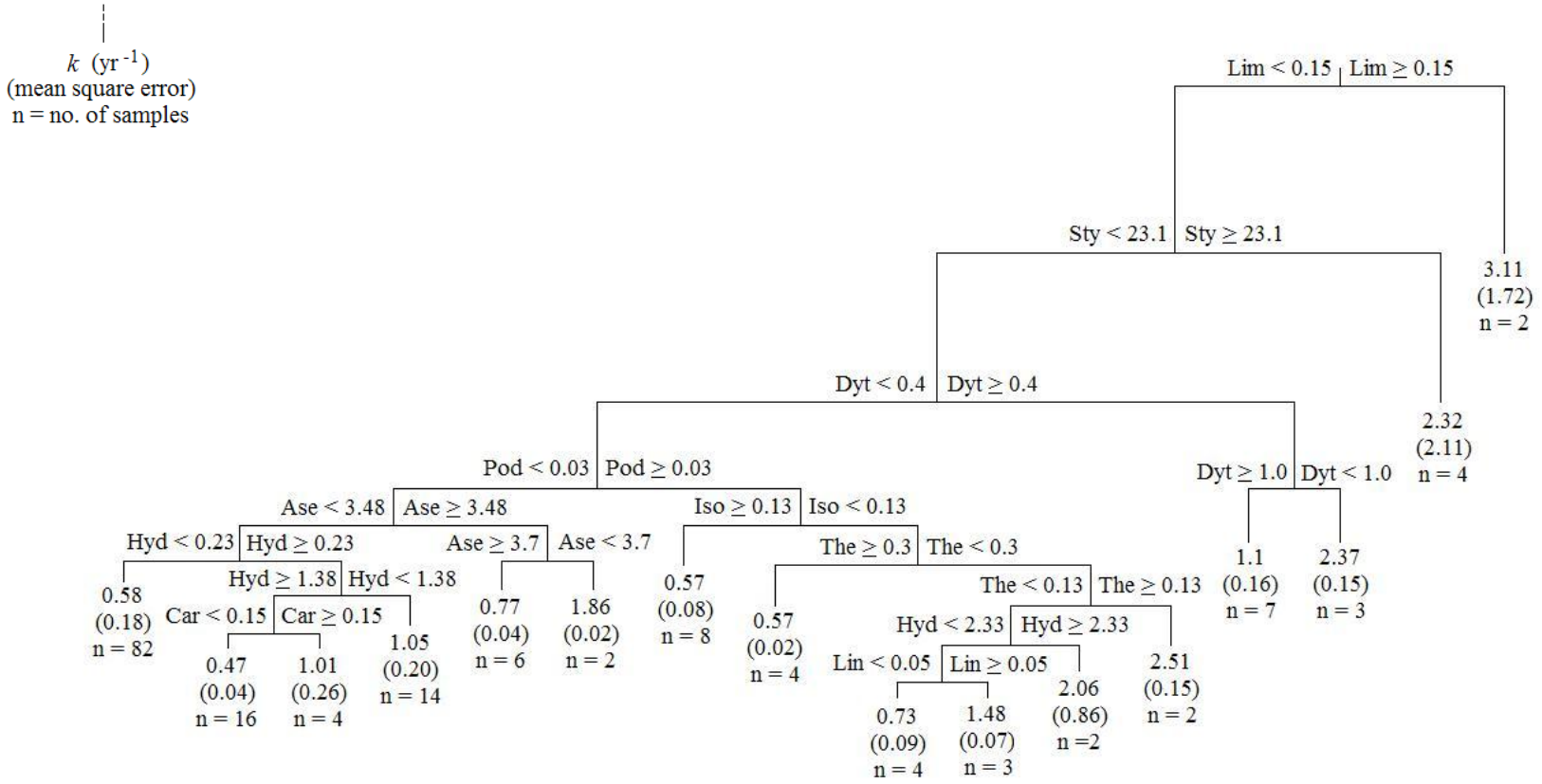
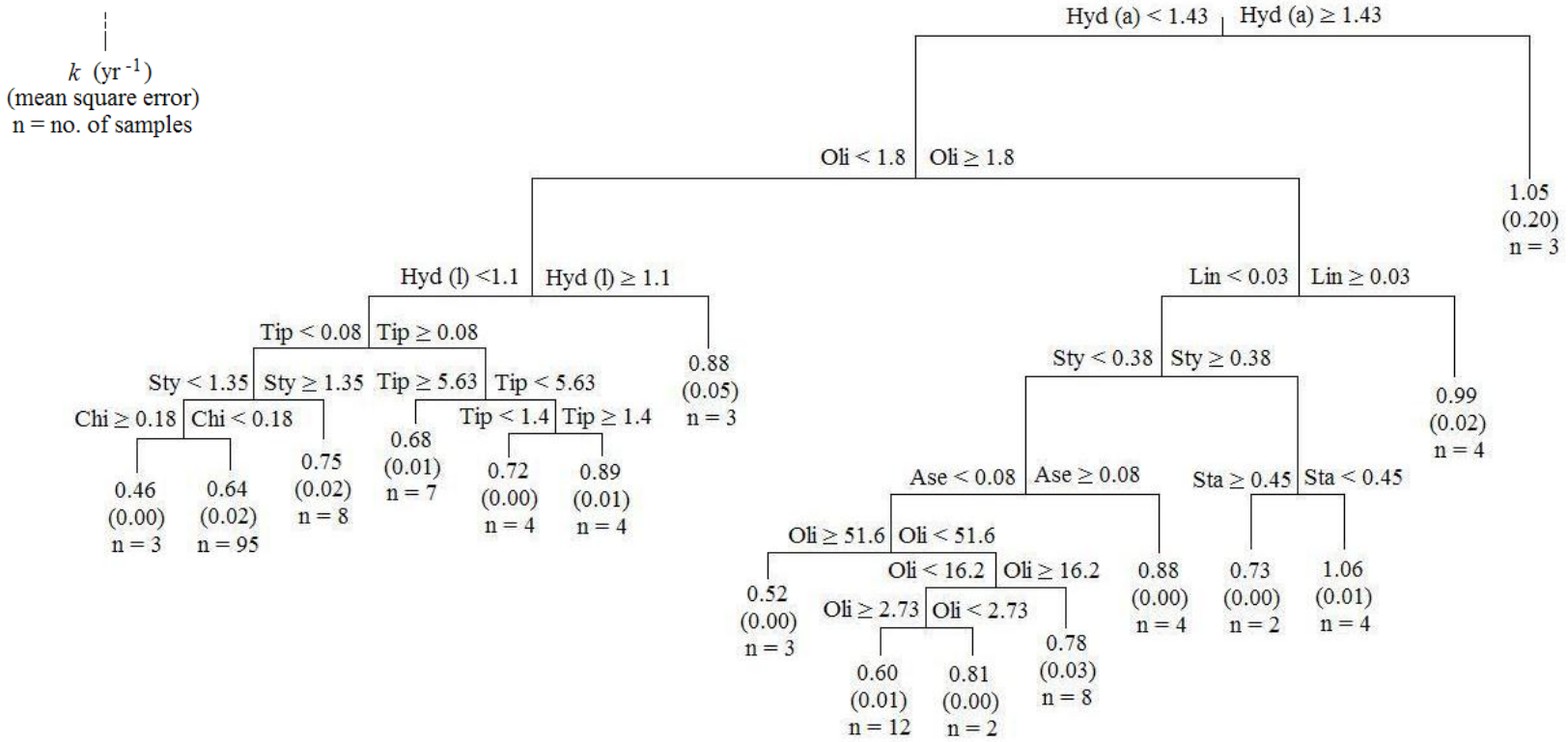
Appendix V. Regression tree analysis to identify invertebrate taxa, by biomass, associated with trends in the early phases (< 224 d) of decomposition. Decomposition was measured over 2 years in 3 mitigated and 3 reference wetlands in the Mid-Atlantic Highlands region, USA, December 2007 to December 2009. Divisions in the regression tree explain 70.2% of variance in decomposition rates.



Taxonomic Groups (mean mg per bag)

Ase = Asellidae, Isopoda (Collector/gatherer)
Car = Carabidae, Coleoptera, adult (Predator)
Dyt = Dytiscidae, Coleoptera, larvae (Predator)
Hyd = Hydrophilidae, Coleoptera, larvae (Predator)
Iso = Isotomidae, Collembola (Collector/gatherer, detritivore)
Lim = Limnephilidae, Trichoptera (Shredder, Filterer)
Lin = Linyphiidae, Araneae (Predator)
Pis = Pisauridae, Araneae (Predator)
Pod = Poduridae, Collembola (Collector/gatherer, detritivore)
Sta = Staphylinidae, Coleoptera, adult (Predator)
Sty = Stylommatophora (Order, omnivore, detritivore)
The = Theridiosomatidae, Araneae (Predator)

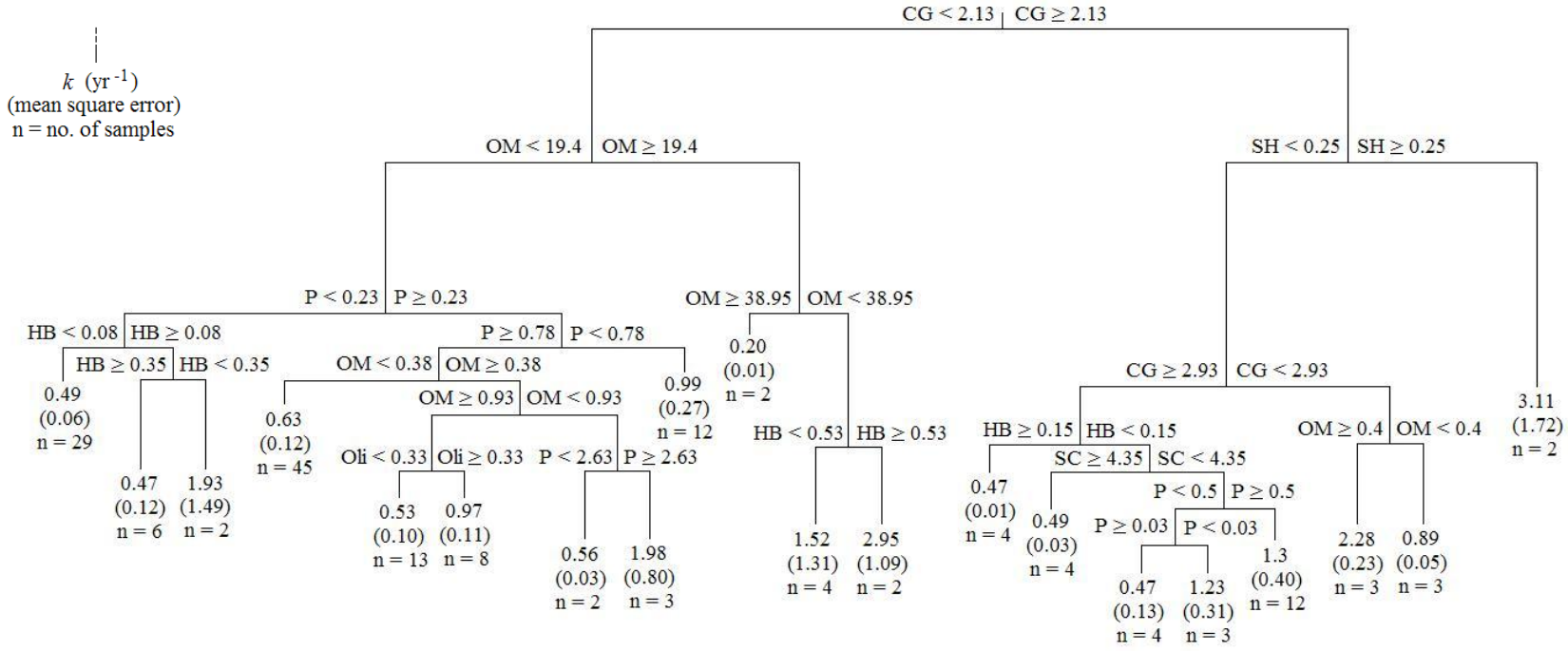
Appendix W. Regression tree analysis to identify invertebrate taxa, by biomass, associated with trends in the late phase (≥ 224 d) of decomposition. Decomposition was measured over 2 years in 3 mitigated and 3 reference wetlands in the Mid-Atlantic Highlands region, USA, December 2007 to December 2009. Divisions in the regression tree explain 41.8% of variance in decomposition rates.



Taxonomic Groups (mg dry mass)

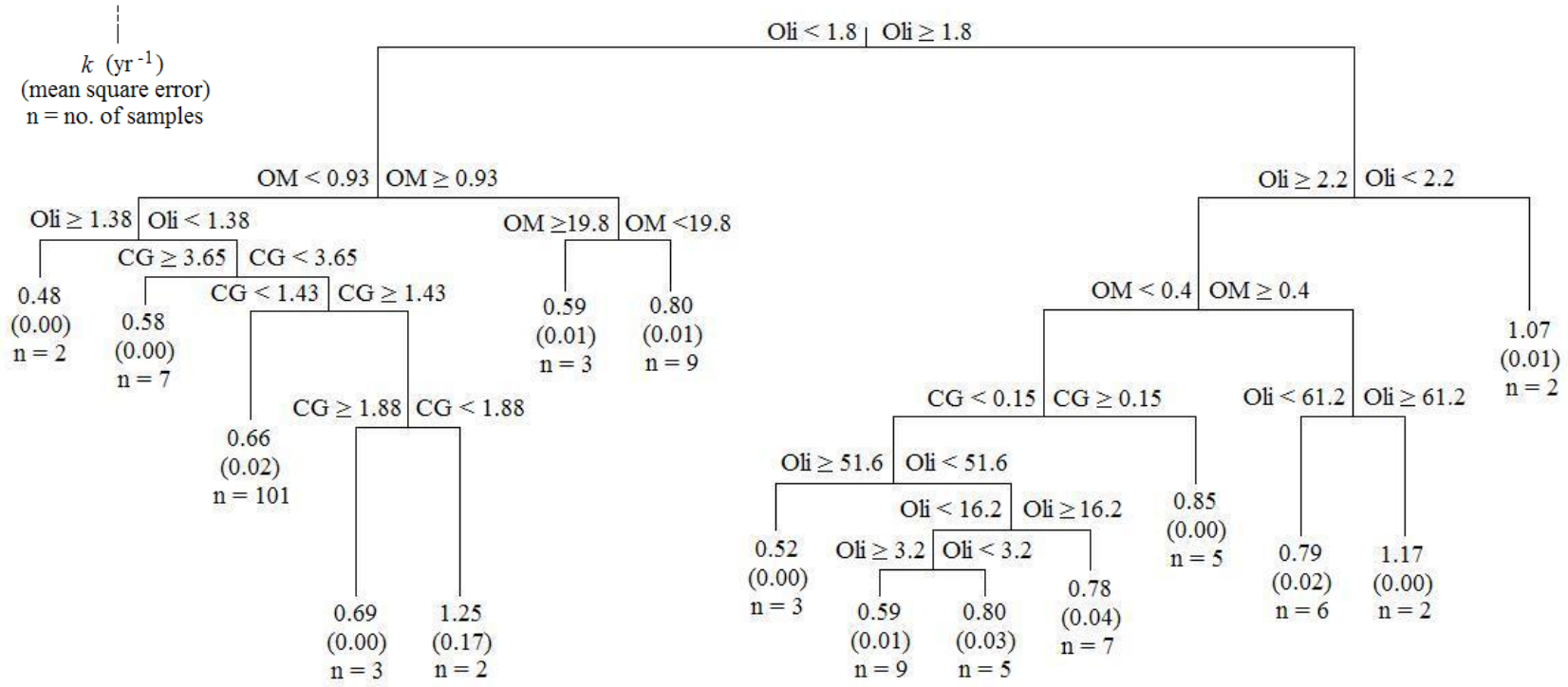
Ase = Asellidae, Isopoda (Collector/gatherer)
Chi = Chironomidae, Diptera, larvae (Collector/gatherer)
Hyd (a) = Hydrophilidae, Coleoptera, adult (Predator)
Hyd (l) = Hydrophilidae, Coleoptera, larvae (Collector/gatherer)
Lin = Linyphiidae, Araneae (Predator)
Oli = Oligochaeta (Subclass, collector/gatherer)
Sta = Staphylinidae, Coleoptera, adult (Predator)
Sty = Stylommatophora (Order, omnivore, detritivore)
Tip = Tipulidae, Diptera, larvae (Collector/gatherer, shredder)

Appendix X. Regression tree analysis to identify invertebrate functional feeding groups (FFG), by biomass, associated with trends in the early phases (< 224 d) of decomposition. Decomposition was measured over 2 years in 3 mitigated and 3 reference wetlands in the Mid-Atlantic Highlands region, USA, December 2007 to December 2009. Divisions in the regression tree explain 46.0% of variance in decomposition rates.



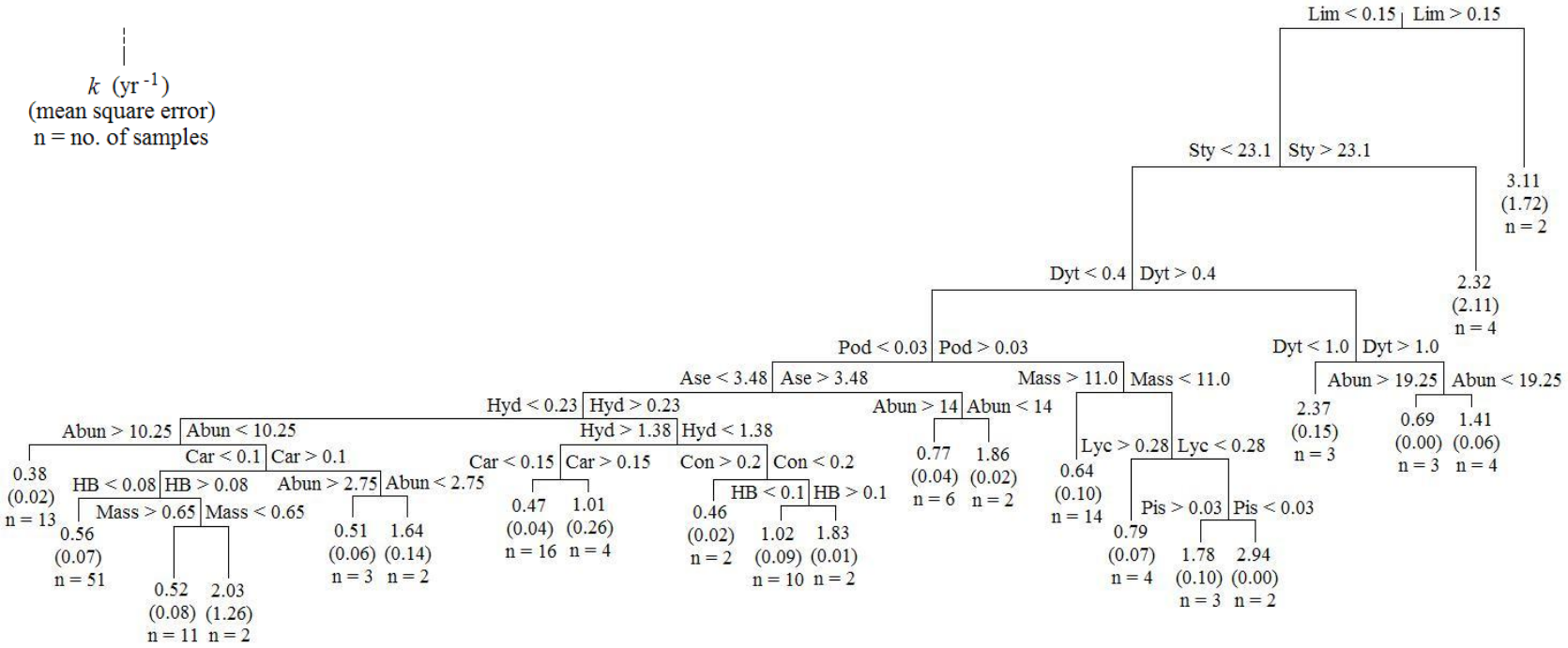
Functional Feeding Groups (mg dry mass)
CG = Collector/gatherer
HB = Herbivore
Oli = Oligochaeta (Subclass, Collector/gatherer)
OM = Omnivore
P = Predator/parasite
SC = Scraper
SH = Shredder

Appendix Y. Regression tree analysis to identify invertebrate functional feeding groups (FFG), by biomass, associated with trends in the late phase (≥ 224 d) of decomposition. Decomposition was measured over 2 years in 3 mitigated and 3 reference wetlands in the Mid-Atlantic Highlands region, USA, December 2007 to December 2009. Divisions in the regression tree explain 38.5% of variance in decomposition rates.



Functional Feeding Groups (mg dry mass)
CG = Collector/gatherer
Oli = Oligochaeta (Subclass, Collector/gatherer)
OM = Omnivore

Appendix Z. Regression tree analysis to identify invertebrate metrics associated with trends in the early phases (< 224 d) of decomposition. Decomposition was measured over 2 years in 3 mitigated and 3 reference wetlands in the Mid-Atlantic Highlands region, USA, December 2007 to December 2009. Divisions in the regression tree explain 70.2% of variance in decomposition rates.

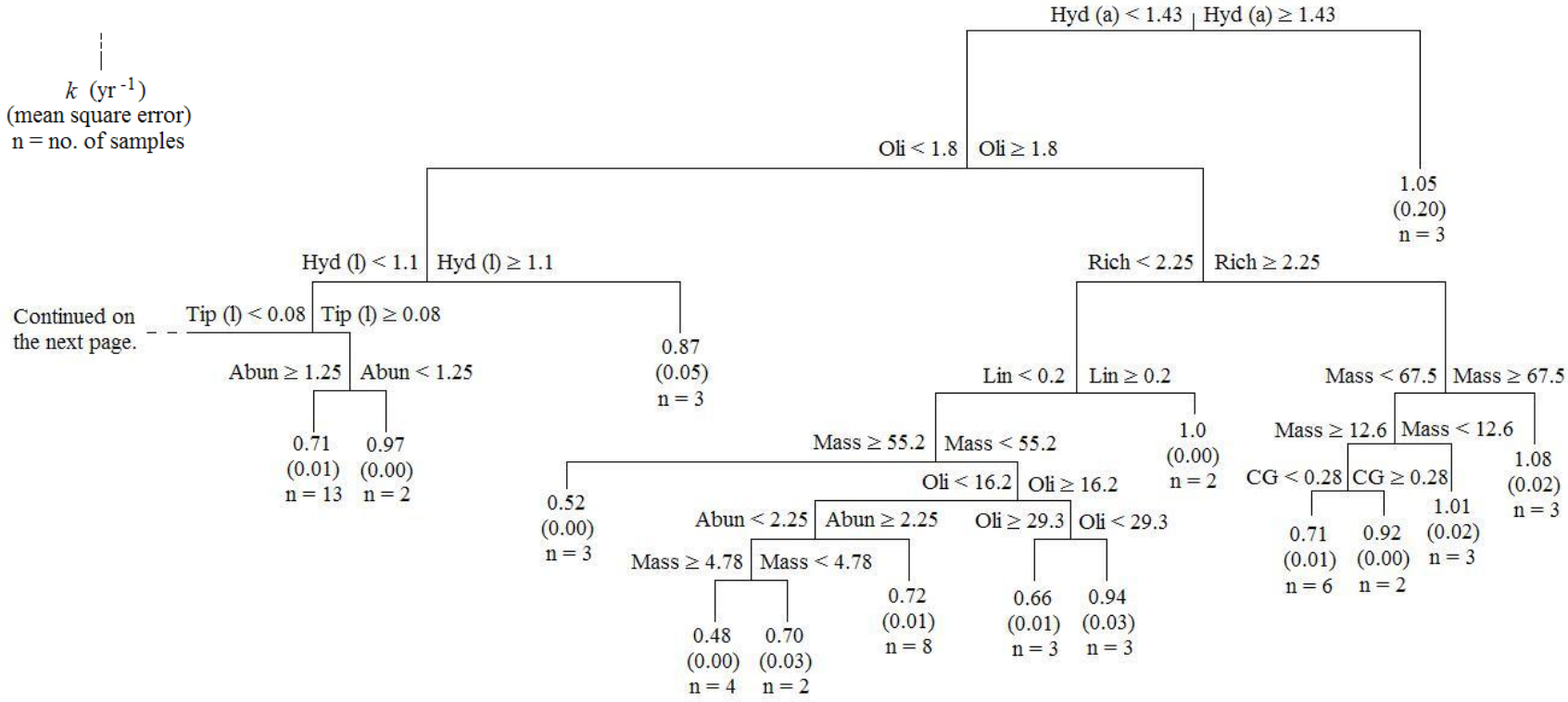


Taxonomic Groups (mg per bag)
Ase = Asellidae, Isopoda (Collector/gatherer)
Car = Carabidae, Coleoptera, adult (Predator)
Con = Conotylidae, Chordeumatida (Herbivore)
Dyt = Dytiscidae, Coleoptera, larvae (Predator)
Hyd = Hydrophilidae, Coleoptera, larvae (Predator)
Lim = Limnephilidae, Trichoptera (Shredder, Filterer)
Lyc = Lycosidae, Araneae (Predator)
Pis = Pisauridae, Araneae (Predator)
Pod = Poduridae, Collembola (Collector/gatherer, detritivore)
Sta = Staphylinidae, Coleoptera, adult (Predator)
Sty = Stylommatophora (Order, omnivore, detritivore)

Functional Feeding Groups (mg dry mass)
HB - Herbivore

Invertebrate Metrics
Abun = Abundance (no. individuals)
Mass = Total Biomass (mg dry mass)

Appendix AA. Regression tree analysis to identify invertebrate metrics associated with trends in the late phase (≥ 224 d) of decomposition. Decomposition was measured over 2 years in 3 mitigated and 3 reference wetlands in the Mid-Atlantic Highlands region, USA, December 2007 to December 2009. Divisions in the regression tree explain 55.7% of variance in decomposition rates.

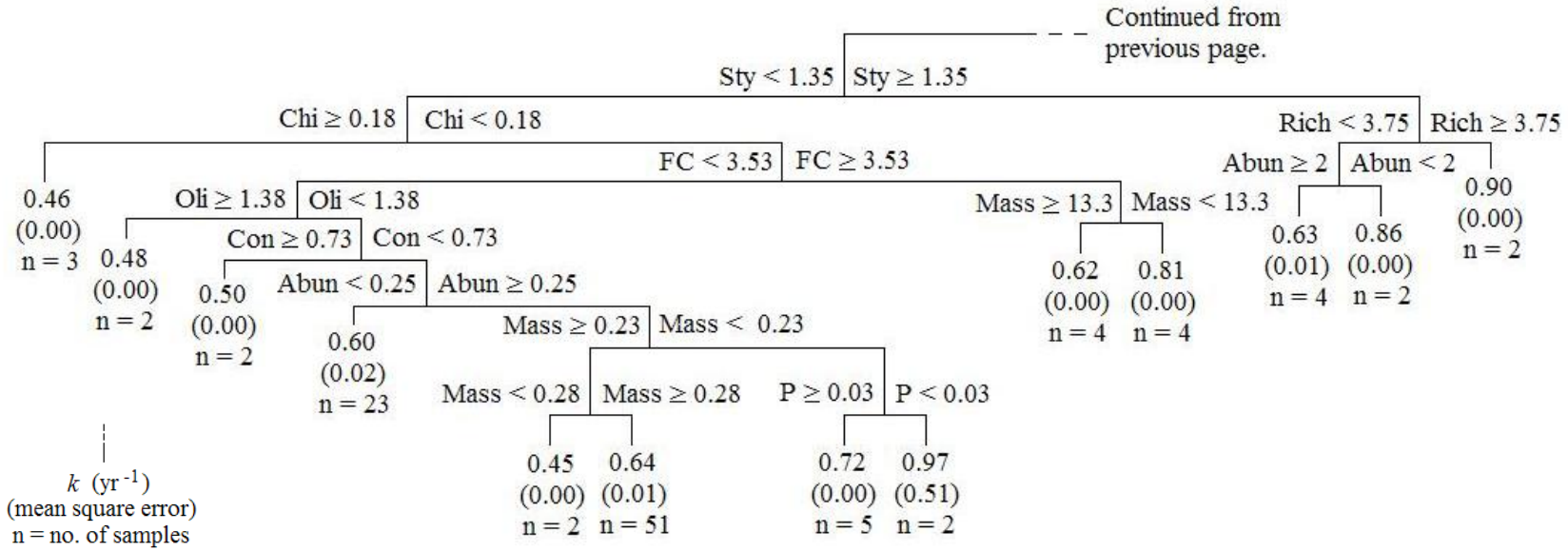


Taxonomic Groups (mg dry mass)
Hyd (a) = Hydrophilidae, Coleoptera, adult (Predator)
Hyd (l) = Hydrophilidae, Coleoptera, larvae (Collector/gatherer)
Lin = Linyphiidae, Araneae (Predator)
Oli = Oligochaeta (Subclass, Collector/gatherer)
Tip = Tipulidae, Diptera, larvae (Collector/gatherer, shredder)

Functional Feeding Groups (mg dry mass)
CG = Collector/gatherers

Invertebrate Metrics
Abun = Abundance (no. individuals)
Mass = Total Biomass (mg dry mass)
Rich = Richness (no. taxa)

Appendix AA. Continued.



Taxonomic Groups (mg dry mass)
Chi = Chironomidae, Diptera, larvae (Collector/gatherer)
Con = Conotylidae, Chordeumatida (Herbivore)
Oli = Oligochaeta (Subclass, Collector/gatherer)
Sty = Stylommatophora (Order, omnivore, detritivore)

Functional Feeding Groups (mg dry mass)
FC = Filterer/collectors
P = Predators

Invertebrate Metrics
Abun = Abundance (no. individuals)
Mass = Total Biomass (mg dry mass)
Rich = Richness (no. taxa)

Appendix BB. Mean, standard error (S.E.), minimum, and maximum fungal biomass (μg ergosterol mg^{-1} litter dry mass) isolated from plant litter bags decomposing in 3 mitigated (M) and 3 reference (R) wetlands in West Virginia, USA, December 2007 to December 2009.

Wetland	Type	Mean	S.E.	Min	Max
Leading Creek	M	0.059	0.006	0.001	0.160
Sugar Creek	M	0.065	0.007	0.002	0.174
Hazelton	M	0.072	0.005	0.003	0.156
Meadowville	R	0.065	0.006	0.000	0.155
Upper Deckers Creek	R	0.062	0.006	0.000	0.156
Bruceton Mills	R	0.074	0.007	0.000	0.171