Litter Decomposition in Created and Adjacent Forested Wetlands of the Coastal Plain of Virginia

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(ABSTRACT)

Litter decomposition is a poorly understood function of constructed and natural forested wetlands. This study compared rates of litter mass loss, changes in litter morphology, and associated macroinvertebrate populations in constructed and natural non-tidal wetlands. Two sets of wetlands (constructed vs. natural) were studied in eastern Virginia; a 9 year-old riparian set near Fort Lee, (FL), and a 2 year-old wet flat set in Charles City County, (CC). Mixed deciduous forest litter collected from the FL natural wetland decayed more rapidly in the created wetlands than the adjacent forested wetlands. Mixed emergent marsh litter collected from the FL created wetland exhibited a similar relationship, although marsh litter decomposed slower than forest litter. Litter area and weight loss followed a similar pattern, although area loss lagged behind weight loss, consistent with an initial leaching phase of decomposition. Both the FL and CC created wetlands exhibited faster litter decomposition than their adjacent forested wetland, however, the FL created wetland had a lower weight:area ratio and higher detritivore abundance than the adjacent forested wetland, while the reverse was true for the CC wetland pair. These relationships suggest macroinvertebrates played an important role in decomposition in the FL created wetland, while other factors were more significant at CC. Faster decomposition in the created wetlands may be of concern for long-term soil organic matter accumulation, or conversely, may indicate quick recovery of the litter decomposition function. Overall, these findings point out the difficulties involved in using certain functional indicators to compare very young and mature systems.

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Chapter 1. Introduction and Literature Review

Estimates and factors affecting litter decomposition in natural and constructed non-tidal freshwater wetlands of the southeastern United States.

Introduction

The primary objective of this study was to compare decomposition rates and the factors affecting decomposition between created and adjacent natural wetlands. Both a mixed deciduous leaf litter and a marsh litter from adjacent natural and created wetlands, respectively, were used to assess the effect of litter type on decomposition. In addition, areas with similar moisture regimes in the created and natural wetlands, and drier and wetter areas within the created wetland were compared.

Following a literature review (Chapter 1), I present the results of a traditional litterbag study of decomposition, where weight loss from litter contained in mesh bags is followed over time (Chapter 2). Along with directly comparing litter weight loss, linear, single and double exponential models were used to describe the pattern of litter weight loss. The litter's C:N ratio was also compared between the different treatments to further estimate and compare the degree of decomposition.

Using a new technique, digital images of the deciduous forest litter were used to measure litter area and perimeter over time (Chapter 3). While litter area can be analyzed in the same ways of litter weight loss, new statistics like area:perimeter ratio and litter weight:area can also be calculated. These new ratios provide added insight into what proportion of litter is being lost as fragments (loss of area and weight) or through leaching and microbial processes (loss of weight only).

Chapter 2 and 3 discuss litter weight and area loss between fine and coarse mesh size litterbags; a traditional means of assessing the relative importance of the effect of macroinvertebrates on decomposition rates. Macroinvertebrates were also collected and identified from the litter in the litterbags (Chapter 4). By combining litterbag decomposition and invertebrate studies which are typically not linked, both macroinvertebrate communities and their influence on decomposition of litter can be analyzed.

Literature Review

With the realization of the important functions and values wetlands provide for society, a "no net loss" national standard has been adopted, which requires the mitigation of wetland losses with in-kind restoration or creation. Wetland impact and mitigation are typically quantified by area of loss or creation. This area based compensation does not necessarily correspond with compensation of ecological functions, which correlate better with societal values of wetlands. For this reason, many have suggested incorporating assessment of wetland function to determine compensatory success such as the hydrogeomorphic (HGM) technique (Brinson, 1993).

Like many other ecosystems, litter decomposition is an important function in wetlands for cycling of nutrients, energy flow and carbon sequestration. Long-term, litter decomposition affects soil organic matter levels, fertility, and many other soil properties. In the case of recently constructed or restored wetlands with low organic matter levels, litter decomposition rates affect whether organic matter accumulates and the associated ecological benefits. There are only a handful of studies that examine decomposition rates in created or restored wetlands, and no reported studies to date comparing decomposition in natural/created wetland pairs such as those described in this study.

A review of the available literature was conducted to examine the different methods used to estimate litter decomposition rates and select appropriate methods for use in this study. For the purposes of this review, only non-woody (i.e. leaves and flowers) litter decomposition was considered. Following a description of the different methods is a discussion of the various factors influencing decomposition rates and models used to describe the pattern of decomposition. Specific factors and decomposition rates are summarized for ecosystems similar to the natural and constructed wetlands examined in this study. Specifically, these ecosystems were natural forested non-tidal wetlands and systems similar to those of the moisture gradient from ponded to wet to upland in the created wetlands.

Methods for Estimating Decomposition

The litterbag method is the predominant reported method for estimating the rates of litter decomposition in terrestrial and wetland environments (Table 1). An unconfined leaf-pack method seems to be the preferred method in aquatic (especially lotic) environments, although a large mesh litterbag also works well. The focus of this review will be upon variations in the litterbag method, with an examination of alternative confined, unconfined and artificial substrate methods such as the cotton burial cloth. Laboratory studies and controlled field or greenhouse studies using simulated soil or litter conditions (e.g. mesocosms) will not be addressed in detail here. While these controlled studies have been useful for examining factors influencing decomposition individually, they do not give realistic estimates of decomposition because they exclude certain processes while examining others (Kemp et al., 1985).

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments.

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Uplands							
Conifer Forests							
Berg et al., 1982	2 g	8 x 8 cm	1 mm	Scots pine (*Pinus silvestris*)	Sweden	120-130 year-old Scots pine stand	14 times in 5 years
Cromack and Monk, 1975	2.5 g, 40 g for mixture	10 x 10 cm, 0.125 m2 for mixture	1 mm, 2.54 cm upper and 2 mm lower for mixture	chestnut oak (*Quercus pinus* L.), white oak (*Quercus alba* L.), red maple (*Acer rubrum* L.), flowering dogwood (*Cornus florida* L.) and mixture in hardwood stand and eastern white pine in pine stand	Coweeta, North Carolina	white pine or mixed hardwood watersheds	monthly in two 1-yr studies
Falconer et al., 1933	129-537 g	galvanized wire baskets w/ bottom covered in cheesecloth	5 mm	white pine, bracken, red pine, and jack pine	Eastern Canada	pine forests	after 1 yr.
Fogel and Cromack, 1977	5 g (needles), 12 g (cones), 15 g (branch), 30-100 g (bark)	20 x 20 cm	1 mm	Douglas fir (*Pseudotsuga menziesii*) green needles, female cones, bark, and branches	Western Oregon	mature Douglas fir forest	15 times in 2 yrs.
Hayes, 1965	100 needles per line		needles glued to nylon fishing line	*Abies grandis* Lindley, *Picea sitchensis* (Bongard) Carrière, *Pinus sylvestris* L.	Wales, Great Britain	30-35 year-old conifer plantation	6-9 times in each of 3 year-long studies
Herlitzius, 1983	3.28 g or 9.48 (spruce)	PVC rings (12 cm dia and 5 cm high)	44 µm, 1100 µm, or 10 mm (lower mesh), 1 mm uniform upper	hazel, oak, beech, spruce, cellulose hydrate foil	Germany, near Ulm	alluvial forest, beech forest, spruce forest	monthly over 1 yr (collected bags were replaced after collection giving a set with variable start instead of collection dates)

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	mass litter (g)	litterbag dimensions	mesh size	litter type	location	environment	sampling frequency
Herlitzius, 1987	3.5 g	PVC ring (12 cm dia.) with gauze closures	10 mm	hazel (*Corylus avellana* L.)	Germany, near Ulm	five forests (elm/ash, ash/maple/oak, beech, oak/hazel, and spruce)	occasionally over 1 year
Hornsby et al., 1995	30 g		6 mm upper, 1 mm lower	loblolly pine (*Pinus taeda* L.)	central Alabama	plexiglass microcosms in loblolly pine stand, varied temp and precip.	12 times in 10 months
Klemmedson et al., 1985	25 g	30 x 30 cm	2 mm	ponderosa pine (*Pinus ponderosa* Laws.)	Arizona	ponderosa pine forests with different stand conditions (clear-cut, dense saplings, large poles, thinned large poles, clear-cut strip)	12 times over 34 months
Lockaby et al., 1995	10 g		6 mm upper, 1 mm lower	mix depending on site; pine, sweetgum, red oak predominately	central Alabama	loblolly pine plantations with different understory suppressions treatments	0, 0.5, 1, 2, 5, 7, 9, 12, 18, 20 months
MacLean and Wein, 1978	20 g and branches tied to lines	10 x 15 cm	1 mm	pine needles, red maple, pin cherry, trembling aspen, white birch, branches (pine and hardwood), understory vegetation, and partially decomposed litter	New Brunswick, Canada	16, 29, and 57 yr. old jack pine stands and 7 and 29 year old mixed hardwood stands	after 9, 12, 14, 21 and 24 months
Mikola, 1960	4.42 (birch) or 9.12 g (pine)	between glass wool		pine or birch	Finland	covered by natural litter layer in several pine and spruce stands	after 1, 2, and 3 years
Rustad and Fernandez, 1998	5 g	10 x 15 cm	0.3 mm (bottom) 1 mm (top)	red spruce (*Picea rubens* Sarg.) and red maple (*Acer rubrum* L.)	Maine	spruce-fir forest (experimentally increased soil temp by 4-5°C)	6, 18, 30 mo.
St. John, 1980	Ten sticks	10 x 15 cm or unconfined	1.9 mm or 3.6 mm	Birchwood swab sticks	California	*Abies concolor* and *Calocedrus decurrens* forest	After 118 days

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Springett, 1976	20 g	30 x 30 cm	2 mm	pine needles	Western Australia	forests with varying burning histories	after 7, 21, 22, 27, 30 months
Suffling and Smith, 1974	10-20 g	10 x 14 cm	0.5, 1, or 4 mm	Mixed coniferous litter	Ontario, Canada	Recently cleared spruce/pine forest	5 times in 1 yr.
Takeda, 1988	3 g	10 x 10 cm	1.5 mm	Japanese red pine (*Pinus densiflora* SIEB. et ZUCC)	Kyoto, Japan	pine forest	every 3 months for 21 mo.
Taylor et al., 1991		8 x 10 cm (or large litter tethered)	1 mm	forb leaves, buffalo-berry leaves, alder leaves, grass, forb stems, spruce needles, forb roots, pine needles, bearberry leaves, conifer coarse roots, bearberry stems, fir needles, moss, twigs, grass roots, female cones, male cones, branches, conifer fine roots	Alberta, Canada	four pine forests	2 times per year for 3 yr.
Thomas, 1968	20 g loblolly w/ and w/o 5 g dogwood	35 x 35 cm	2 mm	loblolly pine (*Pinus taeda* L.) with and without flowering dogwood (*Cornus florida* L.)	Roane Co., Tennessee	19 year-old loblolly pine plantation	monthly for 1 yr.
Titus and Malcolm, 1999	3 g	10 x 10 cm	0.3 x 1.0 mm	Spitka spruce needles from slash	Northumberland, United Kingdom	forest 0, 2, and 5 years after clear-cut	every 3.5 months over 2 yr.
Will, 1967.	50 g		1 mm	*Pinus radiata*	New Zealand	33 year-old *Pinus radiata* stand	18 times in 6 yrs.
Deciduous Forests							
Abbott and Crossley, 1982	woody debris			Chestnut Oak woody litter	Coweeta, North Carolina	hardwood forest	3, 6, 9 and 12 mo.

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Anderson, 1973	0.25 to 1.60 g; tethered leaves additionally	7 x 10 cm	7, 1 and 0.175 mm	beech and sweet chestnut	Kent, Great Britain	hardwood forest	monthly for 1 yr., then after 2 yr.
Anderson, 1975	1.4 – 1.6 g (3.5 cm dia. disks)	10 x 10 cm	48 µm, 1mm, 7 mm	beech and chestnut	Great Britain	sweet chestnut stand	monthly for 1.5 yrs.
Blair et al., 1990	3 g	10 x 10 cm	1.5 mm	flowering dogwood (*Cornus florida* L.), red maple (*Acer rubrum* L.) and chestnut oak (*Quercus prinus*); single species and mixtures	North Carolina (Coweeta)	Appalachian hardwood forest	6 times in 375 d.
Blair and Crossley, 1988	2.5 g	10 x 10 cm fiberglass screen	1.6 x 1.8 mm	dogwood (*Cornus florida* L.), red maple (*Acer rubum* L.), and chestnut oak (*Quercus prinus* L.)	North Carolina (Coweeta)	Appalachian hardwood forest reference and 8 yr. post clear-cutting	bimonthly for first year, every 2 months during second year
Bocock, 1964	1.0-2.5 g and 3-46 leaves or leaflets		1 cm (some 1 mm)	ash (*Fraxinus excelsior*), sessile oak (*Quercus petraea*), hazel (*Corylus avellana*), and alder (*Alnus glutinosa*); more species for initial experiment	England	forest (mull /limestone vs. moder/slate)	
Bocock and Gilbert, 1957	nylon hair nets tethered with fish line			birch (*Betula verrucosa*), lime (*Tilia cordala*), oak (*Quercus robur*) on limestone ridge; oak (*Quercus petraea*) on slate ridge; birch on deep acid peat	England	different forest types (limestone ridge, slate ridge, peat)	approx. 6 months
Bocock et al., 1960	2 g (20 ash leaflets or 8 oak leaves)	nylon hair net	1 cm	oak (*Quercus petraea*) and ash (*Fraxinus excelsior*)	England	forested ridges (slate, pH 3.2-4.7 vs. limestone, pH 5.6-6.3)	6 or 10 times over 14 months
Crossley and Hoglund, 1962	2.5 g	10 x 10 cm (others also tested)	1 mm (others also)	mixed pine, oak and dogwood	Tennessee	forest	

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	mass litter (g)	litterbag dimensions	mesh size	litter type	location	environment	sampling frequency
Dwyer and Merriam, 1981	1.0 g (high), 3.0 g (level), 8.0 g (low)	15 x 15 cm	2 x 1 mm	mixed; 1:1 intact maple & beech (high), 1/3 each intact maple and beech, 1/3 aged maple and beech (level), 25% each intact and aged beech and maple	south of Ottawa, Ontario, Canada	beech-maple forest	periodically over 16 months
Dwyer and Merriam, 1984	3.0 g	15 x 15 cm	2 x 1 mm	mixtures collected at different times: intact beech-maple (spring); cohosh leaves and steams (fall); fresh leek leaves (spring); mixed age beech-maple (spring)	south of Ottawa, Canada	beech and sugar maple forest	after 0, 2, 3, 4, 5, or 6 months (6-mo. exp.); after 0, 3, 4, 5, 9, 10, 14, 15, 16 (16 mo. exp.)
Edwards and Heath, 1975	50 2.5 cm dia. disks per bag	10 x 10 cm	0.7 cm or 0.15 cm	oak and beech (13 different ages)	England	buried below litter layer in oak woodland	unburied every 2-3 months and using a photometer % area disappearance was measured for 2.5 yr.
Elliott et al., 1993	3 g		3 mm (1 mm for hemlock)	beech (*Fagus grandifolia*), red pine (*Pinus resinosa*), hemlock (*Tsuga canadensis*) and mixed hardwood (*Acer saccharum*, *Quercus alba, Fraxinus americana*)	Eastern New York	four forest types; beech, red pine, hemlock and mixed hardwood	monthly for 1 yr.
Gosz et al., 1973	4 g	20 x 20 cm	3 mm	yellow birch, sugar maple, and beech	Hubbard Brook Forest, New Hampshire	hardwood forest	1, 6, 7, 8, 9, 10, 11, and 12 months
Gustafson, 1943	200-300 g or 400 g (pine)	wire baskets, 24 x 24 x 6 cm	½ inch or ¼ inch (pine)	sugar maple, hickory, white oak, black oak, and red pine	Michigan	mixed hardwood or pine stand (pine only)	after 0.5, 1, 1.5, 2, 2.5, 4, and 7.5 yrs (maple and hickory only first 4 collections)
Kelly and Beauchamp, 1987	10 g	30 x 30 cm	2 mm	mixed oak litter or mesic mixed-hardwood (white oak, poplar, maple)	Cumberland Plateau, Tennessee	upland oak and mesic mixed-hardwood forests	approx. monthly for 2.5 or 3 yr.

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Knutson, 1997	used difference between current litter with previous year's litter in quadrats	unconfined		mixed	Northeast Iowa	deciduous forest	yearly for 18 yr.
Kucera, 1959	30-35 g	wooden boxes w/ aluminum screen top and bottom		American elm, sugar maple (leaves and petioles), shagbark hickory (leaves, petiole and rachis), northern red oak, white oak, black-jack oak	central Missouri	forest stands	after 4, 8, 12, 18 mo.
Lee, 1974	4.6-4.9 g	16 x 12 cm	1 mm	white oak or dogwood (picked)	Athens, Georgia	mixed hardwood forest	after 43, 87, 137, 198, and 264 days
Lousier and Parkinson, 1976	9.3 g (mixed, long-term), 5.9 g (balsam, short term), or 10.5 g (aspen, short term)	large hairnets (long term) or 20 x 20 cm (short term)	10 mm (long-term) or 3 mm (short-term)	aspen and balsam	Alberta, Canada	cool temperate aspen woodland	yearly for 5 years (long term) or 7 times in 30 mo. (short term)
Lunt, 1935	75-200 g	litter baskets, 11 x 18.5 x 3 in.	approx. 3 mm	beech, dogwood, red maple, sugar maple, hickory and white oak	Connecticut	mixed hardwood forest or under shade trees surrounded by lawn	after 7 weeks
McClaugherty et al., 1985	2, 4 or 10 g	15 x 15 cm	0.1 mm (buried and in litter layer) or 2.0 mm	red maple wood chips; 5 leaf types (sugar maple, aspen, white oak, white pine, hemlock)	Wisconsin	sugar maple, white oak, bigtooth aspen, white pine, and hemlock forests	2 yr.
Melillo et al., 1982	10 g	20 x 20 cm	4 x 3 mm	beech, sugar maple, paper birch, red maple, white ash, pin cherry	Hubbard Brook, NH	hardwood forest	1, 6, 9, 12 mo.
Mudrick et al., 1994	10 g	33 cm x 21 cm	4 x 5 mm	chestnut oak, red maple, yellow-poplar and mixture	north-central West Virginia	hardwood forest	3, 6, 8, 10, 12 mo.
Nicholson et al., 1966	0.5-0.8 g	4 x 4 cm	0.7 mm	fecal pellets of millipede (*Glomeris Marginata* (Villers))	England	mixed deciduous hardwood	after 0, 3, 7, 14, 28, 42, 56, 84, 140, and 365 d.

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Olson and Crossley, 1961	radioisotope labeled litter	10 x 10 cm	2.3 mm	oak, pine, dogwood	Oak Ridge, Tennessee	pine or oak stand	radiation and weight loss over 30-60 week periods
Pardo et al., 1997	10 g (leaf leaching lab method also)	25 x 25 cm	5 mm	beech and melojo oak	center of the Iberian Peninsula	hardwood forest	60, 120, 180, 260, 360, 470 and 660 days
Rutigliano et al., 1996.	4 g	20 x 20 cm	0.8 mm	beech and fir	near Naples, Italy	beech and beech-fir forests	every 2 months for 7 yrs.
Seastedt and Tate, 1981	40 millipedes or domestic crickets	5 x 5 cm	2 mm	insects	Coweeta, North Carolina and Georgia	hardwood forest litter	periodically over a year
Seastedt et al., 1983	3 g	10 x 10 cm	2 mm	Chestnut Oak	Coweeta, North Carolina	hardwood forest	2 weeks to 2 yr.
Shanks and Olson, 1961	50 g	45 x 60 cm	2.3 mm	mulberry (*Morus rubra*), sugar maple (*Acer saccharum* Marsh.), white oak (*Quercus alba* L.), Shumard red oak (*Quercus shumardii* Buckley), beech (*Fagus grandifolia* Ehrh.)	Southern Appalachians	hardwood forests (beech, cove hardwood, oak, spruce, hemlock and pine sites)	1 year (subset removed and returned after 5.5 mo.)
Stachurski and Zimka, 1976	difference in unconfined litter "standing crop," also weight per area measurements from sub-samples		10 cm2 cores from 1 m2 area	alder (*Carici elongatae-Alnetum*)	Poland	80 year-old alder stand	6 times over 1 yr.
Thomas, 1970.	4 g	25 x 25 cm	2 mm	red maple (Acer rubrum L.), tuliptree (Liriodendron tulipifera L.) and white oak (Quercus alba L.)	Oak Ridge, Tennessee	oak-hickory stand or small stream (30 m downslope)	13 times in 1 yr.
Weary and Merriam, 1978	1 cm2 x 2.5 cm cores			litter separated in cores from humus and mineral soil	Ottawa, Canada	red maple woodlot (w/ and w/o insecticide)	monthly for 16 months

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Witkamp, 1966	2.4 – 9.9 g	10 x 10 cm	1 mm	red mulberry (*Morus rubra* L.), redbud (*Cercis canadensis* L.), white oak (*Quercus alba* L.), loblolly pine (*Pinus taeda*), American beech (*Fagus grandifolia* Ehrh.)	Oak Ridge, Tennessee	white oak, shortleaf pine and red maple stands	every 2 weeks for 1 yr.
Witkamp and Crossley, 1966	2.5 g (tagged with Cs-134)	1 dm2	2 mm	white oak (*Quercus alba* L.)	Oak Ridge, Tennessee	white oak stand (control and 10 – 100g naphthalene monthly)	litterbags collected weekly and then returned after weighing, measuring radiation, and extracting arthropods (1 yr.)
Witkamp and Olson, 1963	5-7.5 g or unconfined attached to strings	10 x 10 cm	1 mm	oak leaves	Oak Ridge, Tennessee	shortleaf pine, white oak, red maple and tulip poplar stands	approx. monthly for 16 months
Witkamp and Van der Drift, 1961	estimated by difference of fresh litter (Dec) with following year's litter weight (Sept.)			leaf litter, filter paper (cellulose) in mesh to exclude invertebrates, lime wood sticks (*Tilia* spp.) vertically in the soil for 6-8 weeks	near Arnhem, Netherlands	deciduous forest (oak, birch, poplar and alder) in mull (pH 7.2) and mor (pH 3.3) sites	3 yr.
Tropical							
Attiwill, 1968	20 g litter and branches	10 x 10 x 2cm boxes	0.75 cm	*Eucalyptus obliqua*	southeastern Australia	*Eucalyptus* forest	8 times in 2 yr.
Budelman, 1988	100 g	spread on 50 x 50 cm wooden frames (13 cm height)		leaf mulches of *Leucaena leucocephala, Gliricidia sepium* and *Flemingia macrophylla*	Ivory Coast	humid tropical climate, open area w/o shade	after 14, 28, 42, 56, and 70 d.
Clark et al., 1998	8-12 g	10 x 15 cm	0.2 mm	epiphytic bryophytes	west-central Costa Rica	tropical montane forest	3, 6, 9, 12, 15, 24 months

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Edwards, 1977	2 – 14 g		up to 8 mm (somewhat elastic bag used to pack fruit & vegetables)	6 tree leaves (*Dacrycarpus cintus, Elaeocarpus ptilanthus, Litsea* sp. 65, *Macaranga albescens, Planchonella firma, Schizomeria* ps. 203) and bamboo (*Nastus productus*)	New Guinea	montane rain forest	periodically over 325 days
Gunadi, 1994	calculated from litterfall before wet/dry season and litter standing crop after wet/dry season			*Pinus merkusii*	Central Java, Indonesia	pine forest plantation (800 m)	6 months
Gunadi et al., 1998	20 g (L) or 30 g (F)	15 x 15 cm	4 mm (L), 2 mm (F)		Central Java, Indonesia	forest plantation (600 or 800 m, L or F layers)	6 times over 1 year
Macauley, 1975	20 leaves	40 x 30 cm	5, 1, and 0.5 mm	*Eucalyptus pauciflora*	Australia	mature *Eucalyptus* stands	7 times in 48 weeks
Maheswaran and Gunatilleke, 1988	2.0-2.5 g	25 x 25 cm	1 mm	*Cullenia ceylanica* (forest) and *Dicranopteris linearis* (fernland)	Sri Lanka	lowland rain forest and deforested area (fernland)	1, 3, 6, 9, 12 months
Tian et al., 1992	stainless steel litterbags	30 x 30 cm	0.5, 2, or 7 mm	three agroforestry species (*Acioa barteri, Gliricidia sepium*, and *Leucaena leucocephala*), maize (*Zea mays*) stover and rice (*Oryza sativa*) straw	Ibadan, Nigeria	maize field	five times in 98 days
Vanlauwe et al., 1995	4.67 t / ha	30 x 30 cm	1.4 mm	*Leucaena leucocephala, Senna siamea, Dactyladenia barteri*	southwestern Nigeria	hedgerow trees in alley cropping system with varying simulated rainfall events	four periods of 115 days (five sampling during each period)

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Vanlauwe et al., 1997	22.3-200 g per bag		1.4 mm	four different prunings of *Leucaena* and *Senna* in alley-cropping systems	southwestern Nigeria	agricultural fields adjacent to hedgerows	five times in 112 days for 4 periods
Wiegert, 1970		22.4 x 22.4 cm	1 mm	mixed litter of mixed age	Puerto Rico	Montane rain forest	periodically for two 1 yr. studies
Wood, 1974	7 g	20 x 16 cm	10 x 7 mm (L) or 0.03 mm (S)	*Eucalyptus delegatensis*	southern Australia	*Eucalyptus* forests	after 1 year
Grasslands and other Ecotypes							
Aerts, 1997					worldwide	shrub and forest	
Berendse et al., 1989	0.8 or 1.8 g	10 x 10 cm	0.25 mm	*Molinia* leaves and culms, *Erica* leaves and flowers and *Erica* branches	Netherlands	wet heathland	10 times in three years
Christensen, 1985	10 g	10 x 30 cm	1 mm	mature spring barley (*Hordeum vulgare* L. cv. Welam) and winter wheat (*Triticum aestivum* L. cv. Solid)	Denmark	buried 10 cm under different field cover types (coarse sand or sandy loam)	10 times in 14 mo.
Curry, 1969a	20 g	22.5 x 18.8 cm	0.003, 0.5, and 7 mm	sward (72% *Agrostis tenuis* and 9.1% *Festuca rubra*)	Ireland	surface and buried under inverted sods	6 times in 10 months
Douce and Crossley, 1982	5 g	10 x 10 cm	2 mm	mixed stems and leaves (Barrow grass *Dupontia fischeri* R. Br., sedges *Carex aquatilis* Wahlenb and *Eriophorium angustifolium* Honck. and small amount of other plants)	Barrow, Alaska	tundra (trough, basin and rim of polygons)	9 times in 13 mo.

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Gallardo and Merino, 1993	2 g	10 x 15 cm	1 mm	five tree species (*Quercus suber, Quercus canariensis, Quercus pyrenaica, Salix atrocinerea, Fraxinus angustifolia*) and four shrub species (*Quercus lusitanica, Quercus coccifera, Halimium halimifolium, Cistus libanotis*)	Spain	shrubland	every 2 mo. for 2 yr.
Golley, 1960	cellulose sheet vertically in soil, measured percent area lost			alpha cellulose sheets between wire screening	Savannah River Plant, South Carolina	light to heavy amount of broomsedge	5 times in 6 months; also 1 month study inserted monthly April-July
Heath et al., 1966	50 disks (2.5 cm dia), measured 'disappearance,' not weight loss	10 x 7 cm	0.003, 0.5 and 7.0 mm	kale, beets, lettuce, beans, oak, beech, elm, ash, birch, lime, and maize	Rothamsted Exp. Station, England	woodland or fallow pasture (buried 2.5 cm)	4 times or 12 times in 14 mo. depending on experiment
Hill et al., 1985	CTSL				England	different soils (woodland, heath, grassland, bog)	variously for up to 2.2 yr.
House and Stinner, 1987	4 g	10 x 10 cm	0.05, 0.20, 1.00, 5.00 mm	crimson clover (*Trifolium incarnatum* L.), hairy vetch (*Vicia villosa* ROTH), rye (*Secale cerale* L.)	North Carolina	no-tillage corn field	4 times in 4 months
Magid et al., 1997	examined particulate organic matter changes to estimate decomposition			oilseed rape (*Brassica napus* L) straw	Denmark	sandy loam soil	approx. monthly for 1 yr. 8 mo.

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Noyd et al., 1997	0.50 g (root), 0.70 g (shoot)	9 x 9 cm	0.5 mm	Native prairie species (above and belowground): *A.gerardii, E. canadensis, S. scoparium, B. kalmii,* and *L. capitata*	northern Minnesota	taconite iron ore tailings	1,2,3,4,11,13,14,15 mo.
Schlesinger and Hasey, 1981	2 g	10 x 10 cm	1 mm	*Ceanothus megacarpus* and *Salvia mellifera*	southern California	chaparral shrubs	monthly for 1 yr.
Vossbrinck et al., 1979	3 g	10 x 10 cm	53 µm or 1 mm	blue grama (Bouteloua gracilis (H.B.K.) Lag. ex Steud.)	Colorado	shortgrass prairie	monthly for 9 mo.
Wiegert, 1974	2.5 or 5 g		2 mm	corn leaves, broom sedge, lespedeza	Savannah River, South Carolina	old field	every 2 weeks for 1 yr.
<u>Wetlands</u>							
Salt Marshes							
Frasco and Good, 1982				*Spartina alterniflora* tall form (SAT) and *Spartina patens* (SP)	New Jersey	salt marsh	monthly for 1 year
Jordan et al., 1989	35 g (15 g blades, 20 g bases)		1 cm	*Typha angustifolia*	Maryland, on Rhode River, sub-estuary of Chesapeake Bay	brackish tidal marsh (also position in litter layer)	periodically over 300 days and again at 860 days
Montagna and Ruber, 1980	15 g (wet)		4.5 x 11 mm diamond	dwarf *Spartina alterniflora (live leaves)*	northern Massachusetts	salt marsh (*Spartina* marsh, tidal ditch, marsh pool)	19 times in first year, another after 2 yr.
Moran et al., 1989	1 g	8 cm diameter cylinder	0.02 mm	*S. alterniflora, C. walteriana*, or lignocellulose	Georgia	salt marsh tidal creek and Okefenokee Swamp	every one or two months for 1 yr.

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Newell et al., 1989	tagged standing leaves			salt-marsh grass (*Spartina alterniflora*)	Georgia	intermediate height *Spartina* salt marsh	4 times in 3-5 mo. (2 seasons)
Scatolini and Zedler, 1996	45 g	30 x 30 cm	5 mm	*Spartina*, plastic grass, *Typha domingensis*, or *Scirpus californicus*	Southern California (San Diego Bay)	natural and created salt marsh	three to eight times over 3 mo. to 1 year
Valiela et al., 1985	50 g		2 x 4 mm	*Spartina patens* (Ait.) Muhl., *S. alterniflora* Loisel.	New England	salt marsh	6 –7 times over 600-700 days
White et al., 1978	20 g	20 x 20 x 5 cm		*Distichlis spicata, Spartina patens, Juncus roemerianus, Spartina alterniflora*	Louisiana	salt marsh	monthly for 1 yr.
Wilson, 1985	50 g		2 x 4 mm	*S. alterniflora*	Cape Cod, Massachusetts	salt marsh	6 times in 2 yr.
Windham, 2001	5 g	15 x 15 cm fiberglass	2 x 2 mm	*Phragmites australis* and *Spartina patens*	New Jersey	brackish tidal marshes	after 0, 1, 2, 4, 7, 12 months
Freshwater Marshes							
Brown et al., 1997					Northern New York	deep water surrounded by fringing marsh	weekly during the summer for three years
Bärlocher and Biddiscombe, 1996	10 cm *Typha* sections or 5 *Lythrum* leaves	standing tagged and litterbag (12 x 15 cm)	tagged or 2.5 mm	*Typha latifolia, Lythrum salicaria*	New Brunswick, Canada	freshwater marsh	after 1, 2, 4, 8, and 12 wks.
Bruquetas de Zozaya and Neiff, 1991	10 g	cylinder (8.5 cm dia., 15 cm height)	300 holes of 5 mm	*Typha latifolia* L.	Argentina	Chaco cattail swamp (aerial, above (submerged in water) and below floating island)	after 7, 15, 30, 45, 75, and 150 d.
Cahoon and Stevenson, 1986	100, 200 or 300 g		2 mm	swamp rose mallow stems (*Hibiscus moscheutos*)	Maryland	low salinity hibiscus marsh on eastern shore of Chesapeake Bay	every three months for 2 yr.

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Davis, 1991	5 g	30 x 30 cm fiberglass screen	1.7 mm	*Cladium jamaicense* Crantz, *Typha domingensis* Pers.	Florida	everglades	1 mo., 1 yr., and 2 yr.
Davis and van der Valk, 1978	50 g (*Typha*) or 20 g (*Scirpus*)	standing and 20 x 40 cm litterbags	standing (1 x 1 m quadrats) or 3 mm	*Typha glauca, Scirpus fluviatilis*	Goose Lake, Iowa	prairie glacial marshes	10 times in 525 d.
DeBusk and Reddy, 1998				cattails or sawgrass	Florida	Everglades	
Emery and Perry, 1996	8 g	10 x 10 cm	1 mm	purple loosetrife (*Lythrum salicaria*), stems or leaves, and Cattail (*Typha* spp.) spring or fall	Minnesota	14 emergent wetlands dominated by cattail or purple loosetrife	4-8 times in 170-180 d.
Findlay et al., 1990	individually tagged leaves (*Nuphar*) or 10 g (*Typha*)		1 cm (mesh cage for tagged leaves)	water chestnut *(Trapa natans)* and *Typha* sp.	Hudson River, New York	tidal freshwater marsh	every 2 wk in late summer and fall for two years
Hietz, 1992	4.5-5.5 (leaves) or 7.5-8.5 g (stalks)	10 x 15 cm	70 µm or 5 mm	reed (*Phragmites australis* (Cav.) Trin. ex Steud.) stalks and leaves	Lake Neusiedl, Austria	fringing reed belt around lake	8 or 11 times in 506 or 863 d.
Hodkinson, 1975a	5, 10 or 20 g	20 x 20 cm	3.5 cm	*Salix, Pinus, Juncus, Deschampsia, Picea*	Alberta, Canada	abandoned beaver ponds	2, 20, 40, 60, 80 weeks
Kittle et al., 1995	5 g	8 x 8 cm	1.5 mm	calamus, common rush, woolgrass and rice cutgrass	N West Virginia	constructed wetlands receiving AMD	66 or 155 days
Kuehn et al., 1999	tagged green shoots in mid-October			*Erianthus giganteus* (plumegrass) culms and leaves	Alabama	freshwater wetland	7 times in 190 days
Mason, 1976	12 1.5 cm pieces	10 x 10 cm	4.6 mm diameter	*Phragmites communis* (Trin)	near Norfolk, England	reedswamp	after 35 and 122 d.
Mason and Bryant, 1975	1.3 (*Typha*) or 1.5 g (*Phragmites*)	10 x 10 cm	4600 or 250 µm	*Phragmites communis* Trin. and *Typha angustifolia* L.	near Norfolk, England	reedswamp	periodically during 314 (phragmites) or 624 (Typha) days

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Morris and Lajtha, 1986	15 – 20 g		2 mm	*Typha latifolia* L., *Carex lacustris* Willd., *Calamagrostis canadensis* (Michx.) Nutt., and *Zizania aquatica* L.	Massachusetts	freshwater tidal marsh	over 30 mo.
Murkin et al., 1989	25 g	12 x 30 cm	1 mm	hybrid cattail (*Typha glauca*), whitetop rivergrass (*Scholochloa festucacea*), common reed (*Phragmites australis*), and hardstem bulrush (*Scripus lacustris glaucus*)	Manitoba	delta marsh (submerged in a channel)	8 times over 1051 days
Neely, 1994	microcosms to simulate wetlands			*Typha latifolia*	Michigan	sterilized marsh water, low and high algae treatments	70 days
Neely and Davis, 1985	10 g	20 x 30 cm	1 mm	*Sparganium eurycarpum* Engelm., *Typha glauca* Godr. (natural and swine waste grown plants(enriched))	Iowa	prairie marsh	1, 14, 30, 50, 100, 150, 350, and 505 days
Polunin, 1982	not specified		10 mm	reed, *Phragmites australis*	Great Britain	freshwater pond/marsh system	varied
Qualls and Richardson, 2000	5 g		4 mm	cattail (*Typha domengensis* Crantz), sawgrass (*Cladium jamaicense* Pers.)	Florida	mesocosms in the Everglades	after 32, 128, 245, 365 days
Ryder and Horwitz, 1995	10 g leaf packs		leafpacks fastened by plastic cables	*Baumea articulata, Typha orientalis*	western Australia	seasonal wetland on Swan Coastal Plain (seasonal and permanently inundated with and w/o vegetation)	3 times in 6 mo.
Sain and Broadbent, 1977	25 g	15 x 23 cm	coarse mesh nylon	Rice (*Oryza sativa*) straw chopped to 1-4 cm or 15-20 cm	California	two rice fields, suspended, soil surface, or incorporated in soil	monthly for 5 mo.

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Schipper and Reddy, 1995	0.5 g per modified porewater equilibrator cell		3 mm	*Typha* sp.	central Florida	cattail dominated marsh, from floodwater to 25 cm deep	after 1, 2, 4, 8, 12 and 16 weeks
Vargo et al., 1998	1.5-2.5 g	12 x 12 cm or 12 x 6 cm	1 cm or 1.5 cm	*Typha latifolia, T. angustifolia,* and *Sparganium eurycarpum* Engelm.	Michigan	enclosures in Typha dominated lakes	10 times in 470 days or 7 times in 117 days
Verhoeven et al., 2001	tensile strength				Netherlands, Belgium and Maryland	tidal and non-tidal riverine wetlands	6 weeks
Wylie, 1987	10 g (pin oak) or 15 g (lotus)		3 mm	pin oak (*Quercus palustris*) and American lotus (*Nelumbo lutea*)	southeast Missouri	wetland moisture gradient, permanently ponded to seasonally inundated for impounded and natural wetlands	monthly for 1 year
Forested Wetlands							
Battle and Golladay, 2001	5 g	30 x 16 cm	5 mm	mixed pond cypress, bald cypress and black gum	southwest Georgia	cypress-gum swamp (depressional)	after 1, 14, 28, 56, 84, 140, 182, 217, 266, and 322 days
Bell et al., 1978	50 g	0.1 m2		white oak, shingle oak, hackberry, silver maple (transition), white oak (upland), silver maple (floodplain)	Illinois	gradient from stream bank to upland	approx. monthly for 10 months
Briggs and Maher, 1983	4 leaves		1.5 mm	River red gum (*Eucalyptus camaldulensis*)	New South Wales, Australia	river red gum swamp	monthly over 1 year (more often during 1st month)
Brinson, 1977	1.17 cellulose 8.07 leaves 10.47 twigs	24 x 32 cm	6 x 7 mm	cellulose *Nyssa aquatica*	North Carolina	swamp, levee, river system	11 times in 56 weeks

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Conner and Day, 1991	10 g		1 mm	mixture of water tupelo, ash and maple	Louisiana	crayfish pond, impounded swamp, natural swamp	12 times in 42 weeks
Cuffney and Wallace, 1987	15 g	35 x 15 cm	5 cm with some 1 x 3 cm mesh	sweetgum (*Liquidambar straciflua* L.), water oak (*Quercus nigra* L.)	Georgia	river and floodplains of two coastal plain streams	7-9 times during 525 days
Day, 1982	5 g		1 mm	mixed litter, single species litter (cypress, cedar, tupelo, maple, oak), red maple branches	Great Dismal Swamp, Virginia	mixed hardwood, cedar, maple-gum, cypress	monthly for 1 yr. and again after 2 yr.
Day, 1983				*Acer rubrum*	microcosms (Styrofoam coolers with maple-gum soil, 22.5 C, darkened room)	different hydroperiod simulations	occasionally over 215 days
Day, 1987	known mass		1 mm	Atlantic white cedar (*Chamaecyparis thyoides*) or mixed species litter	southeastern Virginia	Atlantic white cedar swamp	monthly for 1 year
Deghi et al., 1980	15-25 g	30 x 30 cm	18 x 10 mesh	cypress (*Taxodium*)	Florida	Cypress swamp with sewage effluent additions	monthly for 6 mo., less frequently second six months
Elder and Cairns, 1982	10 g	20 x 20 cm	2.5 mm	water hickory, water tupelo, diamond-leaf oak, baldcypress and sweetgum (both single species and mixtures)	Florida	Apalachicola River flood plain (bottomland hardwood), floodplain (levee), river or bay	every 2-4 weeks over 6 months
Goulter and Allaway, 1979	8-10 g	0.16 m^2	7 mm or 1 mm	*Avicennia marina* (Forsk.) Vierh.	Sydney, Australia	mangrove swamp	every 2 weeks in 8 wks.
Harper and Bolen, 1995	10 g		1 mm w/ only partial closure	longleaf pine, sweetgum, flowering dogwood	North Carolina	blackwater impoundments	1, 3, 4, 5 mo.
Hauer et al., 1986	10 g	40 x 20 cm	5 x 25 mm (0.5 mm for cypress)	American sycamore, sweetgum, and baldcypress	Savannah River Project, South Carolina	thermally impacted and non-impacted streams and swamps	5 times in 16 weeks

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Hill, 1985	2-5 g	15 cm^2	3 mm	*Nelumbo lutea leaves, petioles, Ludigia leptocarpa,* and *Typha angustifolia*	Texas	reservoir wetland	6 to 10 times during five months
Kemp et al., 1985	10 g		1 mm (partially open on one end)	hardwood leaves	Louisiana	swamp forest	12 times in 46 weeks
Lockaby et al., 1996a & 1996b	10 g	12.7 x 12.7 cm	6 mm	mixed (laurel oak, sweetgum, water oak, black gum, swamp tupelo)	Savannah, Georgia	microcosms in a floodplain forest	after 0, 0.25, 11, 14, 17, 20, 23 months
Mader, 1990 (from Trettin et al., 1996)	cotton strip assay			*Equisetum, Carex*, other herbaceous spp., *Myrica* leaves, *Salix* leaves	Alabama	bottomland hardwoods	
McLaughlin et al., 2000	CTSL			cotton strip assay	upper peninsula of Michigan	forest wetland with harvesting and site preparation	two consecutive 5-week incubations during the late spring and summer
Merritt and Lawson, 1979	4 g (also tethered leaves)	10 x 10 cm	50 µm, 500 µm, 8000 µm, and tethered leaves	black ash (*Fraxinus nigra*)	Michigan	floodplain forest	monthly for 1 year
Middleton, 1994	20 g except 10g for *C. occidentalis*	10 x 10 cm	1 mm	*Taxodium distichum, Polygonum pensylvanicum, Jussiaea diffusa, Echinochloa muricata, Eleocharis obtusa, Typha latifolia, Cephalanthus occidentalis*	southern Illinois	bald cypress swamp	9 times in 190 days
Peterson and Rolfe, 1982	70 or 77 g	1650 cm^2 bottom area of hardware cloth containers	7 mm	mixed; *Acer saccharium* dominated floodplain; *Quercus alba* and other oaks comprised the upland litter	Illinois	upland and floodplain forests	every 2 mo. for 2 yr. (upland) or every 6 wk for 1 yr. 2 mo.
Rice et al., 1997				woody debris, pumpkin ash	South-central Louisiana	forested alluvial delta	6 mo. for 2 yr.

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Shure et al., 1986	4 g	15 x 15 cm	1 mm	mixed litter (1974), red ash, black gum, sweet gum, and red maple (1975)	South Carolina	floodplain forest (gradient from river bank)	monthly for 1 year
Trettin et al., 1996	cotton strip assay				Upper Peninsula Michigan	forested outwash plain with histic epipedon	5 wk
Twilley et al., 1986	6.0-8.8 g	20 x 10 cm	1 mm	*Rhizophora mangle, Avicennia germinans*	Southwest Florida	basin mangrove forests	6-7 times in 148 or 353 days
Yates and Day, 1983	5-8 g	20 x 20 cm and tethered leaf packs	1 mm	mixed litter collected from white cedar, maple-gum, cypress, and mixed hardwood sites	Great Dismal Swamp, Virginia	mixed hardwood, cedar, maple-gum, cypress	one collection after 400 days
Boreal and Peatlands							
Alm et al., 1999				*Sphagnum*	Finland	boreal bog	
Arp et al., 1999	3.0 g	10 x 10 cm	1 mm	*Carex Aquatilis*	Colorado	rocky mountain fens affected by acid rock drainage	4 times over 2 years
Bartsch and Moore, 1985	2 g	20 x 20 cm	1.4 mm	*Carex limosa, C. rostrata, C. aquatalis, C. chorodorrhiza, Scirpus cespitosus, Betula glandulosa, Salix pedicellaris, Sphagnum lindbergii*, lawn sphagna, hummock sphagna, cellulose sheet	near Schefferville, Québec, Canada	four mires	after 9 and 12 mo.
Bridgham et al., 1991	cotton strip				E North Carolina	Natural and disturbed peatlands, pocosins	between 1 and 10 weeks
Coulson and Butterfield, 1978	1 g		0.8 mm top, 0.2 mm bottom and 0.02 mm	*Phleum, Festuca, Juncus, Rubus, Eriophorum, Calluna, Sphagnum*	Great Britain	blanket bog	12 mo.

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Heyes et al., 1998	1-5 g	10 x 10 cm	400 µm	*Sphagnum fuscum* (moss), *Picea mariana* (black spruce) needles, and green *Carex rostrata* (sedge) stems	northwest Ontario	headwater bog and impounded riparian wetland	5 times over 2.5 yr.
Marsh et al., 2000	fiberglass mesh bags		2 mm	*Equisetum* spp.	Alaska	shrub wetland	1 or 2 years
Newell et al., 1995	standing litter			*Carex walteriana*	Okefenokee Swamp, Georgia	fens	after 8 mo.
Ohlson, 1987	2 g	20 x 15 cm	1.0 mm	*Carex rostrata*	Sweden	mire (peatland)	1 year
Scheffer et al., 2001	0.5 (*Sphagnum*) or 1.0 g (*Carex*)	10 x 10 cm	0.3 mm	*Carex diandra, C. lasiocarpa, Sphagnum papillosum*, and *S. squarrosum*	Netherlands	fens	after 1.5, 12 and 24 months
Thormann et al., 1999		2.5-6.0 x 2.5-3.0 cm	1 mm	*Sphagnum fuscum, S. teres, S. angustifolium, Betula pumila, Tomenthypnum nitens, Carex* spp., *Typha latifolia*	Alberta, Canada	bog-fen-marsh gradient	after approx. 1 year
Verhoeven and Arts, 1992	1 g	10 x 10 cm	0.2 mm	*Carex diandra* and *C. acutiformis*	Netherlands	fens/mires	12 times during 110 week period
Verhoeven et al., 1996					Poland and Netherlands	mires	
Aquatic Systems							
Streams							
Bärlocher and Schweizer, 1983	0.16, 0.64, 1.44, 2.56, and 4.0 cm^2 squares	10 x 15 cm	0.3 and 3.0 mm	oak (*Quercus petraea* (Mattuschka) Lieblein), maple (*Acer platanoides* L.)	Black Forest, West Germany	soft water stream	after 7, 14, 38, 77, and 108 d.

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Benfield at al., 1977	leaf packs, 15 g		purse-like baskets from chicken wire (tethered to brick)	sycamore (*Platanus occidentalis* L.) (pre-leached)	Virginia	pastureland stream	every 2 weeks over 161 days
Chamier, 1987	1.5 g	15 x 10 cm	1 mm	alder, oak, grass	Lake District, England	7 streams with pH 4.9-6.8	every 2 weeks in 18 wks.
Cuffney and Wallace, 1987	15 g	35 x 15 cm	5 cm with some 1 x 3 cm mesh	sweetgum (*Liquidambar straciflua* L.), water oak (*Quercus nigra* L.)	Georgia	river and floodplains of two coastal plain streams	7-9 times during 525 days
Cummins et al., 1980	5.8 kg loose, 100 6g leafpacks, 100 6 g litterbags	18 cm2 litterbag, leafpacks attached to bricks	naturally entrained, leaf packs or 1 mm litterbags	basswood (*Tilia americana*)	Michigan	1st order stream	every 10-30 days for 3 months
Dangles and Guérold, 1998	4 g	cylindrical baskets w/ 3 compartments, h= 13cm, dia.= 6.5 cm	5 mm	Beech	northeast France	acid (pH 4.5) and nonacid (pH 7.5)) 2nd order mountain streams	33, 69, 99, 140, 176, 203, 225 days
Elwood et al., 1981	6-7 g (leaf packs)	tethered to bricks in stream	3 mm octagonal	red oak	Eastern Tennessee	second order stream	6 times in 3 mo.
Forbes and Magnuson, 1980	0.08 g	22 cm^2	3 x 4 mm	sugar maple (*Acer saccharinum*)	central Wisconsin	streams w/ and w/o coal ash effluent	after 27 and 96 d.
Grattan and Suberkropp, 2001	5 leaf disks (11.6 mm diameter)	disks held together by pins with 2 mm spacers		yellow poplar	Alabama and Tennessee	experimental channels at 1st and 2nd order streams	every 4-5 days over 20-30 days
Herbst, 1980	20-25 leaves in a leaf pack		fastened with plastic buttoneers	silver maple (*Acer*) or cottonwood (*Populus*)	Wisconsin	small stream	4-5 times in 120 or 140 days
Herbst and Reice, 1982	5 g bundles or leaf packs		leaf packs	*Phragmites australis, Eucalyptus rostrata*	Israel	temporary and permanent streams in a semi-arid region	5 times in 10 weeks
Hildrew et al., 1984	CTSL			cotton strips	southeast England	34 streams	3 trials (summer(7d) autumn (28d) and winter(49d))

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Hutchens and Benfield, 2000	8 g	leaf packs	5 mm	chestnut oak (first or second flush)	North Carolina (Coweeta)	clear-cut/reference catchment first order streams	6 times in 250 days
Kirby, 1992	2.5 g	(leaf packs)	fine mesh vs. 1 cm	red maple	north-central Pennsylvania	AMD affected headwater stream	5 times in 142 days
Leff and McArthur, 1990	5 g		4 mm	red maple (*Acer rubum*)	Savannah River, SC	3rd order blackwater stream	weekly for 15 weeks
Maloney and Lambert, 1995	5 g	10 x 15 cm	1 cm	dried green leaves, sugar maple (*Acer saccharium*), speckled alder (*Alnus rugosa*), eastern hemlock (*Tsuga canadensis*), red-stemmed dogwood (*Cornus sericea*) and sweet gale (*Myrica gale*)	Northern Michigan	stream riffle	after 2, 14, 28, and 42 days
McArthur et al., 1986	5 g (tethered in stream)		4 mm	red maple (*Acer rubum*)	Savannah River Plant, SC	thermally impacted and natural 3rd order streams	weekly for 8 weeks
Meyer, 1980	3 g ea. species	20 x 20 cm	1 mm (sewn 1 cm apart)	sugar maple, yellow birch, or beech	New Hampshire	six sites in a forest stream with different rates of sedimentation	1 year
Niyogi et al., 2001	1 g	10 cm long, 5 cm diameter plastic tubes with mesh ends	1 mm	willow (*Salix* spp.)	Colorado	streams affected by acid mine drainage	3-6 times over
Padgett, 1976	10 leaf disks		1.8 mm^2	*Dacryodes excelsa* Vahl., *Sloanea berteriana* Choisy, *Cordia borinquensis* Urban, *Manilkara bidentata* (A. DC.) Chev., *Buchenavia capitata* (Vahl.) Eichl.	Puerto Rico	small stream surrounded by tropical forest	every 2 weeks for 32 wks.
Petersen and Cummins, 1974	10 g leaf pack	attached to 2 lb bricks		15 species	Kalamazoo, Michigan	woodland streams	
Post and De la Cruz, 1977		20 x 30 cm	2.5 mm	mixed deciduous or pine litter	Mississippi	3rd order coastal plain stream	every 2 mo. for 1 yr.

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Qualls and Haines, 1990				disks of *Acer rubrum* L. leaves (three collection sites)	southeast United States	flasks of stream water with varying amounts of humic substances	38 days
Reice, 1974	1, 5, 10, 20, or 40 g		leaf packs (pliable leaves stacked together and fastened by buttoneer)	white ash (*Fraxinus americana*)	south central Michigan	small trout stream (rock, gravel, sand and silt sediments)	one per week over 6-wk periods during 4 seasons
Reice, 1977	5 g		leaf packs (pliable leaves stacked together and fastened by buttoneer)	white ash (*Fraxinus americana*)	piedmont, North Carolina	3rd order stream	weekly for 6 wks.
Sedell et al., 1975	5-15 g leafpacks (strung on monofilament line)		attached to bricks	conifer needles (*Pseudotsuga menziesii* and *Tsuga heterophylla*), vine maple (*Acer circinatum*), bigleaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*)	Oregon	2 streams in the western Cascades	monthly over 200-300 days
Short et al., 1980	5 g leaf packs attached to bricks			alder (*Alnus tenuifolia*), willow (*Salix bebbiana*), aspen (*Populus tremuloides*), and pine (*Pinus ponderosa*)	Colorado	mountain stream	7, 14, 28, 56, 84, 112, and 168 days
Smith, 1986	10 g	(leaf pack attached to bricks)		hackberry, elm, chinquapin oak, bur oak, sycamore	Kansas	tall grass prairie stream (riffles and pools)	every 150 degree days for 900 degree days (approx. 5 months)
Sponseller and Benfield, 2001	8 g	leafpacks	5 mm	sycamore (*Plantanus occidentalis*)	Virginia (upper Roanoke River)	2nd and 3rd order streams (riffles)	after 13, 45, 70, 105, 130 days
Suberkropp et al., 1976	5 g (leaf packs)			white oak (*Quercus alba*) pignut hickory (*Carya glabra*)	SW Michigan	3rd order stream	periodically during 32 weeks

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Thomas, 1970 (see deciduous forests)							
Triska and Sedell, 1976	leaf packs tied to bricks			douglas fir (*Pseudotsuga menziesii*), vine maple (*Acer circinatum*), bigleaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*)	Washington	three experimental steams w/ varying N	periodically over 240 days
Wallace et al., 1982	15 g		5 x 5 mm	rhododendron (*Rhododendron maxima*), white oak (*Quercus alba*), dogwood (*Cornus florida*), red maple (*Acer rubrum*)	Coweeta, North Carolina	reference or insecticide treated streams	0, 8, 14, 49, 117, 144, 207, and 265 days
Webster and Waide, 1982	2-4 g	10 x 10 cm	3 mm octagonal	dogwood (*Cornus florida*), white oak (*Quercus alba*), and rhododendron (*R. Mazimum*)	Coweeta, North Carolina	streams after clear-cutting of forest	periodically during 4 years
Rivers							
Baldy et al., 1995	2-7 g	15 x 15 cm	2 mm	willow, poplar, and London plane	southwestern France	7th order river	2, 4, 8, 12, 16, and 20 weeks
Benfield et al., 1979	1.5 g (1 and 3 mm bags), 10 g (12.5 mm bags), 10 and 20 g packs, 0.5 g (mid-vein or marginal disks in 1 and 3 mm bags)		1, 3, or 12.5 mm or packs	American sycamore (*Plantanus occidentalis* L.) (9 different exposure techniques)	Virginia	New River	6 times in 98 days
Chauvet, 1987	5 g	20 cm long anchored to bank	2 mm	alder, poplar and willow	South Western France	seventh order stream	4 times in 6 mo.

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Kaushik and Hynes, 1971	20 leaf disks (1 cm dia.) (also laboratory studies) (leaves leached prior to field studies)	7 x 7 cm	3 mm (in box with guarded (mesh) and unguarded portions)	elm (*Ulmus americana* L.), maple (*Acer saccharum* MARSH), oak (*Quercus alba* L.) and beech (*Fagus grandifolia* EHRH.)	Ontario, Canada	rivers	monthly for 6 months
Mathews and Kowalczewski, 1969	20 g		0.27 and 3.0 mm (w/ 1 cm plastic support to hold in current)	oak (*Quercus robur* L.), sycamore (*Acer pseudoplatanus* L.), and willow (*Salix* spp.),	England	Thames river near Reading (1.5 m deep)	every 4-5 weeks over 8 months
Lakes							
Barnes et al., 1978	5 g	leafpacks		hickory (*Carya glabra*) and oak (*Quercus alba*)	Gull Lake, Michigan	at 2.5, 6.0 and 12.0 m	5-6 times in 72-85 d.
Best et al., 1990	11.7	10 x 10 x 4 cm (closed by string)	1 mm	*Ceratophyllum demersum*	Lake Vechten, Netherlands	at 2.5 m in littoral zone (also short term laboratory study)	after 0, 17, 49, 127 and 169 d.
Brock et al., 1982	20 -30 g	16 x 16 cm	0.5 mm and 0.25 mm	*Nymphoides Peltata*	Netherlands	river cut-off, euthrophic	varied
Brock et al., 1985	10 leaves	35 x 35 cm	0.27 mm	*Nymphaea alba* L.	Netherlands	oxbow lake and acid moorland pool (also lab portion in flow-through aquaria)	7 times over 105 days during two seasons
Danell and Sjöberg, 1979	15 g	0.1 x 0.25 m	5 mm	*Carex rostrata* and *Equisetum fluviatile*	northern Sweden	lake (sites at 1.0 and 1.2 m)	1, 2, 3, 4, 5, and 12 months (depending on treatment)
Danell and Andersson, 1982	16 g	10 x 25 cm	280 um or 5 mm	sedge (*Carex rostrata*), *Typha latifolia*, wheat straw (*Triticum* sp.), and hay (*Phleum pratense*)	Northern Sweden	oligotrophic and eutrophic lakes	after 3 mo.

Table 1. Summary of decomposition studies in upland, wetland and aquatic environments (Continued).

Study	**mass litter (g)**	**litterbag dimensions**	**mesh size**	**litter type**	**location**	**environment**	**sampling frequency**
Esteves and Barbieri, 1983		20 x 30 cm	2.0 mm	*Nymphoides indica* (L.) O. Kuntze (petioles and leaf blades) and *Polygonum ferrugineum* Wedd. (stems and leaves)	São Paulo, Brazil	tropical reservoir	after 7, 15, 23, 36, 58, 85, 119, and 149 d.
Gasith and Lawacz, 1976	25 leaves (5 ea. species)	165 cm x 15 cm dia. divided into cells	2.25 mm	*Populus deltoides* Marsh., *Salix nigra* Sm., *Acer saccharum* Marsh., *Ulmus americana* Marsh., *Quercus alba* L. (pre-leached)	Madison, Wisconsin	littoral zone of eutrophic lake	7 times in 30 wks.
Hendricks et al., 1984	10-12 leaves (3 g)	leafpacks	some with 6.4 mm hardwire enclosures w/ and w/o bluegill sunfish	maple (*Acer* spp.)	Claytor Lake, western Virginia	At 7 m on bottom of reservoir	1,2, or 3 mo. periods

Litterbag Method

In general, the litterbag method involves the placement of a known amount of litter in a screen or fabric mesh (<1-75 mm) and then examination of the temporal pattern of weight loss with a series of collections over a period of a few months to several years. In early forms (Bocock & Gilbert, 1957; Gilbert & Bocock 1960; Bocock, 1964) nylon hairnets were filled with deciduous forest litter to examine decomposition in hardwood forests of England. Gustafson (1943) was perhaps the first researcher to examine decomposition of confined litter, although he used wire baskets instead of the now familiar bags. The litterbag method's ability to become incorporated into the litter layer is cited as an advantage over the rigid basket or frame used by early researchers (Bocock and Gilbert, 1957). The main advantage of the litterbag method is its ability to track the changes of a known amount of litter over time in a field setting by preventing inputs of additional litter or loss of litter fragments larger than the mesh size. A criticism of the method is that the same mesh that confines the litter can prevent detritivores from accessing litter and thereby cause underestimation of true decomposition. In many systems, both terrestrial and aquatic macroinvertebrates have been shown to be important components of the decomposition process by consuming, and perhaps more importantly, conditioning, fragmenting, and inoculating the litter to allow further biotic processing. This apparent disadvantage of the method can be used as an advantage if multiple mesh sizes are employed. A comparison of fine (< 1mm) to medium (1-5 mm) to coarse mesh (>5 mm) openings can give an idea of the relative importance of leaching/microorganisms, meso-invertebrates and macro-invertebrates during decomposition. Further discussion of litterbag advantages and disadvantages follows in the discussion of the different variations of the litterbag technique.

Amount of Litter Utilized

Typically, the mass of litter contained in litterbags in a given study has been the same in each litterbag regardless of litter type and site differences. Masses studied typically range between 2 and 25 grams, but in some instances, up to several hundred grams have been used (Table 1). These small amounts are likely due to the logistics of the experiments (often factorial designs) requiring hundreds of litterbags. Noyd et al. (1997) calculated the amount of litter used per bag based on the limited supply of different greenhouse-grown native species used for litter. Typically, the amount of litter is chosen to approximate the amount of litter per surface area naturally occurring at the site being examined, or the amount that fits within a bag without crushing the litter. In some instances, where litter-fall is known, the amount is derived from the soil surface area covered by a litterbag (Twilley et al., 1986). Herlitzius (1983) calculated the amount of litter per litterbag for comparison of two forests from litter-fall as 3.23 and 4.21 g, but in practice treated each site the same with 3.28 g per bag. It is unclear whether this was for simplicity or to prevent crushing of leaves.

Brinson (1977) studied decomposition of mixed leaf and branch litter in litterbags in an alluvial swamp forest. The leaf litter in bags were equivalent to approximately 1/3 the measured area equivalent autumn litter fall, while the twigs were twice as dense in the litterbag. While Brinson notes that decomposition rates may be influenced by these different substrate densities, there are no studies to indicate whether this actually is the case.

A common reason for different masses of litter being used in the same experiment is to match the natural litter conditions of different sites being examined (Bocock, 1964). Very often, when coniferous and deciduous litters are being compared, more mass of conifer needles is used to better approximate similar packing volumes. Herlitzius (1983) used three times more mass of spruce (*Picea* spp.) needles than hazel (*Corylus avellana* L.), oak (*Quercus robur* L.) or beech (*Fagus sylvatica* L.) litter for similar volumes while Gustafson (1943) used 400 g of conifer needles versus 200-300 g of deciduous litter. Similarly, variations in the mass of litter used by Edwards (1977) and Baldy et al. (1995) were due to equalization of litter volumes. Dwyer and Merriam (1981) used 1.0, 3.0 or 8.0 g (Table 1) of leaf litter for high, level and low topographic positions, respectively, in a forested study area. Based on analysis of standing litter volumes, they determined that topographically high, level and low sites had 416, 1210 and 2438 g/m^2 of litter respectively and chose the litterbag amounts accordingly.

Varying the mass of material or loading rate in each litterbag is unusual, but gives insight into whether litter density may affect decomposition rates. Vanlauwe et al. (1997) filled litterbags with amounts of leaves proportional to the application rates used for prunings in tropical alley cropping systems (22-71 g per bag) versus a uniform 200-g per bag treatment. Differences between the "real" amounts and the 200-g treatment were only observed in one out of four experiments, when the "real" bags decomposed faster than the 200-g treatment. This slight difference was attributed to greater leaching efficiency in the smaller "real" bags from a dry spell followed by heavy showers just prior to litterbag collection. Brock et al. (1982) also varied the amount of litter in each litterbag, but with a completely different litter (water lilies) and environment (an oxbow lake). Using 20, 40 or 60 g of material in the same size litterbags, the breakdown rate was faster when larger amounts of litter were included in the bag. In a stream environment, Benfield et al. (1979) found the reverse, with 1.5 g and 10-g litterbags losing 68% and 4% of initial weight respectively. The effect of using different amounts of litter on decomposition therefore seems to vary by environment, and warrants further study to determine what factors are responsible.

Litterbag Construction

While some of the earliest litterbag studies (Bocock & Gilbert, 1957; Gilbert & Bocock 1960; Bocock, 1964) used nylon hair nets, and some have used the bags for commercially packaging onions, fruit or peanuts (Edwards, 1977), the majority of litterbags are homemade from either metal, plastic or fiberglass screen or synthetic fabric. Litterbags are typically squares or rectangles with an area of 1-4 dm^2, although some have been much larger or constructed as cylinders or cages.

Differences between litterbag dimensions have not been examined in any of the studies reported here without other confounding factors (e.g. different litter material in the different surface area litterbags). Studies of different sized leaf-packs used in stream environments have shown that differences in rate of decomposition are size-dependant, although variable by season, with greater losses in spring and summer and smaller losses in the fall for the smallest pack (Reice, 1974). A study comparing litterbags of different dimensions may be warranted to determine if there is a size effect or if the effect is related to the lotic environment (e.g. effect of current). Crossley and Hoglund (1962) examined different bag sizes (1 vs. 2 dm^2), but only examined microarthropod numbers, which had higher densities in the smaller bags. This difference may have been due to incomplete extraction instead of an actual difference, as the larger volume of litter may have provided more refuges. The differences in decomposition observed with different amounts of litter suggest litterbag dimensions may also be important.

While a wide range of materials has been used effectively to construct the litterbags, it is important to choose a material that is resistant to degradation itself. Bocock and Gilbert (1957) noted this as an advantage of the nylon litterbags relative to an investigation that used a wooden frame with gauze. Even synthetic materials can pose problems. Wiegert (1974) was forced to transfer litter from nylon bags to fiberglass mesh because exposure to the sunlight in the old field environment was weakening the nylon after several weeks.

There have been a few variations on the litterbag concept where a rigid frame is used instead of the flexible screen or fabric mesh. Falconer et al. (1933), Lunt (1935) and Gustafson's (1943) decomposition studies actually pre-dated the litterbag of Bocock and Gilbert (1957) and used instead galvanized wire baskets. Other rigid litterbag variations have included hardware cloth containers, wooden boxes with screen tops and bottoms, purse-like baskets from poultry fencing, PVC cylinders with mesh closures, and wire cylinders with multiple compartments for sub-samples and have been utilized in a variety of environments from uplands to streams (Attiwill, 1968; Benfield et al., 1977; Dangles and Guérold, 1998; Herlitzius, 1983; Kucera, 1959; Moran et al., 1989; Niyogi et al., 2001; Peterson and Rolfe, 1982). By constructing litterbags with a slightly larger pleated upper side, they have the same advantage of rigid containers; the potential for crushing the litter is eliminated while ensuring proper contact with the soil surface (Dwyer and Merriam, 1981). Schipper and Reddy (1995) modified a pore water equilibrator to determine decomposition with depth. The equilibrator was inserted vertically into the soil profile and consisted of 35 parallel cells along 1-cm increments. By filling the cells with litter and having one face of each cell exposed through a 3-mm mesh, it was analogous to 35 miniature litter containers at different depths. While litterbags have been preferred to more rigid containers because they become incorporated into the litter layer, no comparison of cylinder or baskets and litterbags has been conducted to see if there is really an effect on decomposition.

While the majority of litterbags are sealed identically on all four edges (typically sewn), several studies have used safety pins, staples, twist ties or interrupted stitches to close one side and allow access to organisms larger than the mesh size (Deghi et al., 1980; Harper and Bolen, 1995; Kemp et al., 1985; MacLean and Wein, 1978; Maloney and Lambert; 1995; Meyer, 1980; Shanks and Olson, 1961; Witkamp and Crossley, 1966). Davis (1991) did not even seal the litterbags, instead loosely folding the fiberglass window screen to allow entry of macroinvertebrates. In a similar vein, Niyogi et al. (2001) used fine mesh (1 mm) on each end of litter cylinders oriented with the current in mountain streams, but punctured the mesh on the upstream side of the current to allow macroinvertebrate access.

Mesh Size

Litterbag mesh size is probably the most important variable in litterbag construction because of the potential to exclude certain size classes of organisms and introduce errors from loss of undecomposed litter fragments or changes in the microclimate affecting microbial and fungal activity. Bocock (1964) conducted one of the earliest examinations of the effect of mesh size and the potential to use the litterbag method to assess the differential effects of macroinvertebrates on decomposition. Bocock compared decomposition of ash litter in two woodlands with both coarse meshed nylon hairnets (1-cm mesh) and 15 x 15 cm litterbags with 1-mm diameter circular apertures. This technique assumes fine mesh bags represent decomposition from leaching, microbes and soil fauna smaller than 1 mm, while large mesh bags also include the effects of macroinvertebrates on decomposition. Between 10 and 40% of the decomposition was attributed to the action of macroinvertebrates based on fine and coarse mesh comparisons (Bocock, 1964).

As the litterbag technique developed, three and sometimes four mesh sizes were employed to further explore the relative contributions of different sized animals. Anderson

(1973) utilized three mesh sizes (7 mm, 1 mm and 0.175 mm) and “aerial bags” to analyze the relative importance of leaching, microbes, mesofauna and macrofauna during decomposition in a woodland. Aerial bags, which were suspended above the ground with cord, were used along with laboratory analysis for water-soluble components to estimate leaching separate from microbial activity. The assumption was that bacterial and fungal activity would be inhibited by the low moisture content of the suspended bags. The progressively coarser bags would allow access to the litter by either mesofauna or meso- and macrofauna along with the background microbial and leaching losses in the fine mesh. This study found that the relative importance of biotic and abiotic factors were site-dependant, with biota playing a more important role in beech (*Fagus sylvatica* L.) rather than sweet chestnut (*Castanea sativa* Mill.) forests.

Some investigators have attempted to reduce potential bag effects due to microclimate differences by using uniform 1 mm upper mesh with 0.044 mm, 1.1 mm and 10 mm mesh sizes for the bottom openings of litter cylinders to differentially exclude meso and/or macroinvertebrates (Herlitzius, 1983). While this may have allowed some mesoinvertebrates access to the fine meshed litter cylinders, the added variability due to this design was acceptable in order to ensure the same moisture and temperature conditions in the cylinders. The relative importance of invertebrates, microbes and leaching varied by forest and litter type.

Many authors have used multiple mesh sizes for litterbags as an important tool for understanding the role of meso and macroinvertebrates in decomposition in forests (Bocock, 1964; Anderson, 1973; Herlitzius, 1983; Gustafson, 1943), agroecosystems (House and Stinner, 1987; Tian et al., 1992) swamps, marshes (Mason and Bryant, 1975), bogs (Coulson and Butterfield, 1978), streams (Kirby, 1992), rivers (Mathews and Kowalczewski, 1969) and lakes (Brock et al., 1982; Danell and Andersson, 1982) throughout the world. While many studies have shown differences in decomposition rates between large and small mesh, some environments and treatments exhibit no difference in decomposition (House and Stinner, 1987). Similar to excluding different size classes of invertebrates with mesh size, chemicals such as insecticides, fungicides, and anti-microbials have been used to exclude the effects of other biological decomposition factors, with varying results (Douce and Crossley, 1982; Macauley, 1975; Vossbrinck et al., 1979; Witkamp and Crossley, 1966). Clearly, different abiotic and biotic factors have varying importance for decomposition in different ecosystems.

One of the key drawbacks of litterbags is that meshes large enough to allow access by invertebrates, also allow the loss of fragmented litter (Valiela et al., 1985). By running through the usual procedure of packing, transport and installation in the field, and then immediately returning a subset of bags, they assessed and corrected for some of this fragment loss error. They found litter losses due to handling to be small (< 1% initial mass), and insignificant relative to other losses. Even with this initial correction, there is no estimate of what portion of weight loss from large mesh litterbags is due to loss of partially decomposed fragments throughout the course of litter decomposition.

A study of microarthropod numbers suggests that the comparison between litterbags with different mesh sizes may not be as simple as subtraction (Crossley and Hoglund, 1962). They found that mite numbers (*Tydeus* sp.) in litterbags reached 300 per dm^2, while adjacent core samples collected the same day showed 30-50 per dm^2. Apparently, either due to a more stable microclimate or exclusion of predators larger than 2 mm, the bags dramatically increased mite numbers. Further investigation with 1 mm and 2 mm mesh sizes confirmed this effect, but showed no difference between the mesh sizes. While the effect of increased microarthropod numbers may not have had a significant effect on litter weight loss, it suggests the possibility of confounding "bag effects" from temperature, moisture or other ecological factors.

In some studies, mesh size is varied between litter types to prevent smaller sized litter from falling through the mesh, rather than to compare the relative effect of leaching/microbes and different size fauna. In studies examining both hardwood leaf litter and needles such as pine (*Pinus* spp.), cypress (*Taxodium* spp.) or hemlock (*Tsuga* spp.), a smaller mesh size is used for the needles to prevent error from litter falling through the mesh (Gustafson, 1943; Elliott et al., 1993; Hauer et al., 1986). A better technique seems to be using a smaller mesh bottom and larger mesh top for needles as a compromise to the macroinvertebrate exclusion/litter fragment loss dilemma (Rustad and Fernandez, 1998; Kelly and Beauchamp, 1987).

If a single mesh size must be chosen, it remains a balancing act between one that is too large and artificially overestimates decomposition as leaf fragments are lost, or under-estimates it by exclusion of macrodetritivores. Perhaps, instead of considering litterbag results as direct estimates of decomposition, which assumes any material lost is degraded (Pardo et al., 1997), the term "litter processing," as used in the literature from lotic environments, is more appropriate. During the early stages of exposure, the litterbag may accurately measure decomposition as mass is lost predominately as soluble compounds or as the end-products of respiration and consumption. Longer-term weight losses from litterbags are not entirely from litter decay, as fragments smaller than the mesh size are lost via combined biotic and abiotic fragmentation.

Losing litter fragments may not be the only error associated with the litterbag technique, however. St. John (1980) found litterbags to interfere with the contact and colonization of birchwood sticks by fungal vegetative structures. Unconfined wood in a conifer forest of California, decomposed faster than wood in fine or coarse mesh litterbags (1.9 or 3.6 mm).

Surprisingly, fine mesh litterbags showed similar number of fungal structures and faster decomposition rates than the coarse mesh litterbags. St. John attributed this difference to moisture effects, suggesting the fine mesh litterbags retained more moisture allowing longer periods of microbial activity. A "bag effect" on litter moisture content is not consistent. Witkamp and Olson (1963) found higher moisture content in litterbags relative to unconfined litter, while no difference in moisture content was found between three mesh sizes (Anderson, 1973). Lousier and Parkinson (1976) found the reverse in a long-term 3 year study of litterbag litter. Litterbag confined litter was drier than the surrounding litter because the litterbags became "balled up and matted in an artificial fashion," which prevented the litter from becoming incorporated into the litter layer.

Litter Type

The majority of litterbag studies, including the earliest cited examples, have used single litter species, instead of more realistic mixtures (Table 1). While less realistic, single species litter reduces the variability in decomposition rates and allows for comparison of decomposition rates between plant species. These comparisons further enable examination of the chemical properties of the different plant species to assess how litter nutrient levels, accessory chemical content, or litter quality, affects decomposition.

Gustafson (1943) examined both single species and an oak and pine mixture in an early experiment examining confined litter. When the initial decomposition of the pine and oak incubated together were compared to the single species incubation, both the pine and the oak weight losses were greater in the mixture than in single species litter baskets. This result suggests that there can be a synergistic effect of litter mixtures on decomposition and that mixtures more realistically model decomposition than single species litter.

Dwyer and Merriam (1981) used exclusively mixed litter, but used three different mixtures to better simulate natural litter conditions in high, level and low topographic positions of a beech (*Fagus grandifolia* Ehrh.)/maple (*Acer saccharum* Marsh.) forest near Ottawa, Canada (Table 1), using mixtures of intact and aged beech and maple leaves. The high litter was a 1:1 mixture of intact maple and beech leaves, the level litter was a 2:2:1:1 mixture of intact beech, intact maple, aged beech and aged maple respectively. The low litter consisted of equal portions of intact and aged beech and maple leaves. The litter types were crossed with site (high, level and low) to allow both a realistic topographic estimate of decomposition (i.e. corresponding site and litter) and to compare rates between topographic positions (i.e. same litter on different sites). The interaction between the type of litter from low position being easier to decompose and wetter conditions enhanced decay. Similarly to Dwyer and Merriam (1981), Lockaby et al. (1995) varied the litter mixture utilized based on loblolly pine (*Pinus taeda* L.) stands with different agroforestry practices instead of topographic variation. Depending on treatment, the relative proportions of each component were varied; loblolly pine (34-100%), sweet gum (*Liquidambar straciflua* L.; 0-29%), red oak (*Quercus falcata* Michx.; 0-22%), and miscellaneous (0-15%). The pine-dominated treatments had the slowest decomposition rates.

Several studies examined both single species and mixtures of different species of litter (Mudrick et al., 1994; MacLean and Wein, 1978; Day, 1982). When logistically feasible, studying both single species and mixtures of litter is optimal because it allows species comparisons, more realistic estimates of decomposition, and an ability to assess whether there are synergistic relationships that enhance decomposition as suggested by Gustafson (1943).

Study Duration and Sampling Frequency

The duration of litterbag studies varies between a few months to several years depending on the litter and site conditions. Unless the material decomposes rapidly, studies typically last about 1 year (Table 1). Coupling this annual decomposition rate with litter fall can then give indications of other soil-site characteristics such as long-term organic matter accumulation or degradation.

Sampling frequency varies from a single comparison to several times a month, but typical periods are about a month (Table 1). Often, studies will increase sampling frequency during periods when they believe rapid decomposition will occur such as the initial leaching phase or the beginning of a warm or wet season. Conversely, many long-term studies will wait periods of a year or more during the later slower decomposition phase of relatively recalcitrant litter. Bocock (1964) varied the duration of decomposition based on the expected decomposability of the different litter species being examined. The Bocock experiment had three sub-blocks consisting of a) the most rapidly decomposing, b) more resistant and c) most resistant litters, which were exposed for 27, 148 and 267 days respectively. Some litter types were present in all sub-blocks, giving a better idea of the pattern of decomposition for those species. Herlitzius (1983) varied the typical single litterbag placement with several replacements over a certain period of time. By replacing the litter cylinders with fresh cylinders at each monthly collection, Herlitzius created a so-called “From-sequence” that were all placed in the field in December 1977 and collected between 1 and 12 months later, and a “To-sequence” which were all collected in December 1978 and were placed between 1 and 12 months prior. Herlitzius also placed litter cylinders that were only exposed for 1 month and replaced month-by-month to examine initial seasonal decomposition. Gunadi et al. (1998) used a similar "to-" and “from-sequence” technique in an Indonesia forest plantation, but instead called the samples “equal end” and “equal start.”

Most litterbag experiments collect separate bags at each sampling, followed by drying and processing the litter for chemical analyses. Witkamp and Crossley (1966) deviated from the usual method by removing, processing and replacing the same litterbags on a rotational basis. One litterbag in each block was collected weekly and weighed fresh, measured for Cs^{134} and weighed again after drying for arthropod extraction, then returned to the field after 4-5 days. In this system, each litterbag spent 4-5 days in the laboratory every 4-week period with a fifth bag undisturbed throughout the year-long study. Long-term weight loss was similar for disturbed and undisturbed litterbags. Suffling and Smith (1974) examined the possible handling and drying errors from repeated measurements on the same litterbags. Unlike Witkamp and Crossley (1966), they found spillage to be a significant source of error, although repeated drying did not effect decomposition rates. Titus and Malcolm (1999) used the unique attributes of spruce slash decomposition in clear-cut areas to conduct a 7-year study in 2 years. By identifying sites and collecting litter from slash of 0, 2, and 5 years from the time of harvest, they were able to integrate the three litter mass loss curves into a 7-year composite and identify four separate phases of decomposition.

Unconfined Litter

Tethered leaves

Witkamp and Olson (1963) first used the tethered litter technique to examine decomposition paired with litterbags. They compared the rates of weight loss of oak litter in traditional litterbags (1-mm mesh) with that of unconfined tethered oak leaves. The oak leaves were tethered by inserting their petioles in the twists of nylon strings and positioned near the litterbags. Twenty leaves were spaced along each 1 meter cord, which were then staked in parallel lines about 10 cm apart. Some tethered leaves were lain on top of the existing litter, while others were placed directly on the cleared mineral soil surface and then covered with the leaves that had been removed (Witkamp and Olson, 1963). Litter in bags and on strings lost weight at similar rates for the first few months of the study until the tethered leaves' rate of decomposition increased by 2-3 fold relative to the litter in the litterbags. This pattern was attributed to the loss of easily decomposable compounds by microbial activity and the leaching of the soluble products during the first few months, with the increased rate in tethered leaves coinciding with the onset of fragmentation. It is uncertain whether the fragmentation rate in the litterbags was similar to the rate of tethered leaves and the fragments were larger than the 1 mm mesh size, or if the exclusion of macroinvertebrates resulted in less fragmentation. The breakdown of tethered leaves under the litter was 27% faster than of leaves on top of the litter layer (Witkamp and Olson, 1963). This result is thought to be due to the higher moisture content of the leaves under the litter layer creating a more favorable microclimate for microbial decomposition and subsequent fragmentation by detritivores, which typically prefer bacterial- and fungal-conditioned litter to fresh. Moisture content of litter in litterbags and tethered leaves followed the same trend in different forest stands, but litterbags exhibited less variation among stands and seasons. This result suggests the possibility of a microclimatic difference between the methods, and may favor microbial decomposition of litter in the litterbags with more consistent moisture levels. While litterbags with relatively small mesh sizes clearly underestimate decomposition rates (even with the potential bag moisture effect), tethered leaves overestimate decomposition by assuming all fragments are decomposed immediately and completely when they are shredded. Essentially, the combination of the two methods has given scientists the ability to place bounds on the true rate of decomposition, which neither method estimates alone.

Other authors have used the tethered leaf technique in hardwood forests (Anderson, 1973; Lousier and Parkinson, 1976), coniferous forests (Hayes, 1965), freshwater marshes (Polunin, 1982; only for initial leaching stage), and swamps (Yates and Day, 1983). Anderson's (1973) comparison of tethered and litterbag decomposition in a sweet chestnut stand showed much higher variability, especially after 6-8 months with the tethered leaf method. This variation is not unexpected as the fragments are lost, but could make determining statistical differences more difficult. Yates and Day (1983) used a variation of Witkamp and Olson's method, using packs of 10-12 g of leaves tied together at the petioles instead of individual leaves; a method similar to the leaf pack method used in streams. The 1-mm mesh used by Yates and Day (1983) gave lower estimates of decomposition rates than the unconfined litter, a result consistent with Witkamp and Olson's (1963) findings.

Kuehn et al. (1999) used a variation of the unconfined method while studying an emergent macrophyte, *Erianthus giganteus*, in a freshwater marsh. This macrophyte is a tall reed-like perennial with plant shoots that arise from rhizomes to form circular clumps. Since the culms and leaves of the *E. giganteus* remain standing as they decompose, no tether was necessary and culms and leaves were simply tagged and compared over time with initial weights calculated with a model based on litter length and diameter, developed from a subset of culms and from leaves that were collected green. Leaves and culms lost 32% and 25% of their original weight during senescence and early decay. After the 82nd day of the study, most leaves had become detached from the culms and no longer observable. Similar standing litter decomposition studies have been conducted using emergent wetland species such as *Typha, Scirpus, Lythrum*, and *Spartina* (Bärlocher and Biddiscombe, 1996; Davis and van der Valk, 1978; Newell, 1993; Newell et al., 1989; Newell et al., 1995).

Leaf Packs

Leaf pack is a term coined for a bundle of leaves attached to an anchor, typically used in streams to assess decomposition. Often the term "processing" is used instead of decomposition to describe the leaf pack weight loss of the leaf litter to denote the realization that some weight loss is due to fragmentation by varied abiotic and biotic factors and not from decay. Leaf packs are designed to be analogous to natural leaf accumulations that occur in streams soon after litter fall in forested watersheds (Petersen and Cummins, 1974). Litterbags may induce unnatural microbial conditions by reducing current velocity, exchange rates and possibly anaerobic conditions, so leaf packs are generally considered more realistic estimators of leaf litter processing (Petersen and Cummins, 1974). Leaf packs, similar to unconfined litter decomposition in forests (Witkamp and Olson, 1963), have a potential problem of over-estimation of decomposition rates from the loss of undecomposed litter fragments.

Petersen and Cummins (1974) were the first researchers to use the leaf pack methodology. Leaf packs were constructed by tying 10 g of litter to 1 kg bricks to anchor the packs to the streambed. Other investigators have either tied (Sedell et al, 1975; Suberkropp et al;

1976; Triska and Sedell, 1976; Short et al, 1980; Herbst and Reice, 1982; Ryder and Horwitz, 1995) or stapled together leaf litter using buttoneers, nylon I-bars (Reice, 1974; Herbst, 1980; Smith, 1986), and most used bricks as anchors or attachment to steel bars driven into the stream bed (Herbst and Reice, 1982). In a more controlled environment, Grattan and Suberkropp (2001) used leaf disks (11.6 mm diameter) separated by glass beads on stainless steel insect pins attached to corks to examine fungal activity and decomposition in experimental channels.

Cummins et al. (1980) compared the decomposition rates of naturally entrained leaf litter, leaf packs, and 1 mm mesh litterbags in riffles and alcoves of a woodland stream. Natural leaf litter input was controlled (i.e. only basswood litter in the watershed was collected and added at a known weight) and initial weights of naturally entrained packs were estimated by the relationship between leaf length and weight. Artificial leaf packs had similar processing rates to natural litter in stream riffles, although macroinvertebrate shredder biomass was greater in artificial packs. Naturally entrained alcove litter had a similar decomposition rate as litter in litterbags (Cummins et al., 1980).

Leaf pack size was found to effect the rate of litter decomposition in streams, although the relationship was different depending on the season of the study (Reice, 1974). When comparing the decomposition rates of 1, 5, 10, 20 and 40 gram leaf packs, decomposition rates were highest for 1 gram leaf packs in the spring and summer. The converse was true for the fall, with 1-gram leaf packs exhibiting the least weight loss. During the winter, the 5-gram leaf packs exhibited the greatest rate of loss. While the spring and summer results may be easily explained by the higher surface area to mass ratios of the smaller packs, the fall and winter results support the observation that invertebrate feeding is an important component of litter processing in streams (Reice, 1974).

Annual Difference of Litter Standing Crop and Litter Fall

Witkamp and van der Drift (1961) developed a technique for estimating decomposition rates by comparing weights of fresh litter after litter fall to the weight of the previous year's litter just prior to litter fall (standing crop) on a known area. They measured fresh litter dry weights in December from 0.5 m^2 plots and compared these values to the amount remaining just prior to the next year's litter fall. More extensive observations of the disappearance of litter were made through bimonthly weighing in the field, of fresh litter from previously cleaned quadrats (1 m^2). At each bimonthly sampling, approximately 10% was returned to the laboratory and dried to determine the moisture content correction. Over the three years examined, annual decomposition ranged from 65-80% weight loss in a wet year, to 30-35% in a dry year depending on site (Witkamp and van der Drift, 1961). Decomposition during the wet year on the cleaned surface resulted in 70-100% annual mass loss depending on site.

Other authors have used similar estimates of litter disappearance (Gunadi, 1994; Edwards, 1977), but Knutson (1997) is noteworthy for estimating decomposition for an 18-year period in an Iowa deciduous forest. Litter inputs ranged from 504 to 785 $g/m^2/yr$ and decomposition from 337 to 964 $g/m^2/yr$. Decomposition rates were correlated to the amount of the previous year's litter fall and with precipitation during the period of April to June, with extreme events such as droughts and excessive rainfall having the most dramatic effects on decomposition.

Stachurski and Zimka (1976) and Weary and Merriam (1978) used a coring technique to intensively sample the litter layer of a deciduous forests instead of the quadrat method of Witkamp and van der Drift (1961). By collecting 1 cm^2 x 2.5-cm cores or 10 cm^2 x 5 cm monthly during the year and separating the litter, humus and soil components, estimates of litter decomposition were made. Weary and Merriam (1978) reported summer decay rates between 1.48 and 2.19 g/m^2/d and winter rates approaching zero.

Using the annual difference between standing crop and litter fall to estimate decomposition rates has similar advantages and disadvantages to the tethered leaves and other unconfined methods, namely lack of a invertebrate or microclimate bag effect, yet also no way of accounting for fragmentation. The larger samples associated with this method may eliminate the statistical concern with the high variation of the tethered leaf technique. A disadvantage of this method is its assumption that there is no export or import of material during the year. This assumption limits its applicability to terrestrial systems, as many wetland and aquatic systems have significant litter movement due to flooding, tides or currents. Dwyer and Merriam's (1981) study on the effect of topography on litter decomposition showed litter accumulated differentially even within a forest stand, so perhaps movement via wind and other mechanism may even be an important factor in terrestrial systems.

Standard Materials

A variety of standard materials have been used as an alternative to litterbags for studying decomposition in upland, wetland and aquatic environments. The advantages of these methods are the elimination of litter quality and variability issues, allowing direct comparisons of decomposition rates based on soil and site specific environmental factors (Bridgham et al., 1991). While similar trends should be expected in decomposition of standard substrates and litter, the lack of realistic chemical composition and biotic interaction make the estimates unrealistic.

The most widely used standard material for estimating rates of decomposition is cotton fabric strips. The 10 x 35 cm strips are inserted vertically into the soil and then sub-samples are analyzed for loss of tensile strength (Latter and Howson, 1977). Strips are left in the soil until significant decreases in tensile strength are recorded, yet removed before 85% loss in reached. Latter and Howson (1977) found the percent loss of tensile strength to be greater than the percent weight loss for the cotton fabric, suggesting tensile strength is a more sensitive statistic for decomposition. By testing small (2 cm) sub-samples of each cotton strip, decomposition rates can be compared for the litter surface, litter layer, organic layers and underlying mineral horizons. Litterbag and loss of tensile strength of cotton fabric showed similar trends for a study of decomposition in two fens in the Netherlands (Verhoeven and Arts, 1992).

A variety of sites from uplands to aquatic, have been successfully examined using the cotton fabric tensile strength procedures including grassland/woodland/heath (Hill et al., 1985), tundra (Latter and Howson, 1977), bogs/fens (Hill et al., 1985; Verhoeven and Arts, 1992; Verhoeven et al., 1996), pocosins (Bridgham et al., 1991), forested wetlands (Trettin et al, 1996; McLaughlin et al., 2000), and streams (Hildrew et al., 1984). Similarly, a variety of site treatments have been examined including cultivation/disturbance (Bridgham et al., 1991), water chemistry (Verhoeven and Arts, 1992), harvesting/site preparation (Trettin et al., 1996) and fertilization (McLaughlin et al., 2000).

Hill et al. (1985) modeled decomposition rates at a variety of worldwide locations from their own data using cotton fabric and the literature and found that time to 50% tensile strength loss ranged from 3.2 days in an incubator to 1.2 years in the arctic tundra. Even with this range of tensile strength loss, the 85% loss threshold was reached in a few months in temperate and tropical environments. This short time span necessitates conducting several experiments in different seasons to have a reasonable estimate of annual decomposition.

A variety of other forms of standard substrates including filter paper, cellulose sheets, cellophane, pulp fibers, and popsicle sticks have been used in forests, fields, lakes, rivers and inlets (Golley, 1960; Hofsten and Edberg, 1972; Kormondy, 1968; Went, 1959; Witkamp and Van der Drift, 1961). The cotton fabric strips have the advantage of being used more widely than these materials and therefore their results can be directly compared.

Loss of Area/Leaves

Bocock and Gilbert (1957) and Bocock et al. (1960) were among the first investigators to use the litterbag method to track weight loss as a measure of decomposition. In addition to analyzing the litter for loss of mass, they tracked the loss of whole leaves from the litterbags. The combination of these two data sets gave additional insight into the decomposition process and the role of marcoinvertebrates such as earthworms, which remove whole leaves to their burrows for consumption in the hardwood forests of England. The weight per leaf statistic they developed was the pre-cursor and analog to future studies that measured leaf area loss (Heath and Arnold, 1966; Heath et al., 1964; Heath et al., 1966; Edwards and Heath, 1975) and mass loss simultaneously (Forbes and Magnuson, 1980; this study).

Bocock and Gilbert (1957) and Bocock et al. (1960) recorded the number of leaves along with the litter weight of birch (*Betula verrucosa*), linden (*Tilia cordata*), oak (*Quercus robur*) or ash (*Fraxinus excelsior*) depending on the experiment. When the bags were collected, the contents were sorted, with visible animals and extraneous mineral matter being removed, and the number of leaves remaining counted. When leaves had been significantly fragmented, the number of leaves remaining was estimated by the number of recognizable midribs and petioles. After counting, each litter sample was dried and weighed. Depending on the forest stand examined and litter species, losses from both skeletonization and removal of whole leaves were observed. Ash leaflets were removed as whole leaves more often than oak leaves with the conclusion that earthworms, the dominate macrodetritivore, seemed to prefer N-rich ash leaflets to the less palatable oak leaves (Bocock and Gilbert, 1957). Even examining mass remaining on a per-leaf basis, ash leaflets (<25% per leaf) decomposed more quickly than oak leaves (approx. 45% per leaf).

An analog to measuring litter weight is to measure litter area during decomposition. Heath and Arnold (1966), Heath et al. (1966) and Edwards and Heath (1975) were the first researchers to examine the loss of leaf area. Comparing decomposition with two different mesh sizes in a woodland and fallow agricultural field, they assessed area loss visually (Heath et al., 1966) or with a photometer (Heath and Arnold, 1966; Edwards and Heath, 1975) for 50 2.5 cm diameter leaf disks and reported it as "percentage disappearance." Heath et al. (1966) did not record mass losses, so their results are analogous to the results from traditional litterbag studies with multiple mesh sizes examining weight loss. Mass was not measured because the litter was quickly measured for loss of area, then returned to the site instead of replicates being removed. While Heath et al. (1966) were able to assess the relative contribution of leaching/microbes and macroinvertebrates from multiple mesh sizes, they did not measure weight and area loss simultaneously, so they didn't have the added insight of mass per leaf that Bocock and Gilbert (1957) and Bocock et al. (1960) measured.

Stachurski and Zimka (1976) and Forbes and Magnuson (1980) are the most similar reported studies to my study, which measures litter area, perimeter and weight at each sampling.

Forbes and Magnuson measured litter weight loss over a 96-day period in Wisconsin stream with and without coal ash effluent contamination. Leaf area was only measured after the entire 96 days. Leaf area and weight losses were greater in the stream without coal ash effluent. For decomposition in an alder forest in Poland, Stachurski and Zimka (1976) calculated litter area based on known litter weight and weight per leaf disk of a known area ("litter density" expressed as weight of 1 cm^2 of litter) instead of measuring area directly. From an assumption that detritivore activity exclusively caused loss of litter area (i.e. consumption from the edge of the leaf), and microbial decomposition accounted for loss of litter weight not associated with the area loss (i.e. litter thickness/density), Stachurski and Zimka assigned 73.5% of the litter loss to detritivores per year. While detritivores may affect litter area more than litter density, their assumptions seem to general to make the numerical estimates attributed to each group, especially considering the inter-related relations between detritivores and microbes. By choosing intact, undamaged portions of the litter for weight:area measurements and not measuring the leaf margins or partially consumed areas, the calculated litter area may not be accurate. With better technology such as digital cameras, my study was able to measure the entire litter area and perimeter for comparison with weight remaining and avoided the potential errors from calculating area from the weight of sub-samples.

Isotopes

Olson and Crossley (1961) and Witkamp and Crossley (1966) used both a litterbag method and radioactive labels to study decomposition of coniferous and deciduous litter. Olson and Crossley (1961) tested three litter species, several forest types and five radioisotopes. Witkamp and Crossley (1966) focused on the role of arthropods through application of naphthalene at different rates and by reducing their populations by up to 80%. This reduced arthropod population, particularly mites that prey on bacteria, resulted in bacterial populations increasing up to six-fold. By comparing the weight and ^{134}Cs loss from the bags, the arthropod's direct and indirect effects could be assessed. Witkamp and Crossley (1966) tagged a white oak tree with ^{134}Cs and then collected leaves from it at the time of litter fall. Litterbags were constructed using this tagged litter and wet weights, arthropod population, dry weights and radiocesium content were measured using methods detailed in the previous discussion of litterbag methods. Both weight and ^{134}Cs losses showed similar differences between naphthalene treated and control treatments, decay rates were greater in the control. Cesium losses would have occurred through leaching as water moved through the litter. The lower rate of ^{134}Cs and weight loss in the naphthalene treated plots suggest the gross effects of arthropods is litter fragmentation, thus increasing the surface area of the litter for microbial action and leaching.

Several other studies have reported using radioactive isotopes to label litter for laboratory and field experiments. Using an isotope of a more recalcitrant element, as Wilson (1985) and Benner et al. (1985) utilized with ^{14}C in a laboratory study, could also prove a useful tool. Holland and Coleman (1987) used ^{14}C labeled wheat straw in a field study to compare decomposition of incorporated and surface application. A larger proportion of ^{14}C was retained in the surface-applied straw treatment. By measuring ^{14}C, Holland and Coleman avoided potential litterbag effects and could use unconfined litter.

Particulate Organic Matter Size-Density Fractionation

Magid et al. (1997) have suggested an alternative to the litterbag technique of studying decomposition. They propose recovering and analyzing the particulate organic matter (POM) fractions of paired litter amended and unamended soils. Through this comparison, decomposition rates can potentially be estimated. The main advantage Magid et al. (1997) cite is the direct contact of the unconfined litter with the soil and elimination of any bag effects from changes in microclimate or detritivore exclusion. The technique was designed with agricultural systems in mind, so the issue of sediment contamination of litterbag litter is also avoided. Magid et al. (1996) examined the decomposition of ^{14}C-labeled plant residues by using different density and size-density fractionation methods. They were able to largely recover the plant residue from the soil by size density separations. Magid et al. (1997) based their experiment, which compared the POM fractions and densities of soil amended with oilseed rape straw and an unamended control. Magid et al. (1997) were able to differentiate between 0, 4 and 8 t ha^{-1} straw in the light POM fraction (<1.4 g/cm^3), while no differences were observed in the heavy POM fraction. While these results showed the technique's potential, there are serious limitations to the method. By relying on the difference between amended and unamended soil, the applicability is limited to agricultural settings and precludes studies of native ecosystems with litter layers. Another limitation is that the technique discards soluble compounds and particles smaller than 100 µm. This contraindicates the analysis of litter with highly soluble components or necessitates a paired study to address leaching losses.

Respiration

While CO_2 evolution via respiration from decomposers of plant litter is an important product of decomposition, it is not frequently considered an estimate of decomposition. Early decomposition research used CO_2 evolution as a measure of decomposition in laboratory studies of organic materials and leaf litter along temperature and moisture gradients (Lockett, 1937; Melin, 1930; Waksman and Tenney, 1927). While these laboratory studies were useful for elucidating the relationship between temperature, moisture and the action of microbes, they were not realistic because they excluded the effects of invertebrates. Theoretically, for certain systems with little or no leaching or other transport of particulate organic material, respiration should be a good estimate of decay rate. The effect of N on *Spartina alterniflora* decomposition was measured via CO_2 evolution in laboratory percolators and converted to weight loss estimates (Marinucci et al., 1983). Hodkinson (1975b) measured respiration as a component of an energy balance for an abandoned beaver pond ecosystem, with respiration and downstream drift being the ultimate exports. Mason (1976) and Elliott et al. (1993) also used respiration as a tool to assess relative importance of bacteria and fungi in a laboratory study on litter with and without antibiotic treatment, with a paired litterbag field estimate of decomposition. Yavitt (1994) and DeBusk and Reddy (1998) examined net CO_2 flux to answer one of the main questions involving decomposition, whether organic matter is accumulated or lost on a net basis in a (1) mountain bog with an organic soil and (2) along a P fertilization gradient in the everglades.

Magid et al. (1997) report one of the few field studies that explicitly considers respiration rate as an estimate of decomposition. They measured CO_2 fluxes in agricultural fields that received different amounts (0-8 Mg/ha) of oilseed rape straw amendments. They found respiration expressed as cumulative CO_2 evolution gave a good separation of treatment differences. An advantage of using the cumulative CO_2 evolution is that assuming respiration is never negative, it will give a readily acceptable long-term picture of decomposition. Magid et al. (1997) also noted that absolute decomposition rates must be greater than that measured via respiration to account for microbial growth.

Several laboratory and field studies have examined microbial respiration models (Bunnell et al., 1977; Howard and Howard, 1979; Witkamp, 1966). They found effective models relating respiration to several factors including temperature, moisture, O_2, substrate, bacterial density, and weeks since leaf drop. Bunnell et al. (1977) used their model to simulate losses due to microbial respiration relative to litterbag decomposition studies; the model estimates were 70-90% of the measured litterbag decomposition weight losses. These results suggest respiration is a reasonable estimate of decomposition (although underestimated) and useful for predicting seasonal changes in decomposition due to changes in temperature and moisture.

Summary and Preferred Methods

The method chosen to examine decomposition clearly depends on the purpose of the investigation. While a combination of several of the methods described earlier would usually be ideal, the constraints of time and resources typically necessitate that only one or two techniques be employed. Using multiple mesh sized litterbags and perhaps measurement of litter area presents a good option for examining the different factors involved in leaf litter processing. If only one technique is chosen, a relatively large mesh sized litterbag method for estimation of natural site conditions or cotton fabric strips for comparison among different sites may be the best choices.

Factors Affecting Overall Rates of Decomposition

The factors affecting litter decomposition have been examined for many years in terrestrial, aquatic and more recently wetland environments. Extensive review article have been published by Brinson et al. (1981), Webster and Benfield (1986), and Coûteaux et al. (1995) which cover decomposition in freshwater wetlands, aquatic and terrestrial systems respectively. Brinson et al. (1981) also drew on terrestrial studies where wetland specific information was not available. The following will be a relatively cursory overview of the factors affecting decomposition rates. Refer to the above-mentioned review articles for more in-depth analysis.

The two main environmental factors influencing decomposition are moisture and temperature, i.e. climate (Waksman and Gerretsen, 1931). In terrestrial ecosystems, higher moisture levels increase the rates of decomposition (Enríquez et al., 1993), but as upland zones transition to aquatic systems via wetlands, the relationship becomes more complex. In an early laboratory study, Acharya (1935) reported decomposition rates of rice straw decreased from aerobic, to waterlogged, to anaerobic conditions. In wetlands, increased frequency or duration of flooding increases the rate of decomposition (Brinson et al., 1981). Brinson et al. (1981) described an optimal regime of wetting and drying under aerobic conditions that would provide the most rapid rates of decomposition. Alternating anaerobic and aerobic regimes showed somewhat slower decomposition, with continually anaerobic systems even slower. In wetland and aquatic systems, the redox levels must also be considered, not just the presence of water. If dissolved oxygen is present in the water (oxidized), the more efficient aerobic pathways can continue even while flooded. Without dissolved oxygen (reduced), other electron acceptors are used and decomposition is less efficient.

It has long been understood that chemical and biological reactions such as decomposition are affected by temperature (Waksman and Gerretsen, 1931). If temperatures are low enough, a threshold or "biological zero" can be crossed where biologically mediated decomposition ceases, and frozen precipitation prevents leaching. Temperature's effects can best be seen on a global scale, with very slow rates of decomposition in the boreal regions and rapid decomposition in much of the temperate and tropical zones (Brinson et al., 1981). Meentemeyer (1978) used actual evapotranspiration (AET) as a climatic index, combining energy and moisture, for modeling annual decomposition rates at five locations ranging from sub-polar to warm temperate. AET was superior to temperature and precipitation for modeling the annual decay rates.

Litter quality is a term used to describe the ease of decomposition, with high quality litter having relatively labile and palatable elements and low quality litter having more refractory components. These specific litter characteristics affecting quality vary by litter species and even plant part and age of the litter (Heath and Arnold, 1966; Waksman and Tenney, 1928; Webster and Benfield, 1986). Bocock (1964) even used this variable (decomposability) to count leaves remaining in their litterbags when leaves were extensively fragmented, with the more refractory mid-ribs and stems of the hardwood tree leaves used.

Several elemental and molecular analyses have been conducted to help predict and explain the influence of litter quality. The importance of the C:N ratio of organic material has long been understood in decomposition and for assessing soil nitrogen availability. Enríquez et al. (1993) examined P along with C and N, and found positive relationships between N and P content and decomposition rates. Differences in the C:N:P ratios accounted for 89% of the variance in detritus decomposition for plants ranging from unicellular algae to trees.

Considering lignin instead of C in the models did not improve the relationships. In a microcosm study of 8 litter types, Taylor et al. (1989) found C:N ratios to be a better predictor of decomposition rate than lignin content. Despite this observation, lignin can be an important decomposition factor for litter with high lignin content or in the later phases of decomposition (Rutigliano et al., 1996; Taylor et al., 1991).

Other authors have found lignin to be an important factor in decomposition when combined with AET and N content (Meentemeyer, 1978; Melillo et al., 1982). Coûteaux et al. (1993) described two phases of decomposition. In the first phase, decomposition is controlled by the N, P, and S content of non-lignified compounds along with the loss of easily degraded soluble carbohydrates and celluloses. This initial rapid loss has been seen by many researchers as shown in the initial weight loss columns that are summarized in Table 2. Table 2 summarizes studies of litter decomposition in the Southeast United States by percent weight loss after certain periods, single exponential rate constants and half-lives. During the second phase, only highly lignified tissue remains and decomposition is ruled by lignin mass loss dynamics. During the second phase of decomposition, high N concentrations in lignin negatively effect decomposition, opposite of the early phase, while high cellulose concentrations have a positive effect on decomposition (Coûteaux et al., 1993). High polyphenol litter content, similar to lignin, has also been reported to slow decomposition rates (King and Heath, 1967).

Biotic influences on litter decomposition have been grouped by fungi and bacteria, and different size classes of invertebrates. While practically all ecosystems have some decomposition due to each component, the relative magnitude of each one is highly variable (Anderson, 1973; Benfield et al., 1979; Heath et al., 1966; Heath and Arnold, 1966; House and Stinner, 1987; Mason and Bryant, 1975; Merritt and Lawson, 1979; Seastedt, 1984; Tian et al.,

Table 2. Selected confined and unconfined litter decomposition studies in the Southeast United States (Note: numbers in *italics* indicate they were extrapolated from graphs or tables or from maximum weight loss for annual decay rates).

Study	**location**	**environment**	**duration**	**number of samplings**	**litter type**	**% wt. loss (initial period)**	**% wt. loss (3 mo)**	**% wt. loss (6 mo)**	**% wt. loss (12 mo)**	**% wt. loss (max)**	**annual decay rate ($-k\ yr^{-1}$)**	**r^2**	**$T_{1/2}$ (yr)**	**$T_{0.95}$ (yr)**
Forested wetlands														
Baker et al., 2001	Cache River, AR	mixed oak floodplain forest	700 d	14	mixed	-	-	-	-	67.10%	0.686	-	1.01	4.37
			700 d	14	cherrybark oak	-	-	-	-	46.50%	0.416	-	1.67	7.20
	Coosawhatchie River, SC	laurel oak floodplain forest	700 d	14	mixed	-	-	-	-	82.20%	0.841	-	0.82	3.56
			700 d	14	cherrybark oak	-	-	-	-	84.20%	0.788	-	0.88	3.80
	Coosawhatchie River, SC	Sweetgum / Swamp Tupelo floodplain forest	700 d	14	mixed	-	-	-	-	91.90%	0.995	-	0.70	3.01
			700 d	14	cherrybark oak	-	-	-	-	n/a	n/a	-		
	Iatt Creek, LA	Sweetgum / Cherrybark Oak floodplain forest	700 d	14	mixed	-	-	-	-	94.80%	1.268	-	0.55	2.36
			700 d	14	cherrybark oak	-	-	-	-	93.10%	1.330	-	0.52	2.25
Battle and Golladay, 2001	southwest Georgia	cypress-gum swamp, flooded exposed	322 d	10	mixed pond and bald cypress	<2% (1 d)	*20%*	*40-45%*	-	*60%*	1.040	0.840	0.67	2.88
			322 d	10	black gum	>15% (1 d)	*35%*	*40-45%*	-	*50-55%*	0.770	0.770	0.90	3.89
		cypress-gum swamp, multiple flooded exposed	322 d	10	mixed pond and bald cypress	<2% (1 d)	*25%*	*65%*	-	*80%*	2.330	0.570	0.30	1.29
			322 d	10	black gum	>15% (1 d)	*30%*	*50%*	-	*70%*	1.260	0.900	0.55	2.38

Table 2. Selected confined and unconfined litter decomposition studies in the Southeast United States (Note: numbers in *italics* indicate they were extrapolated from graphs or tables or from maximum weight loss for annual decay rates). (Continued).

Study	**location**	**environment**	**duration**	**number of samplings**	**litter type**	**% wt. loss (initial period)**	**% wt. loss (3 mo)**	**% wt. loss (6 mo)**	**% wt. loss (12 mo)**	**% wt. loss (max)**	**annual decay rate ($-k$ yr^{-1})**	**r^2**	**$T_{1/2}$ (yr)**	**$T_{0.95}$ (yr)**
		cypress-gum swamp, permanently flooded	322 d	10	mixed pond and bald cypress	<2% (1 d)	*20%*	*50-55%*	-	*60-65%*	1.470	0.630	0.47	2.04
			322 d	10	black gum	>15% (1 d)	*35%*	*50-55%*	-	*60-65%*	1.040	0.860	0.67	2.88
Brinson, 1977	North Carolina	swamp	392 d	11	cellulose sheets	n/a	*23%*	*>90%*	*100.0%*	100%	-	-	-	-
		swamp	392 d	11	Nyssa aquatica leaves	*18% (14 d)*	*22%*	*55%*	*73.0%*	75%	1.890	-	0.37	1.59
		swamp	392 d	11	Nyssa aquatica twigs	*5% (14 d)*	*7%*	*7%*	*18.0%*	20%	0.280	-	2.48	10.70
		levee	392 d	11	cellulose sheets	n/a	*1%*	*35%*	*100.0%*	100%	-	-	-	-
		river	392 d	11	cellulose sheets	n/a	*80%*	*>99%*	*100.0%*	100%	-	-	-	-
Conner and Day, 1991	Louisiana	crayfish pond	322 d	12	mixture (water tupelo, ash, maple)	*8% (7 d)*	*33%*	*55%*	-	80%	2.081	0.870	0.33	1.44
		impounded swamp	322 d	12	mixture	*14% (7 d)*	*29%*	*35%*	-	56%	0.769	0.980	0.90	3.90
		natural swamp	322 d	12	mixture	*7% (7 d)*	*23%*	*37%*	-	59%	0.832	0.960	0.83	3.60

Table 2. Selected confined and unconfined litter decomposition studies in the Southeast United States (Note: numbers in *italics* indicate they were extrapolated from graphs or tables or from maximum weight loss for annual decay rates). (Continued).

Study	**location**	**environment**	**duration**	**number of samplings**	**litter type**	**% wt. loss (initial period)**	**% wt. loss (3 mo)**	**% wt. loss (6 mo)**	**% wt. loss (12 mo)**	**% wt. loss (max)**	**annual decay rate ($-k\ yr^{-1}$)**	**r^2**	**$T_{1/2}$ (yr)**	**$T_{0.95}$ (yr)**
Cuffney and Wallace, 1987	Georgia, Ogeechee East	high floodplain	525 d	7	sweetgum	*8% (6 d)*	*17%*	*30%*	*78%*	*84%*	1.607	-	0.43	1.86
			525 d	7	water oak	*2% (6 d)*	*10%*	*25%*	*70%*	*77%*	1.205	-	0.58	2.49
		low floodplain	525 d	7	sweetgum	*6% (6 d)*	*20%*	*33%*	*60%*	*80%*	1.023	-	0.68	2.93
			525 d	7	water oak	*3% (6 d)*	*10%*	*23%*	*40%*	*45%*	0.548	-	1.27	5.47
		wet floodplain	525 d	8	sweetgum	*23% (6 d)*	*27%*	*40%*	*67%*	*74%*	1.059	-	0.65	2.83
			525 d	8	water oak	*2% (6 d)*	*8%*	*15%*	*33%*	*40%*	0.402	-	1.73	7.46
	Georgia, Ogeechee West	high floodplain	525 d	7	sweetgum	*8% (6 d)*	*9%*	*30%*	*65%*	*70%*	1.096	-	0.63	2.73
			525 d	7	water oak	*5% (6 d)*	*5%*	*17%*	*50%*	*80%*	0.767	-	0.90	3.91
		low floodplain	525 d	7	sweetgum	*7% (6 d)*	*22%*	*53%*	*65%*	*77%*	1.498	-	0.46	2.00
			525 d	7	water oak	*4% (6 d)*	*12%*	*30%*	*40%*	*64%*	0.584	-	1.19	5.13
		wet floodplain	401 d	7	sweetgum	*27% (6 d)*	*40%*	*75%*	*95%*	*95%*	3.324	-	0.21	0.90
			401 d	7	water oak	*8% (6 d)*	*20%*	*35%*	*60%*	*65%*	0.950	-	0.73	3.15
	Georgia, Black Creek	high floodplain	525 d	7	sweetgum	*4% (6 d)*	*23%*	*30%*	*50%*	*54%*	0.657	-	1.05	4.56
			525 d	7	water oak	*4% (6 d)*	*15%*	*25%*	*40%*	*40%*	0.511	-	1.36	5.86

Table 2. Selected confined and unconfined litter decomposition studies in the Southeast United States (Note: numbers in *italics* indicate they were extrapolated from graphs or tables or from maximum weight loss for annual decay rates). (Continued).

Study	**location**	**environment**	**duration**	**number of samplings**	**litter type**	**% wt. loss (initial period)**	**% wt. loss (3 mo)**	**% wt. loss (6 mo)**	**% wt. loss (12 mo)**	**% wt. loss (max)**	**annual decay rate (-k yr^{-1})**	**r^2**	**$T_{1/2}$ (yr)**	**$T_{0.95}$ (yr)**
		low floodplain	525 d	7	sweetgum	*8% (6 d)*	*32%*	*60%*	*60%*	*67%*	1.059	-	0.65	2.83
			525 d	7	water oak	*1% (6 d)*	*17%*	*30%*	*35%*	*49%*	0.511	-	1.36	5.86
		riffle	401 d	7	sweetgum	*24% (6 d)*	*45%*	*75%*	*92%*	*95%*	3.324	-	0.21	0.90
			401 d	7	water oak	*4% (6 d)*	*25%*	*54%*	*75%*	*82%*	1.717	-	0.40	1.75
		backwater	216 d	5	sweetgum	*22% (6 d)*	*43%*	*70%*	-	82%	2.484	-	0.28	1.21
			216 d	5	water oak	*9% (6 d)*	*27%*	*37%*	-	*46%*	0.950	-	0.73	3.15
	Georgia, Ogeechee River	riffle	299 d	7	sweetgum	*21% (6 d)*	*95%*	*95%*	-	*96%*	21.769	-	0.03	0.14
			299 d	7	water oak	*6% (6 d)*	*80%*	*65%*	-	*87%*	2.520	-	0.28	1.19
		backwater	525 d	9	sweetgum	*21% (6 d)*	*37%*	*60%*	*90%*	*90%*	2.192	-	0.32	1.37
			525 d	9	water oak	*5% (6 d)*	*15%*	*40%*	*70%*	*70%*	1.132	-	0.61	2.65
Day, 1982	Great Dismal Swamp, Virginia	mixed hardwood forest (drier)	712 d	13	mixed oak species	*7% (30 d)*	*10%*	*10%*	50.7%	75.90%	0.294	0.834	2.36	10.19
			712 d	13	mixed species	*7% (30 d)*	*15%*	*10%*	49.3%	69.70%	0.341	0.822	2.03	8.79
			712 d	13	red maple	*0% (30 d)*	*8%*	*6%*	48.2%	53.90%	0.553	0.885	1.25	5.42
		atlantic white cedar forest	712 d	13	atlantic white cedar	*4 % (30 d)*	*12%*	*15%*	37.0%	45.20%	0.340	0.897	2.04	8.81
			712 d	13	mixed species	*9% (30 d)*	*16%*	*17%*	43.2%	57.00%	0.348	0.881	1.99	8.61

Table 2. Selected confined and unconfined litter decomposition studies in the Southeast United States (Note: numbers in *italics* indicate they were extrapolated from graphs or tables or from maximum weight loss for annual decay rates). (Continued).

Study	**location**	**environment**	**duration**	**number of samplings**	**litter type**	**% wt. loss (initial period)**	**% wt. loss (3 mo)**	**% wt. loss (6 mo)**	**% wt. loss (12 mo)**	**% wt. loss (max)**	**annual decay rate $(-k\ yr^{-1})$**	**r^2**	**$T_{1/2}$ (yr)**	**$T_{0.95}$ (yr)**
			712 d	13	red maple	*0 %* *(30 d)*	*16%*	*13%*	40.7%	48.20%	0.403	0.775	1.72	7.43
		maple-gum forest	712 d	13	tupelo gum	*7%* *(30 d)*	*15%*	*14%*	57.0%	66.20%	0.65 (based on yr 1)	0.830	1.07	4.61
			712 d	13	mixed species	*4%* *(30 d)*	*13%*	*10%*	47.0%	54.10%	0.509	0.830	1.36	5.89
			712 d	13	red maple	*2%* *(30 d)*	*11%*	*9%*	46.4%	55.40%	0.468	0.812	1.48	6.40
		cypress forest (wettest)	712 d	13	cypress	*7%* *(30 d)*	*15%*	*12%*	29.7%	31.50%	0.327	0.819	2.12	9.16
			712 d	13	mixed species	*11%* *(30 d)*	*20%*	*23%*	51.2%	58.00%	0.587	0.826	1.18	5.10
			712 d	13	red maple	*4%* *(30 d)*	*10%*	*11%*	49.5%	57.20%	0.541	0.753	1.28	5.54
Elder and Cairns, 1982	Florida, Apalachicola River and floodplain	floodplain forest (dry)	183 d	6	water hickory	4% (30 d)	*23%*	*30%*	-	*30%*	0.621	-	1.12	4.82
			183 d	6	diamondlaef oak	1% (30 d)	*4%*	*7%*	-	*7%*	0.146	-	4.74	20.50
			183 d	6	bald cypress	3% (30 d)	*5%*	*10%*	-	*10%*	0.183	-	3.80	16.40
			183 d	6	tupelo	8% (30 d)	*16%*	*36%*	-	*36%*	0.767	-	0.90	3.91
			183 d	6	sweetgum	6% (30 d)	*16%*	*36%*	-	*36%*	0.804	-	0.86	3.73
			183 d	6	average	4% (30 d)	*15%*	*23%*	-	*23%*	0.511	-	1.36	5.86

Table 2. Selected confined and unconfined litter decomposition studies in the Southeast United States (Note: numbers in *italics* indicate they were extrapolated from graphs or tables or from maximum weight loss for annual decay rates). (Continued).

Study	**location**	**environment**	**duration**	**number of samplings**	**litter type**	**% wt. loss (initial period)**	**% wt. loss (3 mo)**	**% wt. loss (6 mo)**	**% wt. loss (12 mo)**	**% wt. loss (max)**	**annual decay rate (-k yr^{-1})**	**r^2**	**$T_{1/2}$ (yr)**	**$T_{0.95}$ (yr)**
		river or estuary (saturated)	183 d	6	water hickory	*17% (30 d)*	*34%*	*51%*	-	*51%*	1.461	-	0.47	2.05
			183 d	6	diamondlaef oak	*6% (30 d)*	*18%*	*37%*	-	*37%*	0.767	-	0.90	3.91
			183 d	6	bald cypress	*9% (30 d)*	*27%*	42%	-	42%	0.804	-	0.86	3.73
			183 d	6	tupelo	*18% (30 d)*	*62%*	*100%*	-	*100%*	2.045	-	0.34	1.46
			183 d	6	sweetgum	*15% (30 d)*	*40%*	*100%*	-	*100%*	2.009	-	0.35	1.49
		river (2 sites)	183 d	6	average	*13% (30 d)*	*25%*	*63%*	-	*63%*	1.333	-	0.52	2.25
		estuary	183 d	6	average	*16% (30 d)*	*29%*	*74%*	-	*74%*	1.571	-	0.44	1.91
	Sweetyard transect	plot 1 (flooded tupelo stand)	183 d	6	site specific mix.	*20% (30 d)*	66%	*100%*	-	*100%*	2.045	-	0.34	1.46
		plot 2 (flooded cypress stand)	183 d	6	site specific mix.	*24% (30 d)*	*53%*	*62%*	-	*62%*	1.242	-	0.56	2.41
		plot 4 (levee, rel. dry)	183 d	6	site specific mix.	*8% (30 d)*	*27%*	*33%*	-	*33%*	0.694	-	1.00	4.32
	Brickyard transect	plot 12 (floodplain)	183 d	6	site specific mix.	*8% (30 d)*	*33%*	*87%*	-	*87%*	1.790	-	0.39	1.67
		plot 14 (rel. dry)	183 d	6	site specific mix.	*5% (30 d)*	*23%*	*43%*	-	*43%*	0.877	-	0.79	3.42
		plot 15 (floodplain)	183 d	6	site specific mix.	*2% (30 d)*	*18%*	84%	-	84%	1.247	-	0.56	2.40
Hauer et al., 1986	Savannah River Project, South Carolina	thermally impacted swamp	112 d	5	sycamore	*0-5% (7d)*	*30%*	-	-	*30%*	*1.163*	-	*0.60*	*2.58*
			112 d	5	sweetgum	*5% (7 d)*	*35-40%*	-	-	*48%*	*2.133*	-	*0.33*	*1.40*

Table 2. Selected confined and unconfined litter decomposition studies in the Southeast United States (Note: numbers in *italics* indicate they were extrapolated from graphs or tables or from maximum weight loss for annual decay rates). (Continued).

Study	**location**	**environment**	**duration**	**number of samplings**	**litter type**	**% wt. loss (initial period)**	**% wt. loss (3 mo)**	**% wt. loss (6 mo)**	**% wt. loss (12 mo)**	**% wt. loss (max)**	**annual decay rate (-k yr^{-1})**	**r^2**	**T$_{1/2}$ (yr)**	**T$_{0.95}$ (yr)**
			112 d	5	baldcypress	*5-10% (7 d)*	*30%*	-	-	35%	*1.405*	-	*0.49*	*2.13*
		post-thermally impacted swamp	112 d	5	sycamore	*10% (7 d)*	*20%*	-	-	*30%*	*1.163*	-	*0.60*	*2.58*
			112 d	5	sweetgum	*10% (7 d)*	*35%*	-	-	*52%*	*2.394*	-	*0.29*	*1.25*
			112 d	5	baldcypress	*15% (7 d)*	*20%*	-	-	*25%*	*0.938*	-	*0.74*	*3.19*
		control swamp	112 d	5	sycamore	*10-15% (7 d)*	*60%*	-	-	*78%*	*4.938*	-	*0.14*	*0.61*
			112 d	5	sweetgum	*10-15% (7 d)*	*90%*	-	-	*95%*	*9.770*	-	*0.07*	*0.31*
			112 d	5	baldcypress	*10% (7 d)*	*30%*	-	-	*40%*	*1.666*	-	*0.42*	*1.80*
Kemp et al., 1985	Louisiana	swamp forest	322 d	12	hardwood leaves	-	-	-	-	*80%*	*1.826*	-	*0.38*	*1.64*
Shure et al., 1986	South Carolina, floodplain forest	streambank (1974)	ca. 395 d	13	mixed	*12% (30 d)*	*30%*	*50%*	*83.0%*	ca. 85%	*1.754*	-	*0.40*	*1.71*
		30 m from bank (1974)	ca. 395 d	13	mixed	*12% (30 d)*	*32%*	*50%*	*80.0%*	ca. 85%	*1.754*	-	*0.40*	*1.71*
		15-45 m from bank (1975)	ca. 395 d	13	red ash	*13% (30 d)*	*27%*	*49%*	*65.0%*	64-69%	1.170	-	0.59	2.56
			ca. 395 d	13	black gum	*10% (30 d)*	*20%*	*45%*	*60.0%*	64-69%	1.080	-	0.64	2.77
			ca. 395 d	13	sweet gum	*16% (30 d)*	*22%*	*40%*	*52.0%*	52%	0.730	-	0.95	4.10
			ca. 395 d	13	red maple	*19% (30 d)*	*31%*	*51%*	*60.0%*	64-69%	1.020	-	0.68	2.94
		60 m from bank (1974)	ca. 395 d	13	mixed	*17% (30 d)*	*25%*	*35%*	*65.0%*	68%	*1.054*	-	*0.66*	*2.84*

Table 2. Selected confined and unconfined litter decomposition studies in the Southeast United States (Note: numbers in *italics* indicate they were extrapolated from graphs or tables or from maximum weight loss for annual decay rates). (Continued).

Study	**location**	**environment**	**duration**	**number of samplings**	**litter type**	**% wt. loss (initial period)**	**% wt. loss (3 mo)**	**% wt. loss (6 mo)**	**% wt. loss (12 mo)**	**% wt. loss (max)**	**annual decay rate ($-k\ yr^{-1}$)**	**r^2**	**$T_{1/2}$ (yr)**	**$T_{0.95}$ (yr)**
		upland terrace, 90 m (1974)	ca. 395 d	13	mixed	*7% (30 d)*	*17%*	*20%*	*55.0%*	58%	*0.802*	-	*0.86*	*3.73*
Yates and Day, 1983	Great Dismal Swamp, Virginia	mixed hardwood forest (drier)	400 d	12	mixed (site specific) - litterbag	*5% (30 d)*	*8%*	*13%*	*18.0%*	21.50%	0.242	0.891	2.86	12.38
			400 d	12	mixed - leafpack	*0% (30 d)*	*12%*	*13%*	*34.0%*	39.30%	0.498	0.821	1.39	6.02
		atlantic white cedar forest	400 d	12	mixed - litterbag	*11% (30 d)*	*28%*	*35%*	*40.0%*	38.60%	0.488	0.873	1.42	6.14
			400 d	12	mixed - leafpack	*10% (30 d)*	*34%*	*58%*	82.0%	83.60%	1.810	0.681	0.38	1.66
		maple-gum forest	400 d	12	mixed - litterbag	*17% (30 d)*	*20%*	*30%*	*35.0%*	24.90%	0.286	0.614	2.42	10.47
			400 d	12	mixed - leafpack	*10% (30 d)*	*20%*	*39%*	*82.0%*	81.90%	1.710	0.872	0.41	1.75
		cypress forest (wettest)	400 d	12	mixed - litterbag	*7% (30 d)*	*13%*	*20%*	*33.0%*	24.10%	0.276	0.737	2.51	10.85
			400 d	12	mixed - leafpack	*10% (30 d)*	*4%*	*32%*	*70.0%*	79.40%	1.581	0.749	0.44	1.89
Upland field														
Curry, 1969a	Ireland, grassland	surface, 0.003 mm mesh	293 d	6	sward (*Agrositis tenuis* and *Festuca rubra*)	17.5% (28 d)	29.0%	47.2%	-	59.8%	*1.136*	-	*0.61*	*2.64*
		buried, 0.003 mm mesh	293 d	6	sward	21% (28 d)	33.9%	53.4%	-	70.6%	*1.526*	-	*0.45*	*1.96*
		surface, 0.5 mm mesh	293 d	6	sward	19.2% (28 d)	45.1%	47.4%	-	62.4%	*1.219*	-	*0.57*	*2.46*

Table 2. Selected confined and unconfined litter decomposition studies in the Southeast United States (Note: numbers in *italics* indicate they were extrapolated from graphs or tables or from maximum weight loss for annual decay rates). (Continued).

Study	**location**	**environment**	**duration**	**number of samplings**	**litter type**	**% wt. loss (initial period)**	**% wt. loss (3 mo)**	**% wt. loss (6 mo)**	**% wt. loss (12 mo)**	**% wt. loss (max)**	**annual decay rate ($-k\ yr^{-1}$)**	**r^2**	**$T_{1/2}$ (yr)**	**$T_{0.95}$ (yr)**
		buried, 0.5 mm mesh	293 d	6	sward	20.6% (28 d)	35.5%	55.4%	-	65.5%	*1.327*	-	*0.52*	*2.26*
		surface, 7 mm mesh	293 d	6	sward	21.6% (28 d)	43.2%	55.7%	-	63.4%	*1.253*	-	*0.55*	*2.39*
		buried, 7 mm mesh	293 d	6	sward	20.2% (28 d)	35.2%	55.6%	-	72.5%	*1.609*	-	*0.43*	*1.86*
Heath et al., 1966*	fallow pasture (buried 2.5 cm), Rothamsted, England	Exp. 1, 0.5 mm mesh	424 d	4	beech	1.09% (49 d)	*1.5%*	1.93%	*14%*	22.18%	*0.216*	-	*3.21*	*13.87*
			424 d	4	oak	3.02% (49 d)	*4%*	6.52%	*23%*	33.22%	*0.348*	-	*1.99*	*8.61*
			240 d	4	elm	85.72% (49 d)	*87%*	88.52%	*91%*	93.38%	*4.132*	-	*0.17*	*0.73*
			424 d	4	birch	26.37% (49 d)	*32%*	41.31%	*68%*	87.03%	*1.760*	-	*0.39*	*1.70*
			424 d	4	linden	27.30% (49 d)	*30%*	38.58%	*64%*	81.87%	*1.471*	-	*0.47*	*2.04*
			424 d	4	maize	46.16% (49 d)	*55%*	72.54%	*88%*	98.87%	*3.862*	-	*0.18*	*0.78*
		Exp. 1, 7 mm mesh	424 d	4	beech	2.18% (49 d)	*3%*	5.44%	*70%*	90.00%	*1.984*	-	*0.35*	*1.51*
			240 d	4	oak	16.67% (49 d)	*25%*	39.60%	-	93.81%	*4.234*	-	*0.16*	*0.71*
			49 d	4	elm	99.84% (49 d)	-	-	-	99.84%	*47.988*	-	*0.01*	*0.06*
			182 d	4	birch	34.55% (49 d)	*58%*	96.15%	-	96.15%	*6.537*	-	*0.11*	*0.46*

* note: % area loss, not % weight loss

Table 2. Selected confined and unconfined litter decomposition studies in the Southeast United States (Note: numbers in *italics* indicate they were extrapolated from graphs or tables or from maximum weight loss for annual decay rates). (Continued).

Study	**location**	**environment**	**duration**	**number of samplings**	**litter type**	**% wt. loss (initial period)**	**% wt. loss (3 mo)**	**% wt. loss (6 mo)**	**% wt. loss (12 mo)**	**% wt. loss (max)**	**annual decay rate (-k yr^{-1})**	**r^2**	**$T_{1/2}$ (yr)**	**$T_{0.95}$ (yr)**
			240 d	4	linden	54.53% (49 d)	*68%*	90.95%	-	99.99%	*14.017*	-	*0.05*	*0.21*
			240 d	4	maize	87.04% (49 d)	*91%*	98.63%	-	99.94%	*7.786*	-	*0.09*	*0.38*
		Exp. 2, 0.5 mm mesh	367 d	12	ash	0.01% (7 d)	22.76 %	*33%*	92.95%	92.95%	*2.639*	-	*0.26*	*1.13*
			367 d	12	elm	0.35% (7 d)	28.39 %	*43%*	91.55%	91.55%	*2.459*	-	*0.28*	*1.22*
			367 d	12	beet	0.72% (7 d)	80.08 %	*89%*	99.33%	99.33%	*4.982*	-	*0.14*	*0.60*
			367 d	12	maize	0.01% (7 d)	19.21 %	*35%*	89.40%	89.40%	*2.234*	-	*0.31*	*1.34*
			50 d	6	lettuce	25.75% (7 d)	-	-	-	99.27%	*35.940*	-	*0.02*	*0.08*
House and Stinner, 1987	North Carolina, no-tillage corn field	0.05 mm mesh	120 d	4	crimson clover	*44% (30 d)*	*73%*	-	-	*74%*	4.100	-	*0.17*	*0.73*
			120 d	4	hairy vetch	*44% (30 d)*	*73%*	-	-	*74%*	4.100	-	*0.17*	*0.73*
			120 d	4	rye	*20% (30 d)*	*52%*	-	-	*54%*	2.364	-	*0.29*	*1.27*
		0.2 mm mesh	120 d	4	crimson clover	*44% (30 d)*	*72%*	-	-	*73%*	3.985	-	*0.17*	*0.75*
			120 d	4	hairy vetch	*47% (30 d)*	*68%*	-	-	*71%*	3.768	-	*0.18*	*0.80*
			120 d	4	rye	*19% (30 d)*	*48%*	-	-	*52%*	2.234	-	*0.31*	*1.34*
		1.0 mm mesh	120 d	4	crimson clover	*43% (30 d)*	*69%*	-	-	*71%*	3.768	-	*0.18*	*0.80*
			120 d	4	hairy vetch	*50% (30 d)*	*71%*	-	-	*73%*	3.985	-	*0.17*	*0.75*

Table 2. Selected confined and unconfined litter decomposition studies in the Southeast United States (Note: numbers in *italics* indicate they were extrapolated from graphs or tables or from maximum weight loss for annual decay rates). (Continued).

Study	**location**	**environment**	**duration**	**number of samplings**	**litter type**	**% wt. loss (initial period)**	**% wt. loss (3 mo)**	**% wt. loss (6 mo)**	**% wt. loss (12 mo)**	**% wt. loss (max)**	**annual decay rate ($-k\ yr^{-1}$)**	**r^2**	**$T_{1/2}$ (yr)**	**$T_{0.95}$ (yr)**
			120 d	4	rye	*17% (30 d)*	*47%*	-	-	*54%*	*2.364*	-	*0.29*	*1.27*
		5.0 mm mesh	120 d	4	crimson clover	*49% (30 d)*	*66%*	-	-	*71%*	*3.284*	-	*0.21*	*0.91*
			120 d	4	hairy vetch	*56% (30 d)*	*71%*	-	-	*73%*	*3.985*	-	*0.17*	*0.75*
			120 d	4	rye	*22% (30 d)*	*43%*	-	-	*46%*	*1.876*	-	*0.37*	*1.60*
Noyd et al., 1997	taconite mine, Minnesota	no amendment	457 d	8	mixed prairie species	*30-33% (30 d)*	*51%*	*58%*	*68%*	*72%*	*1.017*	-	*0.68*	*2.94*
		22.4 Mg ha-1 composted yard waste	457 d	8	mixed native prairie species	*30-33% (30 d)*	*53%*	*55%*	*63%*	*69%*	*0.936*	-	*0.74*	*3.20*
		44.8 Mg ha-1 composted yard waste	457 d	8	mixed native prairie species	*30-33% (30 d)*	*53%*	*55%*	*58%*	*63%*	*0.795*	-	*0.87*	*3.77*
Parker, 1962	Iowa	corn field, surface	140 d	7	cornstalk residue	5.3% (5 d)	*36%*	-	-	50.2%	*1.819*	-	*0.38*	*1.65*
		corn field, buried 15 cm	145 d	7	cornstalk residue	6.1% (5 d)	*58%*	-	-	65.2%	*2.659*	-	*0.26*	*1.13*
Wiegert and Evans, 1964	Southern Michigan	old field	367 d	4	Poa compressa	25% (61 d)	*29%*	47.2%	54.5%	54.5%	*0.784*	-	*0.88*	*3.82*
			367 d	4	Aristida purpurascens	6.1 % (61 d)	*12%*	35.0%	36.9%	36.9%	*0.458*	-	*1.51*	*6.54*
			367 d	4	Lespedeza capitata	1.22% (61 d)	*4%*	17.2%	22.7%	22.7%	*0.256*	-	*2.70*	*11.69*
			367 d	4	Solidago rigida	28.1% (61 d)	*35%*	62.6%	68.1%	68.1%	*1.137*	-	*0.61*	*2.63*

Table 2. Selected confined and unconfined litter decomposition studies in the Southeast United States (Note: numbers in *italics* indicate they were extrapolated from graphs or tables or from maximum weight loss for annual decay rates). (Continued).

Study	**location**	**environment**	**duration**	**number of samplings**	**litter type**	**% wt. loss (initial period)**	**% wt. loss (3 mo)**	**% wt. loss (6 mo)**	**% wt. loss (12 mo)**	**% wt. loss (max)**	**annual decay rate (-k yr^{-1})**	**r^2**	**$T_{1/2}$ (yr)**	**$T_{0.95}$ (yr)**
Freshwater marsh														
Atkinson and Cairns, 2001	Western Virginia	20-yr old created depressional wetland	507 d	5	Scirpus cyperinus	*8% (2 d)*	-	*17%*	19%	23%	*0.188*	-	*3.68*	*15.91*
			507 d	5	Typha latifolia	*7% (2 d)*	-	*22%*	28%	35%	*0.310*	-	*2.23*	*9.65*
		2-yr old created depressional wetland	507 d	5	Scirpus cyperinus	*5% (2 d)*	-	*7%*	9%	15%	*0.117*	-	*5.92*	*25.59*
			507 d	5	Typha latifolia	*7% (2 d)*	-	*22%*	20%	32%	*0.278*	-	*2.49*	*10.78*
Boyd, 1970	South Carolina	freshwater marsh	180 d	8	Typha latifolia (suspended)	*5% (20 d)*	*10%*	*10-15%*	-	*10-15%*	*0.214-0.330*	-	*2.1-3.2*	*9.1-14.0*
			180 d	8	Typha latifolia (submerged)	*20% (20 d)*	*30%*	*45%*	-	*45%*	*1.213*	-	*0.57*	*2.47*
Davis, 1991	Florida, everglades	nutrient enriched	730 d	7	Cladium jamaicense	*10% (30 d)*	*20%*	*27%*	*40%*	*53%*	*0.378*	-	*1.83*	*7.93*
			730 d	7	Typha domingensis	*10% (30 d)*	*23%*	*35%*	*60%*	*65%*	*0.525*	-	*1.32*	*5.70*
		transitional	730 d	7	Cladium jamaicense	*8% (30 d)*	*12%*	*12%*	*25%*	*42%*	*0.273*	-	*2.54*	*10.99*
			730 d	7	Typha domingensis	*10% (30 d)*	*14%*	*20%*	*32%*	*53%*	*0.378*	-	*1.83*	*7.93*
		control marsh	730 d	7	Cladium jamaicense	*10% (30 d)*	*16%*	*22%*	*42%*	*35%*	*0.273*	-	*2.54*	*10.99*
			730 d	7	Typha domingensis	*10% (30 d)*	*12%*	*18%*	*35%*	*47%*	*0.318*	-	*2.18*	*9.43*

Table 2. Selected confined and unconfined litter decomposition studies in the Southeast United States (Note: numbers in *italics* indicate they were extrapolated from graphs or tables or from maximum weight loss for annual decay rates). (Continued).

Study	**location**	**environment**	**duration**	**number of samplings**	**litter type**	**% wt. loss (initial period)**	**% wt. loss (3 mo)**	**% wt. loss (6 mo)**	**% wt. loss (12 mo)**	**% wt. loss (max)**	**annual decay rate (-k yr^{-1})**	**r^2**	**$T_{1/2}$ (yr)**	**$T_{0.95}$ (yr)**
Kittle et al., 1995	N West Virginia, marshes with AMD	pH 3.85 marsh	155 d	1	common rush	-	-	-	-	*48%*	*1.541*	-	*0.45*	*1.94*
			155 d	1	woolgrass	-	-	-	-	*37%*	*1.089*	-	*0.64*	*2.75*
			155 d	1	cattail	-	-	-	-	*65%*	*2.474*	-	*0.28*	*1.21*
			155 d	1	calamus	-	-	-	-	*58%*	*2.044*	-	*0.34*	*1.47*
			155 d	1	rice cutgrass	-	-	-	-	*67%*	*2.613*	-	*0.27*	*1.15*
		pH 4.83 marsh	155 d	1	common rush	-	-	-	-	*36%*	*2.542*	-	*0.27*	*1.18*
			155 d	1	woolgrass	-	-	-	-	*32%*	*0.585*	-	*1.18*	*5.12*
			155 d	1	cattail	-	-	-	-	*55%*	*1.882*	-	*0.37*	*1.59*
			155 d	1	calamus	-	-	-	-	*50%*	*1.633*	-	*0.42*	*1.83*
			155 d	1	rice cutgrass	-	-	-	-	*53%*	*1.779*	-	*0.39*	*1.68*
		pH 7.93 marsh	155 d	1	common rush	-	-	-	-	*59%*	*2.101*	-	*0.33*	*1.43*
			155 d	1	woolgrass	-	-	-	-	*43%*	*1.325*	-	*0.52*	*2.26*
			155 d	1	cattail	-	-	-	-	*63%*	*2.343*	-	*0.30*	*1.28*
			155 d	1	calamus	-	-	-	-	*65%*	*2.474*	-	*0.28*	*1.21*
			155 d	1	rice cutgrass	-	-	-	-	*77%*	*3.463*	-	*0.20*	*0.87*
Kuehn and Suberkropp, 1998	Alabama	freshwater fringing marsh	*780 d*	15	Juncus effusus (standing)	*2-3% (10 d)*	*10%*	*25-30%*	*30-35%*	49%	0.400	0.990	1.73	7.49
Kuehn et al., 1999	Alabama	freshwater wetland	190 d	7	Erianthus giganteus (plumegrass) culms	*18% (30 d)*	*23%*	-	-	25%	*0.553*	-	*1.25*	*5.42*
			82 d	5	E. giganteus leaves	*6% (30 d)*	-	-	-	32%	*1.718*	-	*0.40*	*1.74*

Table 2. Selected confined and unconfined litter decomposition studies in the Southeast United States (Note: numbers in *italics* indicate they were extrapolated from graphs or tables or from maximum weight loss for annual decay rates). (Continued).

Study	**location**	**environment**	**duration**	**number of samplings**	**litter type**	**% wt. loss (initial period)**	**% wt. loss (3 mo)**	**% wt. loss (6 mo)**	**% wt. loss (12 mo)**	**% wt. loss (max)**	**annual decay rate (-k yr^{-1})**	**r^2**	**$T_{1/2}$ (yr)**	**$T_{0.95}$ (yr)**
Moran at al., 1989	Okefenokee Swamp, Georgia	carex wetland (1985)	*325 d*	8	Carex walteriana	*18% (30 d)*	*21%*	25%	-	35%	*0.484*	-	*1.43*	*6.19*
		carex wetland (1986)	*225 d*	4	Carex walteriana	*25% (30 d)*	*37%*	43%	-	48%	*1.062*	-	*0.65*	*2.82*
Schipper and Reddy, 1995	Florida, Typha marsh	floodwater	84 d	5	Typha sp.	*27-31% (7 d)*	-	-	-	-	*1.5-2.5*	-	*0.3-0.5*	*1.2-2.0*
		soil/water interface	84 d	5	Typha sp.	*26-30% (7 d)*	-	-	-	-	*1.5-2.2*	-	*0.3-0.5*	*1.4-2.0*
		10 cm deep	84 d	5	Typha sp.	*26-30% (7 d)*	-	-	-	-	*0.9-1.8*	-	*0.4-0.8*	*1.7-3.3*
		20 cm deep	84 d	5	Typha sp.	*22-27% (7 d)*	-	-	-	-	*0.7-1.4*	-	*0.5-1.0*	*2.1-4.3*
Permanently ponded														
Carpenter et al., 1983	Lake Anna, Virginia	AMD and natural arms of a reservior	99 d	5	flowering dogwood (control sites only)	31.9% (6 d)	*90%*	-	-	*90%*	9.935	-	0.07	0.30
			149 d	6	white oak	20.7% (6 d)	*55%*	-	-	*60%*	1.826	-	0.38	1.64
			149 d	6	soft rush	17.8% (6 d)	*35%*	-	-	*45%*	1.169	-	0.59	2.56
			99 d	5	yellow birch	29.6% (6 d)	*65%*	-	-	*65%*	3.068	-	0.23	0.98

Table 2. Selected confined and unconfined litter decomposition studies in the Southeast United States (Note: numbers in *italics* indicate they were extrapolated from graphs or tables or from maximum weight loss for annual decay rates). (Continued).

Study	**location**	**environment**	**duration**	**number of samplings**	**litter type**	**% wt. loss (initial period)**	**% wt. loss (3 mo)**	**% wt. loss (6 mo)**	**% wt. loss (12 mo)**	**% wt. loss (max)**	**annual decay rate ($-k$ yr^{-1})**	**r^2**	**$T_{1/2}$ (yr)**	**$T_{0.95}$ (yr)**
Harper and Bolen, 1995	North Carolina	blackwater impoundment 1	136 d	4	longleaf pine	9.8% (21 d)	12%	-	-	39.80%	*1.363*	-	*0.51*	*2.20*
			136 d	4	sweetgum	35.3% (21 d)	37%	-	-	58%	*2.330*	-	*0.30*	*1.29*
			136 d	4	flowering dogwood	35.1% (21 d)	45%	-	-	68.20%	*3.077*	-	*0.23*	*0.97*
		blackwater impoundment 2	136 d	4	longleaf pine	8.9% (21 d)	8%	-	-	40.50%	*1.394*	-	*0.50*	*2.15*
			136 d	4	sweetgum	33.3% (21 d)	38%	-	-	62.10%	*2.606*	-	*0.27*	*1.15*
			136 d	4	flowering dogwood	36.2% (21 d)	49%	-	-	74.10%	*3.628*	-	*0.19*	*0.83*
		natural pond	136 d	4	longleaf pine	9.8% (21 d)	13%	-	-	41%	*1.417*	-	*0.49*	*2.11*
			136 d	4	sweetgum	33.5% (21 d)	34%	-	-	56.90%	*2.260*	-	*0.31*	*1.33*
			136 d	4	flowering dogwood	30.4% (21 d)	47%	-	-	68.30%	*3.085*	-	*0.22*	*0.97*
Hill, 1985	Texas	Reservior wetland	154 d	10	Nelumbo leaves	*10-15% (7d)*	*80%*	-	-	*90%*	3.945	0.671	0.18	0.76
			154 d	10	Nelumbo petioles	*10-15% (7d)*	*35-40%*	-	-	*45%*	1.205	0.428	0.58	2.49
			154 d	10	Typha leaves	*10-15% (7d)*	*45-50%*	-	-	*55%*	1.717	0.726	0.40	1.75
			154 d	10	Ludwigia (whole plant)	*10-15% (7d)*	*45-50%*	-	-	*55%*	1.826	0.681	0.38	1.64

1992). Each component is difficult to predict since many environmental and litter variables influence the biota such as litter quality, litter age, moisture, temperature, pH, soils, and salinity. While each of these biotic components are considered separately, they are often strongly interrelated. Invertebrates prefer feeding on microbially conditioned litter to fresh litter (Bärlocher and Kendrick, 1975; Cummins et al., 1973) or litter components can effect microbial decomposition, such as tannins inhibiting fungi growth (Harrison, 1971). The fragmentation and re-deposition as feces of the litter by the invertebrates also assists microbial decay by increasing the surface area.

Several methods have been used to compare the relative magnitude of the different decomposer biota. One of the earliest and most common techniques was to vary the size of the litterbag mesh (Table 1). The theory is that progressively smaller mesh sizes would exclude different size classes of detritivores. While these results are useful for assessing the relative importance of different size-classes, accurately estimating the contribution of each size class is limited by confounding bag effects on moisture content, predator-prey effects, and smaller mesh sizes retaining smaller fragments of litter. Insecticide treatment of some litterbags relative to untreated bags with the same mesh size reduces the litterbag effects, but changes in the relationships in the litter community also make this an unrealistic estimate (Witkamp and Crossley, 1966). To compare the relative contribution of fungi and bacteria to decomposition rates, antibiotic treatments (Elliott et al., 1993) and comparison of fungal and bacteria abundance (Holland and Coleman, 1987) have been effective. Still, with the complex relationships and symbiotic conditioning of litter and fragmentation by micro and macroorganisms respectively, these methods suggest relative importance, but not realistic estimates of actual proportions.

While typically secondary to biological factors, physical forces can play an important role in decomposition. Leaching of soluble compounds has been shown to be a significant loss (10-20%) during early decomposition (Table 2). Some investigators even pre-leach the litter they examine to remove this factor (Mason and Bryant, 1975; Benfield et al., 1977; Kaushik and Hynes, 1971). In tidal systems, flushing has been shown as an important factor in removal of detritus (White and Trapani, 1982). In wetlands seasonal flooding may have a similar effect. Considering the documented weakening and bleaching of cotton fabric by sunlight, exposure/shading may even have also some effect on decomposition.

With so many different factors influencing decay rates and different factors being more or less important in different ecosystems, it is difficult to predict site-specific decomposition. While some researchers have been successful at predicting decomposition rates within a climatic zone or with small data sets, there is typically a large variation between ecosystems (Vogt et al., 1986). By combining climatic and litter quality data in models (AET and lignin), Meentemeyer (1978) was able to explain 72% of the variation versus 51% being explained by latitude alone. With the added factor of frequency and duration of flooding for wetland systems, there are no models that accurately predict decomposition. Clearly, decomposition needs to be directly measured with examination of the relative importance of each of these factors.

Models of Decomposition

There have been many models used to describe decomposition over time. The most common model used is an exponential model, $Y=Y_o e^{-kt}$ (Jenny et al., 1949). Typically, results are then compared based on the rate constant, k. This model works well for many systems and was used by Brinson et al. (1981) to compare rates among different wetland systems in their review article. Some systems do not match the exponential model at all or initially during the rapid leaching phase of decomposition.

The initial rapid loss of mass attributed to leaching can pose difficulties for the models used to describe the pattern of decomposition. Laboratory leaching of litter has show significant differences in initial leaching depending on litter type and size. Harrison and Mann (1975) found initial leaching of litter particles smaller than 1 mm to be double that of whole leaves. Many deciduous litter species such as aspen (*Populus tremuloides* Michx.), ash (*Fraxinus excelsior*), and alder (*Alnus glutinosa*) produced relatively large weight losses of 20-25%, 22%, and 12% after 1 day of leaching, respectively. Conifers and some low litter quality deciduous species, such as lodgepole-jack *pine (Pinus contorta* Loud. x *P. banksiana* Lamb.), Scots pine (*Pinus silvestris*), beech (*Fagus silvatica*) and oak (*Quercus robur*) are relatively resistant to leaching weight losses, <5%, 1%, 3.8%, and 7% weight loss after 1-2 days, respectively (Nykvist, 1959a; 1959b; 1959c; Taylor and Parkinson, 1988). Some researchers have pre-leached the litter and found the results better match the exponential models (Benfield et al., 1977; Gasith and Lawacz, 1976; Kaushik and Hynes, 1971; Mason and Bryant, 1975). Mason and Bryant (1975) even found a linear model satisfactory with pre-leached *Phragmites* and *Typha* litter. Similar to results of Mason and Bryant (1975) using pre-leached litter, several studies in tropical forests have found decomposition follows a linear pattern after an initial phase of rapid leaching, although exponential decay constants were still calculated (Edwards, 1977). Other researchers have used more complex mathematical models (Elliott et al., 1993; Kelly and Beachamp, 1987; House and Stinner, 1987) or included environmental variables such as temperature or precipitation (Bell et al., 1978; Morris and Lajtha, 1986) to better fit the data.

Very few studies examine decomposition for periods longer than one year (Table 1 and 2). Titus and Malcolm (1999) studied the decomposition of Sitka spruce slash over a seven-year period. They identified four distinct phases of decomposition each fitted with a different exponential model with decay constants ranging from 0.51 yr^{-1} for the first 105 days to 0.10 yr^{-1} for years 6 and 7. These results suggest that while the single exponential model is the most common and convenient for comparing results, it may not be an accurate model of long-term decomposition. It also indicates that studies of relatively short duration may overestimate decay rates if the litter is still in the initial rapid phase of decomposition.

Decomposition in Wetlands and Surrounding Environments of the Southeast United States

In this section, I will examine in detail the findings of litterbag and unconfined litter studies in the Southeast United States in similar environments to the created and natural reference wetlands examined in my study. Therefore, sites similar to the created wetland moisture gradient from an upland field down to intermittently to permanently flooded non-tidal freshwater marsh and the natural freshwater non-tidal forested wetlands will be examined (Table 2). Since there are few studies of decomposition in created wetlands, occasionally other systems such as agricultural fields or systems outside the geographical area have been used for comparison.

Considering the lack of agreement in the literature on which model to use to describe the expected pattern of decomposition, Table 2 provides both weight loss estimates after different periods of time, from the initial weight loss to the maximum observed, along with single-exponential annual rate constants with half-lives and estimated time to 95% weight loss. Considering the four separate rates described by Titus and Malcolm (1999) for Sitka spruce decomposition, caution should be used when extrapolating decomposition rates beyond the duration of the study.

Non-tidal Forested Wetlands

There are relatively good estimates of the rates of decomposition in floodplain forests and swamps of the southeast United States (Table 2). Differences in decomposition rates have been examined along gradients from streambank to upland forest, between different forest types, with mixtures and single species litter and with various human disturbances (Table 2). Even within similar ecosystems in the same geographic area, there is considerable variation with decay rates ranging from 0.242 to 2.081 yr^{-1} (2.86 and 0.33 yr $T_{1/2}$ respectively) for mixed litter. As would be expected, single species litter showed greater variation and ranged from 0.146 to 9.770 yr^{-1} or $T_{1/2}$ of 4.74 and 0.07 yr respectively. The overall average of 78 litter/site combinations found in literature was 1.17 yr^{-1} and is consistent with estimates calculated by Lockaby and Walbridge (1998) of 1.01 yr^{-1} which together represent half-lives of between 0.59 and 0.69 yr.

Flooding has a positive or negative effect on decomposition in floodplain forests depending on the frequency and duration (Baker et al., 2001; Battle and Gollady, 2001). Multiple brief flooding events stimulate decomposition as seen at the Iatt Creek and Coosawhatchie River sweetgum/swamp tupelo forests reported by Baker et al. (2001) and cypress-gum swamp of Battle and Golladay (2001). Presumably due to anaerobic conditions developing, long periods of flooding have an inhibitory effect on decomposition as seen for the Cache River (Baker et al., 2001), and for single long flood events or permanently flooded sites (Battle and Gollady, 2001).

Moisture's influence on decomposition has also been examined along topographic gradients in floodplains and swamps (Brinson, 1977; Cuffney and Wallace, 1987; Day, 1982; Elder and Cairns, 1982; Shure et al., 1986; Yates and Day, 1983). In general, the higher and drier topographic sites such as levees or mixed hardwood forests have slower rates of decomposition (Table 2). When decomposition is also estimated in permanently inundated rivers or bays with associated forests, the inhibitory effect of flooding seen by Baker et al. (2001) and Battle and Golladay (2001) is not observed (Brinson, 1977; Cuffney and Wallace, 1987; Elder and Cairns, 1982). With currents in the rivers, streams and bays, conditions likely never became sufficiently anaerobic to limit decomposition.

Upland Fields

There has been little litter decomposition research on pastures or fields similar to the upland area examined in this study. For this reason, additional studies of grasslands from different geographical regions in the temperate zone were examined (Table 2). There was a wide range in annual decay rates reported for upland fields (from 0.216 to 47.99) which corresponds to half-lives of 3.21, and 0.01 years respectively (Table 2). If only grasses and legumes typical for pastures are examined, the range narrows to between 0.256 yr^{-1} for *Lespedeza capitata* and 4.100 yr^{-1} for crimson clover or hairy vetch. Heath et al. (1966) were the only investigators to examine tree leaf litter in a pasture environment. They found a wide range of decomposition rates, with elm litter in coarse mesh litterbags essentially disappearing in 49 days and >75% of beech litter in fine mesh bags remaining after 424 days (Table 2).

Since some of the studies examined were simulating incorporation of crop residue into the soil, some litterbags were buried (Curry, 1969a; Heath et al., 1966; Parker, 1962; Sain and

Broadbent, 1977). Burial of litter increases the decomposition rate relative to surface-applied litter (Curry, 1969a; Parker 1962; Sain and Broadbent, 1977). Since the litter used in my study was surface-applied, buried litter was not used to calculate average values. The average reported (Table 2) annual decay coefficient of coarse mesh litterbags containing grasses and legumes typical for pastures was 1.43 yr^{-1} or a half-life of 0.48 year. While this average value suggests more rapid decomposition than in forested wetlands, it is confounded by differences in litter types and litter age, as some litter examined was not senescent when harvested.

Freshwater Non-tidal Marshes

Decomposition rates in freshwater non-tidal marshes of the southeast United States range from 0.117 to 3.463 yr^{-1} with corresponding half-lives of 5.9 and 0.20 yr (Table 2). Excluding buried litter and acid mine drainage impaired marshes, the average decay rate is 0.969 yr^{-1} or a 0.72 year half life. The smaller upper range and somewhat lower decay rate for the emergent litter suggests that the litter may more recalcitrant than tree leaf litter in the forested wetlands. Another reason for the lower decomposition rates may be that emergent litter has more material leached from it as it stands in the marsh prior to collection than leaf litter collected from traps at litterfall.

Atkinson and Cairns (2001) are the only investigators to examine decomposition in created marshes of the southeast United States. They found slightly higher rates of decomposition in the 20 year-old than the 2 year-old created wetlands, suggesting decomposition rates increase as ecosystems become established (Table 2). Decomposition rates were slower in the created wetlands than the average rate for freshwater non-tidal marshes and reported studies examining similar litter species (Table 2). It is unclear whether this lower rate is due to their recent creation, or difference in climate, flooding, or other factors.

Results from several freshwater marsh studies suggest litter position/microclimate plays an important factor in decomposition rates. Litter that is suspended above the water which would simulate the decomposition of standing litter, decomposed at rates 4 times slower than litter submerged and in contact with the soil (Boyd, 1970). Burial under sediments also has a inhibitory effect on decomposition relative to litter at or above the soil surface (Schipper and Reddy, 1995). So, along with lateral gradients in decomposition rates from streambank to upland terrace as observed in forested wetlands, there is a vertical decomposition gradient from standing litter to buried litter, both exhibiting apparently optimal conditions for decomposition between the extremes.

Permanently Ponded

There is limited information on decomposition of litter in freshwater lakes and ponds of the Southeast United States (Table 2). While none of the studies are completely analogous with the shallow ponds examined in this study, some general information is useful. Hardwood leaf litter decomposition rates range from 1.826 to 9.935 yr^{-1} with corresponding half-lives of 0.38 to 0.07 year (Table 2). Similar to forested wetlands, litter species and quality accounts for this range with oak litter more recalcitrant than dogwood or birch (Table 2).

Emergent litter such as rushes (*Scripus*) and cattails (*Typha*) decompose slowly relative to the hardwood leaf litter, with rates of 1.17 and 1.72 yr^{-1} respectively (Table 2). These rates are within the range for similar species in the freshwater marsh environments and the range of 0.5-3.8 yr^{-1} cited by Hill (1985), although much faster than some studies of cattail species (Davis, 1991; Atkinson and Cairns; 2001). From these limited studies, it does not appear that there was an inhibitory effect on decomposition by permanent ponding, although the shallow stagnant ponds examined in my study may be more prone to developing anaerobic conditions that could inhibit decomposition.

Summary

The limited number of litter decomposition studies reported for the Southeast United States makes it difficult to predict the relative decomposition rates for the natural and created wetlands examined in my study. The ranges of the forested non-tidal wetlands, upland fields, emergent marshes and permanently ponded sites all overlapped (0.2-2.1, 0.3-4.1, 0.1-3.5, and 1.8-9.9 yr^{-1} respectively). The average values were even counter-intuitive along the moisture gradient, with drier upland and wetter ponded sites averaging faster rates of decomposition. In this case, the average results likely represent differences in other factors that influence decomposition such as litter quality, soils or vegetation structure. When the same litter is examined across a moisture gradient in a floodplain or swamp, the pattern matches the theoretical concept better; drier and many permanently inundated sites have slower rates of decomposition than the intermittently innundated sites where moisture levels are sufficient for decomposition, yet remaining aerobic (Brinson, 1977; Cuffney and Wallace, 1987; Day, 1982; Elder and Cairns, 1982; Shure et al., 1986; Yates and Day, 1983).

Predicting whether constructed wetlands would have similar litter decomposition rates to the adjacent natural wetlands from the literature is also difficult. The average annual decay rates for emergent marshes and forested wetlands were 0.97 and 1.0 - 1.2 yr^{-1} respectively. Created wetlands may not have the same decomposition function as the predominately natural emergent marshes in the literature considering the young age and less developed soils and litter layers. Atkinson and Cairns (2001) found slightly faster rates of decomposition in 20 year-old relative to 2 year-old constructed wetlands (Table 2). Therefore, it seems probable that the adjacent natural wetlands will have faster rates of decomposition than the constructed wetlands with a similar moisture regime in my study. Although, considering the number of factors that influence decomposition rates, no difference or a reverse relationship are also conceivable.

Chapter 2. Litter Weight Loss, Decomposition Models and C:N Ratios

Introduction

With the realization of the important functions and values that wetlands generate for society, a "no net loss" national standard has been adopted, which requires the mitigation of destroyed wetlands with in-kind on-site restoration or off-site creation. The initial focus of wetlands protection was on wetland delineation and losses and gains were typically quantified by area. However, more recently there has been increased interest in whether wetland functions are being replaced through restoration and creation (Brinson and Rheinhardt, 1996; Hruby et al., 1995; Richardson, 1994; Wilson and Mitsch, 1996).

Litter processing is an important function of wetlands as evidenced by many wetland systems with high organic matter levels or even organic soils. Considering the numerous types of wetlands relative to upland and aquatic systems, there is limited information available on decomposition rates in natural wetlands. There are only a handful of studies that report decomposition rates in created or restored wetlands and no studies comparing decomposition in natural/created wetland pairs such as reported here.

The litterbag method is the predominant method for estimating the rates of litter decomposition in terrestrial and wetland environments (see Chapter 1). The litterbag method typically tracks weight loss from litter confined in fabric or wire bags. Many replicate litterbags are installed simultaneously and then collected periodically during the period of the study, typically at least one year. Rates of weight loss are expressed on an ash-free basis and typically fitted to exponential decay models, although initial rapid leaching losses and other site- and litter-specific variables can cause more complex patterns of loss. Litter decomposition is affected by many different factors including temperature, moisture, litter species, biota, community type, and flooding regime (see Chapter 1). In this study, the effects of litter differences were assessed by using two mixed litter types, emergent litter dominated by *Typha* from created wetland areas and mixed deciduous tree litter from reference forested wetlands.

There are relatively good estimates of the rates of decomposition in floodplain forests and swamps of the southeastern United States (see Chapter 1, Table 2). Differences in decomposition rates have been examined along gradients from streambank to upland forest, between different forest types, with mixtures and single species litter and with various human disturbances (Table 2). The most common model used is an exponential model, $Y=Y_0e^{-kt}$, where k is the rate of decomposition (Jenny et al., 1949). Half-life ($T_{1/2}$), or the time required for 50% litter weight loss, is calculated from a given rate (k) with the exponential model. Even within similar ecosystems in the same geographic area, there is considerable variation with decay rates ranging from 0.242 to 2.081 yr^{-1} (2.86 and 0.33 yr. $T_{1/2}$ respectively) for mixed litter. As would be expected, single species litter showed greater variation and ranged from 0.146 to 9.770 yr^{-1} or $T_{1/2}$ of 4.74 and 0.07 yr. respectively. The overall average of 78 litter/site combinations examined was 1.17 yr^{-1} and is consistent with that calculated by Lockaby and Walbridge (1998) of 1.01 yr^{-1} which together represent half-lives of between 0.59 and 0.69 yr.

Flooding has a positive or negative effect on decomposition in floodplain forests depending on the frequency and duration (Baker et al., 2001; Battle and Gollady, 2001). Multiple brief flooding events stimulate decomposition as seen at the Iatt Creek and Coosawhatchie River sweetgum/swamp tupelo forests studied by Baker et al. (2001) and a cypress-gum swamp of Battle and Golladay (2001). Presumably, due to anaerobic conditions developing, long periods of flooding have an inhibitory effect on decomposition as seen for the Cache River study of Baker et al. (2001) and in single long flood event and permanently flooded sites reported by Battle and Gollady (2001).

Moisture's influence on decomposition has also been examined along topographic gradients in floodplains and swamps (Brinson, 1977; Cuffney and Wallace, 1987; Day, 1982; Elder and Cairns, 1982; Shure et al., 1986; Yates and Day, 1983). In general, the higher and drier topographic sites such as levees or mixed hardwood forests have slower rates of decomposition (Table 2). When decomposition has been estimated in the associated permanently inundated rivers or bays, often the inhibitory effect of flooding reported by Baker et al. (2001) and Battle and Gollady (2001) has not been observed (Brinson, 1977; Cuffney and Wallace, 1987; Elder and Cairns, 1982). Presumably, currents in the rivers, streams and bays studied by the later authors never allowed conditions to become sufficiently anaerobic to limit decomposition.

There is little information available on decomposition in wetlands created for replacement of freshwater non-tidal forests (see Chapter 1, Table 2). In my study, created and natural wetland pairs with similar moisture regimes (2-4 cm standing water in winter) and the effect of moisture (i.e. wetter and drier areas) within the created wetlands were compared. I hypothesized that the moisture gradient from upland to emergent marsh to permanently flooded likely would follow the same patterns of decomposition as seen in the forested wetland systems cited above, with slower rates in the uplands and flooded locations if they became anaerobic.

Two different fabric mesh sizes were used in this study for the construction of litterbags to assess the relative importance of different sized detritivores. Bocock (1964) conducted one of the earliest examinations of the effect of mesh size and potential to use the litterbag method to assess the effects of macroinvertebrates on decomposition. Bocock compared decomposition of ash litter in two woodlands with both coarse meshed nylon hairnets (1-cm mesh) and 15 x 15 cm litterbags with 1-mm diameter circular apertures. That technique assumes fine mesh bags represent decomposition from leaching, microbes and soil fauna < 1 mm, while large mesh bags also include the effects of macroinvertebrates on decomposition. Between 10 and 40% of the decomposition was attributed to the action of macroinvertebrates based upon fine versus coarse mesh comparisons (Bocock, 1964).

As the litterbag technique developed, three and sometimes four mesh sizes were employed by successive studies to further explore the relative contributions of different sized animals. Anderson (1973) utilized three mesh sizes (7 mm, 1 mm and 0.175 mm) and "aerial bags" to analyze the relative importance of leaching, microbes, mesofauna and macrofauna during decomposition in a woodland. Aerial bags, which were suspended above the ground with cord, were used along with laboratory analysis for water-soluble components to estimate leaching separate from microbial activity. The assumption was that bacterial and fungal activity would be inhibited by the low moisture content of the suspended bags. The progressively coarser bags would allow access to the litter by either mesofauna or meso- and macrofauna along with the background microbial and leaching losses in the fine mesh. Anderson's study found that the relative importance of biotic and abiotic factors were site-dependant, with biota playing a more important role in beech (*Fagus sylvatica* L.) rather than sweet chestnut (*Castanea sativa* Mill.) forests.

Many authors have used multiple mesh sizes for litterbags as an important tool for understanding the relative roles of microbes, meso- and macroinvertebrates in decomposition in forests (Bocock, 1964; Anderson, 1973; Herlitzius, 1983; Gustafson, 1943), agroecosystems

(House and Stinner, 1987; Tian et al., 1992) swamps, marshes (Mason and Bryant, 1975), bogs (Coulson and Butterfield, 1978), streams (Kirby, 1992), rivers (Mathews and Kowalczewski, 1969) and lakes (Brock et al., 1982; Danell and Andersson, 1982) throughout the world. While many studies have shown differences in decomposition rates between large and small mesh sizes, some environments and treatments exhibit no difference in decomposition (House and Stinner, 1987). Clearly, different abiotic and biotic factors have varying importance for decomposition in different ecosystems.

One of the drawbacks of litterbags is that mesh sizes large enough to allow ready access by invertebrates also allows the loss of litter fragments (Valiela et al., 1985). By running through the usual procedure of packing, transport and installation in the field, then immediately returning a sub-set of bags, they assessed and corrected for some of this fragment loss error. They found litter losses due to handling to be small (< 1% initial mass), and not significant relative to other losses. Even with this initial correction, there is no estimate of what portion of weight loss from litterbags is from physical losses of partially decomposed fragments later in decomposition.

A study of microarthropod numbers suggests that the comparison between litterbags with different mesh sizes may not be as simple as subtraction (Crossley and Hoglund, 1962). They found that mite numbers (*Tydeus* sp.) in litterbags reached 300 per dm^2, while adjacent core samples collected the same day showed 30-50 per dm^2. Apparently, either due to a more stable microclimate or exclusion of predators larger than 2 mm, the bags utilized dramatically increased mite numbers. Further investigation with 1 mm and 2 mm mesh sizes confirmed this effect, but showed no difference between the mesh sizes. While the effect of increased microarthropod numbers may not have had a significant effect on litter weight loss, it suggests the possibility of confounding "bag effects" from temperature, moisture or other ecological factors.

If a single mesh size must be chosen, it remains a balancing act to select one that is not too large and artificially over-estimates decomposition as leaf fragments are lost, or under-estimates it by exclusion of macrodetritivores. Perhaps, instead of considering the litterbag results as direct estimates of decomposition, which assumes any material lost is degraded (Pardo et al., 1997), the term "litter processing," as used in the literature concerning lotic environments, is more appropriate. During early stages of exposure, the litterbag may accurately measure decomposition as mass is lost predominately as soluble compounds or as the end-products of respiration and consumption. Longer-term weight losses from litterbags are not entirely from litter decay, as fragments smaller than the mesh size are lost via biotic and abiotic fragmentation.

The primary objective of this portion of my overall study was to compare decomposition rates in created wetlands of two different ages and adjacent natural forested wetlands using a litterbag approach. Two types of litter were used in the litterbags, a mixture representative of the marsh vegetation in the created wetlands and a mixture of the deciduous tree leaves representative of the natural wetlands. To further understand the litter decomposition dynamics, two mesh sizes of litterbags were constructed to assess the relative importance of leaching and microbial activity alone versus these mechanisms in concert with the effects of macroinvertebrate consumption and fragmentation of the litter. We hypothesized that the intact litter layer and associated biota of the adjacent natural wetlands would result in faster decomposition than areas with similar moisture regimes in the created wetlands. A secondary objective was to examine the effects of moisture along a gradient in the created wetlands, from areas that supported dominantly upland vegetation down to permanently flooded areas. From information in the literature, it appeared that litter placed into the intermediate moisture regimes (i.e. areas than flood and dry periodically) should decompose the most rapidly, with the lack of moisture and anoxic conditions reducing relative decomposition in the upland and permanently flooded areas, respectively.

Methods and Materials

Site Description

Fort Lee – The Fort Lee (FL) constructed wetland is located at milepost 10 along north-bound Interstate 295 adjacent to the Ft. Lee Military Reservation and the town of Hopewell in Prince George County. The Virginia Department of Transportation constructed the site in 1989/1990. An upland site was excavated to an average depth of -4 m below natural grade adjacent to the interstate to approximately -0.5 m where it borders the reference wetland (Fig. 1). Upland topsoil (~ 0.25 m) was added to the site prior to final planting. The site contains three small ponded areas that contain water throughout the year. Surrounding these ponds and in other low-lying zones are wet areas which are flooded throughout the winter and early spring. These "wet areas" support predominately cattails (*Typha* sp.), bulrushes (*Scirpus* spp.) and woolgrass (*Scirpus cyperinus*). A significant linear ridged area between the deeper wet areas adjacent to the interstate and the reference wetland supports drier "upland" conditions. These areas are infrequently saturated and support tall fescue (*Fescue arundinacea* Schreb.), *Sericea lespedeza* and other grasses. Between the "wet" and "upland" areas, there are "intermediate" transition zones that support a mixture of both wetland and upland species (Cummings, 1999).

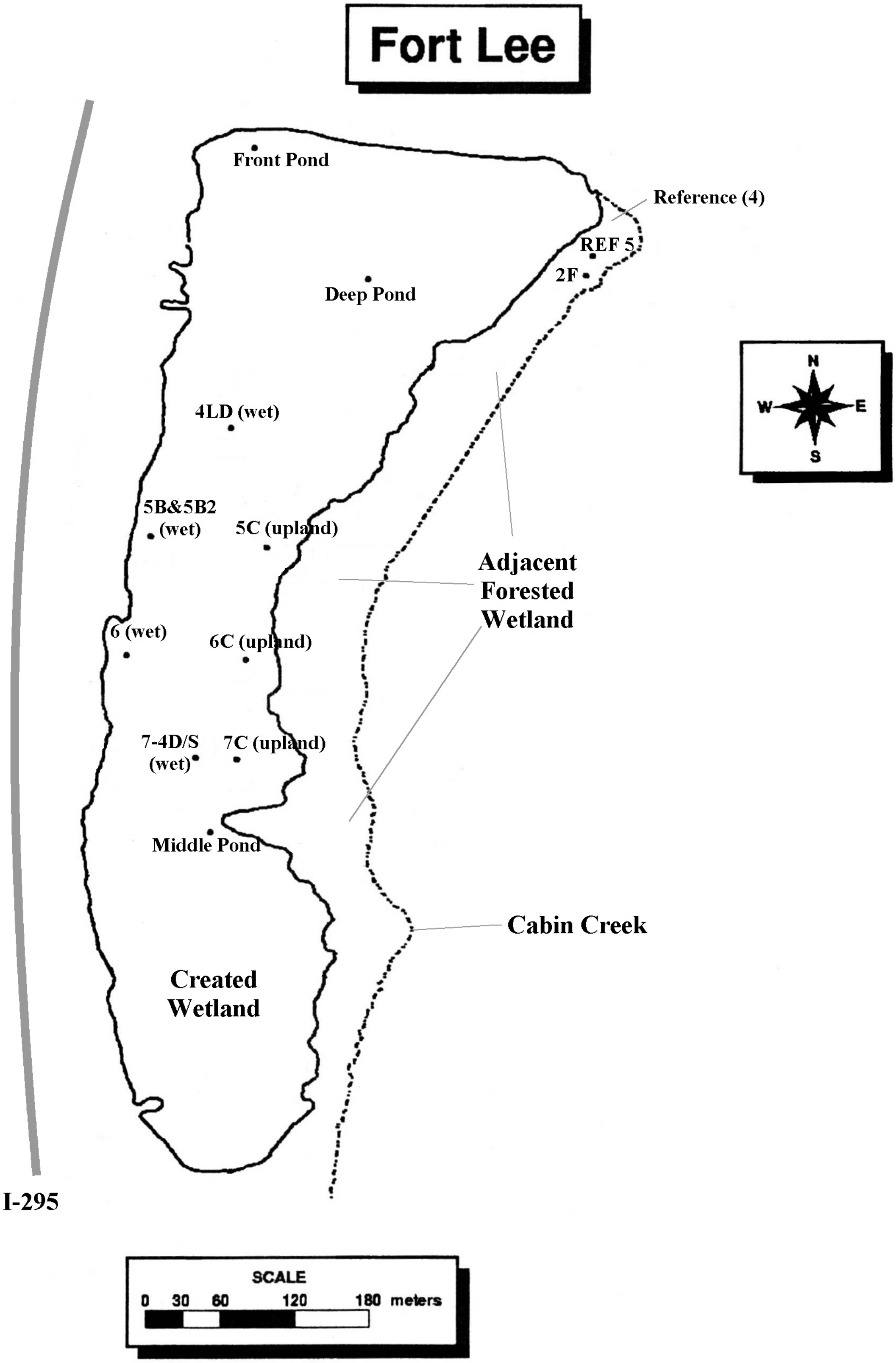

Figure 1. Map of Fort Lee created and adjacent natural wetlands with well and litterbag moisture regime treatments indicated.

The reference area consists of a strip of forested wetland between the constructed wetland and Cabin Creek, a small creek. On the opposite side of the creek there are several homes. While the site is a natural riparian wetland, it has been affected by several impacts. There is evidence of past beaver disturbance, although no current evidence was apparent during this study. The proximity of the houses and overland sheet flow from the constructed wetland during high rain events also impacts the site. There is also evidence of some trees being cut by trespassers onto the site. Extensive urban development upstream has certainly affected the stream's hydroperiod as well. The reference area was dominated by a mixture of red maple (*Acer rubrum* L.), sweetgum (*Liquidambar styraciflua* L.) and swamp chestnut oak (*Quercus michauxii* Nutt.; Cummings, 1999). Appendix III provides some soil chemical properties, but more detailed discussion of the FL created and adjacent natural wetlands, especially soils and soil development, can be found in Cummings (1999).

A water budget was calculated for the FL wetland to assess the relative importance of different sources of water. Detailed discussion of the techniques utilized and calculations are found in Daniels et al. (2000). Surface water runoff, precipitation and groundwater inflow were all found to be important sources of water, with ground water providing the largest portion consistently during the year (Figures 2a & b). The adjacent natural wetland may also receive some water from over-bank flooding from Cabin Creek along with being along the surface and groundwater flow paths from the created wetland. Nearby well levels and surface moisture conditions for the different FL moisture regimes are in Appendix I.

Charles City - The Charles City (CC) constructed wetland (Route 199 mitigation) is located in Charles City County west of Route 623, just north of the Chickahominy State Wildlife

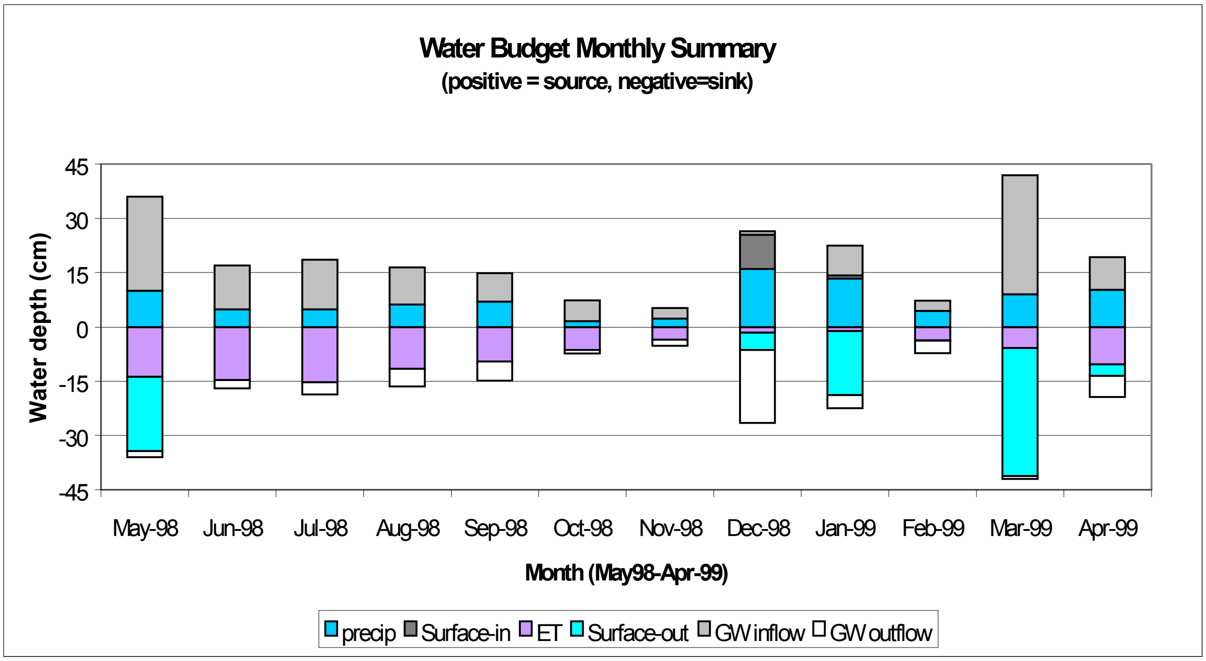

Figure 2a. Monthly total of each water budget parameter during the year from May 1, 1998 to April 30, 1999, negative values indicate losses (i.e. surface water outflow, ET, and net groundwater and soil water storage during periods of recharge) and positive values indicate sources (i.e. precipitation, surface water inflow, and net discharge of groundwater and soil water storage). (Daniels et al., 2000)

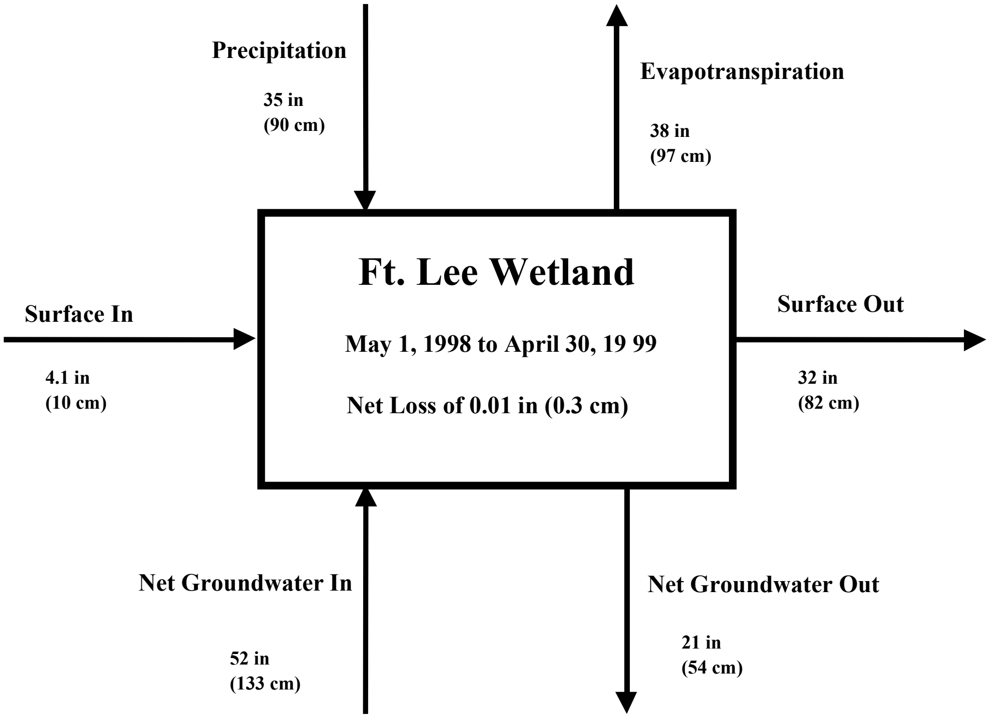

Figure 2b. Water Budget summary for the Fort Lee created wetland. (Daniels et al., 2000)

Management Area (Fig. 3). It was constructed during the winter of 1997/1998 in a similar manner to the FL site. An upland field was excavated from between -0.5 to -1.5 meters below natural grade adjacent to a natural forested wetland. While the plan called for topsoil to be returned to the site, little evidence of this can be seen in the areas examined. The final surface in most areas is a relatively compact clay that was formerly the argillic (Btg) horizon. The constructed wetland area studied slopes down from a natural wetland to an area that is permanently ponded. The site was excavated such that much of it is wet to +0.5 m of standing water during the winter, except for several areas where mature trees were left on islands of soil (e.g. irregular shaped areas near well 16 and 17 as shown in Fig. 3). *Eleocharis obtusa* (Willd.) J.A. Schultes and *Juncus acuminatus* Michx. were the dominant species in the created wetland during the summer of 1998 (DeBerry and Perry, 2002).

The reference site adjacent to the constructed wetland was identified as jurisdictional based upon indicators such as sphagnum and canopy species composition along with identification of hydric soils. The adjacent natural wetland could be characterized as a wet hardwood flat or wet woods, where in a relatively low slope area of the Coastal Plain without any nearby watercourses for drainage, water accumulates in and above a relatively low permeability clayey subsoil, especially during the winter months. While there is standing water in vernal pools throughout the natural wetland during the winter and early spring, they quickly disappear as the trees leaf-out. Other than the disturbance caused by the construction of the wetland, the reference site has not been disturbed recently. It is likely that the site was logged several decades ago.

The soils at the site are mapped as the Chickahominy or Newflat soil series (Fine, mixed, semiactive, thermic Typic Endoaquults), with the reference wetland belonging to a ponded phase

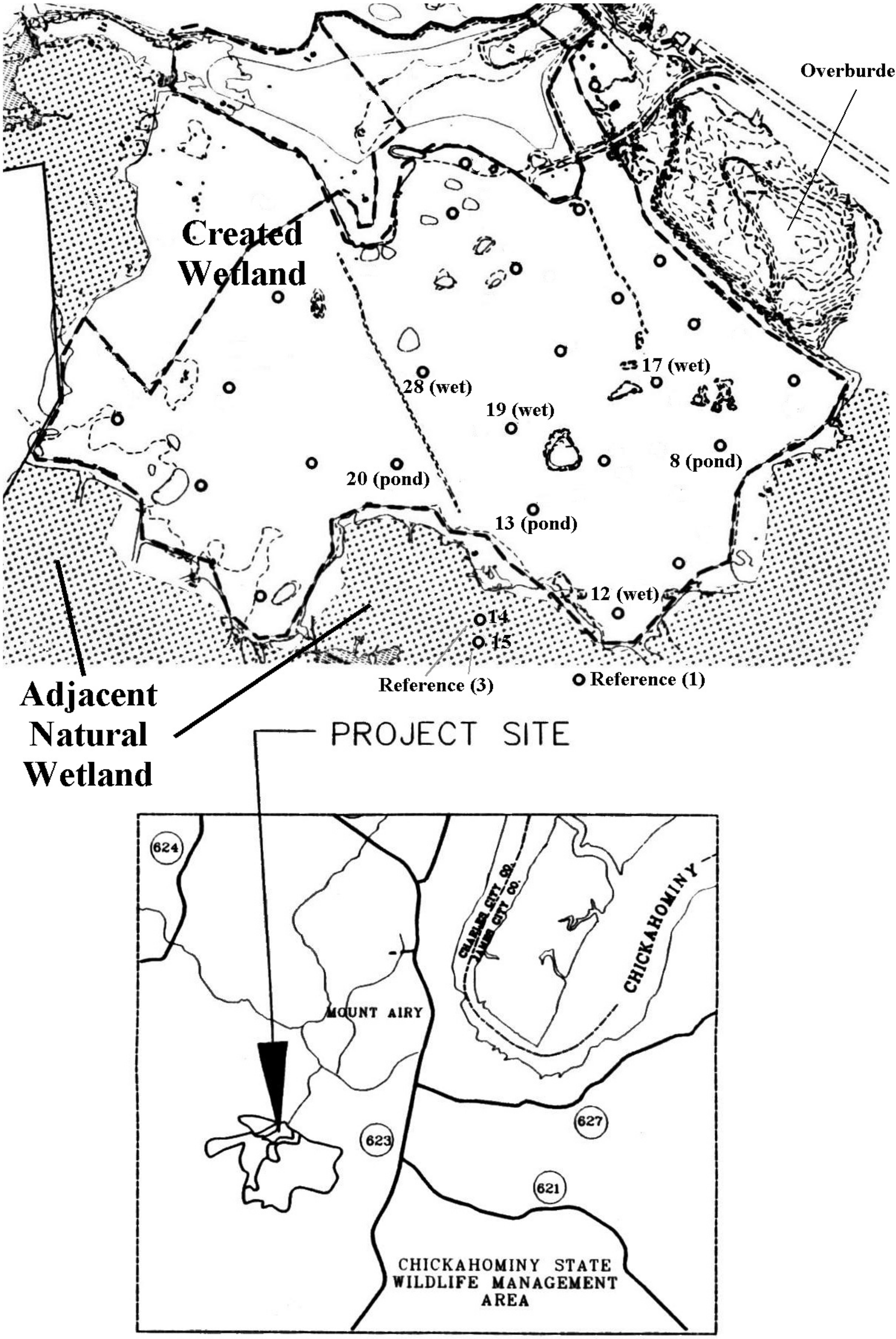

Figure 3. Charles City created and adjacent forested wetlands with well and litterbag moisture regime locations indicated.

of the Chickahominy series (Hodges et al., 1990; Robert Hodges, pers. comm.). A high shrink/swell clay content in the soil results in cracks opening and closing during the seasonal wet/dry cycles in the exposed Btg horizon in the created wetland. While the adjacent natural wetland has similar wet/dry cycles, no open cracks were observed within the intact litter layer and A horizon. Further information on the construction and hydrologic monitoring of the CC created wetland or Route 199 Mitigation Wetland is found in VHB (1998). Appendix II and IV provide additional hydrology / soil moisture and soil chemical properties, respectively.

While an extensive water budget was not calculated for the CC created wetland, some inferences about its sources of water can be made. On several occasions 5-10 cm of water was ponded on the surface of the created wetland, while wells screened below the truncated Btg horizon were dry, indicating that the water was perched and not from groundwater. Therefore, it appears that precipitation and some minor (<10%) surface runoff from adjacent forested areas are the only sources of water for the CC created and adjacent natural wetlands.

Litterbag Design

The litterbags utilized in this study were constructed from 2 different types of polyester/nylon mesh (Figure 4). The fine mesh bags were constructed out of nylon sheer with average 380 x 380 μm square openings. The coarse mesh bags were constructed from polyester crinoline fabric with 3 x 4 mm oval openings. The litter bag dimensions were 15 x 15 cm (interior). One side of each bag was formed by folding the fabric, with two other sides being sewn with a serged seam. The fourth side was either taped (fine mesh) or stapled (coarse mesh). The staples for the coarse mesh bags were spaced so those organisms larger than the mesh size

Figure 4. Coarse and fine mesh size litterbags with forest litter.

could access the bags. The fine mesh bags should exclude any arthropods and therefore primarily estimated leaching and microbial decomposition losses.

The litterbags were filled with material collected from either the FL marsh area (near the weather station on transect 7) or freshly fallen leaves from the FL reference area collected in November 1998. The marsh vegetation was collected by clipping and collecting all standing material from several 1 m^2 quadrats. The dominant species were cattails (*Typha*) and woolgrass (*Scirpus cyperinus*), with some other minor components (smartweed (*Polygonum* spp.), rushes (*Juncus* spp.), beggar ticks (*Bidens* spp.), and other unidentified material. Litter traps were constructed in the reference area to collect freshly fallen leaves, and consisted of a coarse mesh fabric fastened to the ground prior to leaf fall. The leaf litter contained predominately swamp white oak (*Quercus bicolor* Willd.), sweet gum (*Liquidambar styraciflua* L.), red maple (*Acer rubrum* L.), swamp chestnut oak (*Quercus michauxii* Nutt.) and sweet bay magnolia (*Magnolia virginiana* L.). One set of litter traps also contained loblolly pine (*Pinus taeda* L.) needles, which were excluded from the litterbags to reduce variability. Litter traps were spread throughout the reference area, typically clustered near the ground water wells (Fig. 1).

Each litterbag was filled with approximately the same amount of material. The marsh vegetation collected from the created wetland contained two dominant species, cattails and woolgrass. To reduce variability, the ratio of these materials was kept constant by adding approximately 9 g of oven-dried (40 hrs at 55° C) cattails and 3.5 g of woolgrass and other material to each bag. The exact weight of each bag was recorded, but all litterbags with marsh litter weighed around 12.5 g. The leaf litter from the reference or adjacent natural forested wetland was air-dried and then thoroughly mixed. Any conifer litter was removed and discarded to reduce variability. After being oven-dried, approximately 5.0 grams of the mixed leaf litter was placed in each litterbag with "forest" litter.

Experimental Design

To keep the number of litterbags required for the study to a reasonable number the design was not a complete block design and some moisture/site treatments received fewer or no litterbags of certain mesh size/litter type combinations (Table 3). The "wet" in the created wetlands and "reference" moisture treatments in the adjacent forested wetlands were matched as close as possible by winter water levels (i.e. 2-10 cm standing water). The moisture gradient treatments within the created wetlands were located such that "pond" moisture regimes would be permanently flooded (FL) or flooded longer (CC) than the "wet" (or similar "reference") treatment. Drier "upland" areas were only examined within the FL created wetland and while they had saturated soils during the winter and early spring, they did not support a dominance of hydrophytic vegetation (Table 3, Figure 5-8).

Bags were placed to lie flat on the soil surface/litter layer. When possible, each replicate of litterbags was located within 15 m of pre-existing ground-water monitoring wells (Fig. 1 & 3) and a detailed study of soil redoximorphic features in the FL created and natural wetlands (Cummings, 1999). Ground-water measurements were made monthly and used along with previous groundwater well data to characterize moisture levels. The bags were secured to the surface with landscape staples to prevent movement. Bags were placed at each site during mid to late December 1998. Prior to placement, vegetation and/or litter from the previous year was removed from beneath each litterbag. Care was taken to ensure the soil and humus layers were not disturbed.

Table 3. Experimental design and treatment descriptions for the Fort Lee and Charles City wetlands. For each replicate/collection, a fine/coarse mesh pair of litterbags was collected.

Moisture Regime	Litter Type	Fort Lee			Charles City		
		# replicates	# collections	description	# replicates	# collections	description
wet	forest	4	12	2-10 cm standing water in winter cattails dominated emergent veg.	4	12	2-10 cm standing water in winter cattails dominated emergent veg.
	marsh	4	12		4	12	
reference	forest	4	12	2-10 cm standing water in winter deciduous wetland tree species	4	12	2-10 cm standing water in winter deciduous wetland tree species
	marsh	4	12		4	12	
pond	forest	3	12	20-40 cm permanent standing water no emergent vegetation	3	12	15-30 cm standing water in ruts during winter (not permanent) no emergent vegetation
	marsh	3	6		0	0	
upland	forest	3	12	saturated at soil surface in winter tall fescue, sericea lespedeza veg.	0	0	n/a
	marsh	3	6		0	0	

Figure 5a. Fort Lee adjacent natural forested wetland (wet moisture regime; 2/00).

Figure 5b. Charles City adjacent natural forested wetland (wet moisture regime; 2/00).

Figure 6a. Fort Lee wet moisture regime in the created wetland (2/00).

Figure 6b. Charles City wet moisture regime in the created wetland (2/00).

Figure 7a. Fort Lee pond moisture regime in the created wetland (2/00).

Figure 7b. Charles City pond moisture regime in the created wetland (2/00).

Figure 8. Fort Lee upland moisture regime in the created wetland (2/00).

Litterbags were collected monthly or every other month for a year, depending on the site-specific sampling design (Table 3). Four or five litterbags of each litter type/mesh size combination were used as field quality controls (QC) to assess the weight lost from bag placement and recovery. Field quality control bags were placed as described above and then re-collected the same day for dry weight determination. The amount of weight lost therefore compensates for the loss due to particles falling from the bag instead of being decomposed, at least initially. These losses were found to be minimal, typically 1-3%.

Litterbag Collection, Preparation and Analysis

Litterbags were collected from each location once a month for a year. After removing the landscape staples, bags were placed into separate plastic bags to prevent the escape of arthropods. Upon return to the lab, any debris adhering to the outside of the bag was carefully removed. Each bag was opened and any macroinvertebrates were picked from the litter and preserved in ethanol for later identification (see Chapter 4). The litter was then rinsed in distilled water to remove both sediments and any remaining arthropods.

After removing the arthropods, litter was dried at 55 °C for 72 hours and then weighed to determine gross decomposition rates. Litter was then ground and a litter sub-sample was ashed at 500 ° C to determine ash-free weight. Sub-samples from the quality control litterbags were ashed to estimate the initial ash content and all decomposition rates and weights were expressed on an ash-free basis. Another sub-sample of each ground litter was dried overnight at 55 °C and analyzed simultaneously for C and N via a furnace and tungsten reduction, respectively, using an elemntar Americas Inc., VarioMAX CNS analyzer.

Statistical Analyses

Along with modeling weight loss with linear, single exponential and double exponential equations, the design was analyzed as a 4-way (date, litter type, mesh size, moisture regime) ANOVA with LSD mean separations among treatments for differences in weight loss or C:N ratio at the FL and CC constructed and adjacent natural wetlands using the PROC GLM procedure in the SAS System for Windows, Version 7 (1998). If overall treatment differences were significant, differences at a given date were also compared (e.g. assuming overall moisture regime differences were significant, regimes were then compared for each month (slice). Although a 90% probability level was occasionally utilized, a 95% level was used unless stated otherwise.

Results and Discussion

Decay Rates and Models of Litter Decomposition

Litter decomposition was modeled using three different models; linear, single and double exponential (Table 4). While many different models have been used to describe litter decomposition patterns, the single and double exponential are commonly used because they typically describe the data more accurately and correspond to theoretical knowledge about litter decay. As soluble and readily decomposable material is degraded, the absolute rate of decay decreases as proportionally more and more recalcitrant material remains. The single exponential is more commonly used than the double exponential model for simplicity and ease of comparison with other reported studies (Wieder and Lang, 1982). Often, double exponential models have a better fit than single exponential models, especially when there is an extremely rapid

Table 4. Linear, single and double exponential models along a moisture gradient in the Fort Lee and Charles City wetlands with r^2 values as indicators of goodness of fit.

Wetland	Litter Type	Mesh Size	Moisture Regime	Linear			Single Exponential			Double Exponential				
				$y = (-k)\,t + 1$			$y = e^{-kt}$			$y = (a)e^{-(k1)t} + (1-a)e^{-(k2)t}$				
				k (d^{-1})	k (yr^{-1})	r^2	k (d^{-1})	k (yr^{-1})	r^2	a	k1	(1-a)	k2	r^2
Fort Lee	Forest	fine	wet	0.0019	0.69	0.0000	0.0031	1.13	0.5118	0.207	0.0808	0.793	0.0019	0.8139
			reference	0.0018	0.66	0.3704	0.0027	0.99	0.6536	0.157	9536	0.843	0.0019	0.8364
			pond	0.0017	0.62	0.0546	0.0027	0.99	0.4543	0.568	0.0083	0.432	$1.17e^{-11}$	0.6967
			upland	0.0015	0.55	0.6490	0.0020	0.73	0.7332	0.080	4170	0.920	0.0017	0.7818
		coarse	wet	0.0023	0.84	0.2962	0.0040	1.46	0.7309	0.181	0.0482	0.819	0.0029	0.8203
			reference	0.0020	0.73	0.6484	0.0030	1.10	0.7101	0.474	0.0032	0.526	0.0028	0.7101
			pond	0.0020	0.73	0.5192	0.0033	1.21	0.6929	0.798	0.0049	0.202	$8.34e^{-11}$	0.7096
			upland	0.0017	0.62	0.6759	0.0025	0.91	0.7752	0.090	1.356	0.910	0.0021	0.8187
	Cattail	fine	wet	0.0015	0.55	0.6878	0.0020	0.73	0.7338	0.814	0.0027	0.186	$2.80e^{-11}$	0.7365
			reference	0.0016	0.58	0.7643	0.0020	0.73	0.7492	0.480	0.0020	0.520	0.0020	0.7492
			pond	0.0013	0.47	0.7021	0.0017	0.62	0.6900	0.486	0.0017	0.514	0.0017	0.6900
			upland	0.0011	0.40	0.7941	0.0013	0.47	0.7610	0.460	0.0013	0.540	0.0013	0.7610
		coarse	wet	0.0018	0.66	0.8261	0.0025	0.91	0.8335	0.508	0.0025	0.492	0.0025	0.8335
			reference	0.0016	0.58	0.8069	0.0022	0.80	0.7898	0.477	0.0022	0.523	0.0022	0.7898
			pond	0.0016	0.58	0.7383	0.0021	0.77	0.7314	0.490	0.0021	0.510	0.0021	0.7314
			upland	0.0014	0.51	0.7601	0.0018	0.66	0.7350	0.501	0.0018	0.499	0.0018	0.7350
Charles City	Forest	fine	wet	0.0019	0.69	0.3052	0.0030	1.10	0.6034	0.163	4.037	0.837	0.0021	0.7512
			reference	0.0017	0.62	0.2554	0.0026	0.95	0.6408	0.325	0.0137	0.675	0.0011	0.8426
			pond	0.0017	0.62	0.1834	0.0025	0.91	0.5929	0.309	0.0154	0.691	0.0011	0.8378
		coarse	wet	0.0021	0.77	0.7362	0.0033	1.21	0.8494	0.073	1.069	0.927	0.0029	0.8678
			reference	0.0018	0.66	0.6017	0.0026	0.95	0.7787	0.112	3.087	0.888	0.0021	0.8516
			pond	0.0019	0.69	0.5009	0.0029	1.06	0.7348	0.128	545.5	0.872	0.0022	0.8170
	Cattail	fine	wet	0.0014	0.51	0.6992	0.0018	0.66	0.6890	0.480	0.0018	0.520	0.0018	0.6890
			reference	0.0012	0.44	0.6795	0.0014	0.51	0.7003	0.860	0.0017	0.140	$1.86e^{-11}$	0.7009
		coarse	wet	0.0017	0.62	0.7887	0.0022	0.80	0.7475	0.510	0.0022	0.490	0.0022	0.7475
			reference	0.0012	0.44	0.8079	0.0015	0.55	0.8037	0.460	0.0015	0.540	0.0015	0.8037

initial loss of weight followed by a more typical exponential decay curve. While a linear model of decomposition has limited extrapolative value due to the assumption of a constant decay rate, for materials with little soluble or readily labile constituents, the linear model can fit the data for the first year or two of decomposition (Wieder and Lang, 1982). In my study, double exponential and single exponential or linear models best described the forest and marsh litter decomposition patterns, respectively.

Within the litter decomposition variables examined, litter type generated the most dramatic differences in modeled decay rates. Forest litter decomposed faster than marsh litter and had single exponential decay rates of 0.91 - 1.46 yr^{-1} and 0.47-0.91 yr^{-1} respectively (Table 4). Due to clear differences between marsh and forest litter decomposition, the site and litterbag mesh size treatment differences will be discussed separately for marsh and forest litter.

Forest Litter Decomposition

As expected, coarse meshed litterbags exhibited faster or equal rates of decay than fine meshed litterbags (Table 4). This difference is attributed to the action of macroinvertebrates along with a potential bag effect of fragments being more easily lost from the coarse mesh litterbags. Fine and coarse-meshed litterbags exhibited similar patterns of decomposition between moisture regimes and sites, so only graphs of coarse mesh litterbags are shown (Figure 9-12) with fine mesh litterbag results given in Appendix V.

Linear models of decomposition did not fit the data well, while single and double exponential models generally provided a better fit. Linear models underestimated decomposition initially, and over-estimated decomposition after 8-9 months when relatively recalcitrant material remained. Single exponential models did not accurately estimate the relatively large weight loss

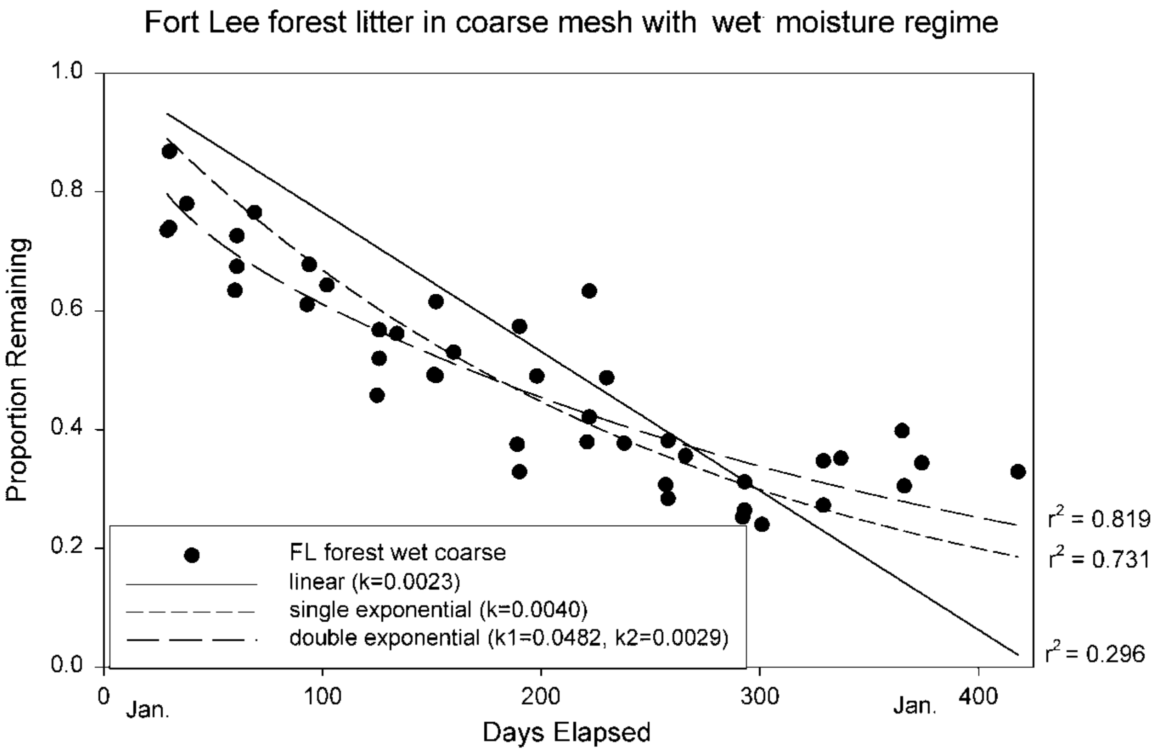

Figure 9a. Decomposition models for forest litter in coarse mesh litterbags with a wet moisture regime in the Fort Lee created wetland.

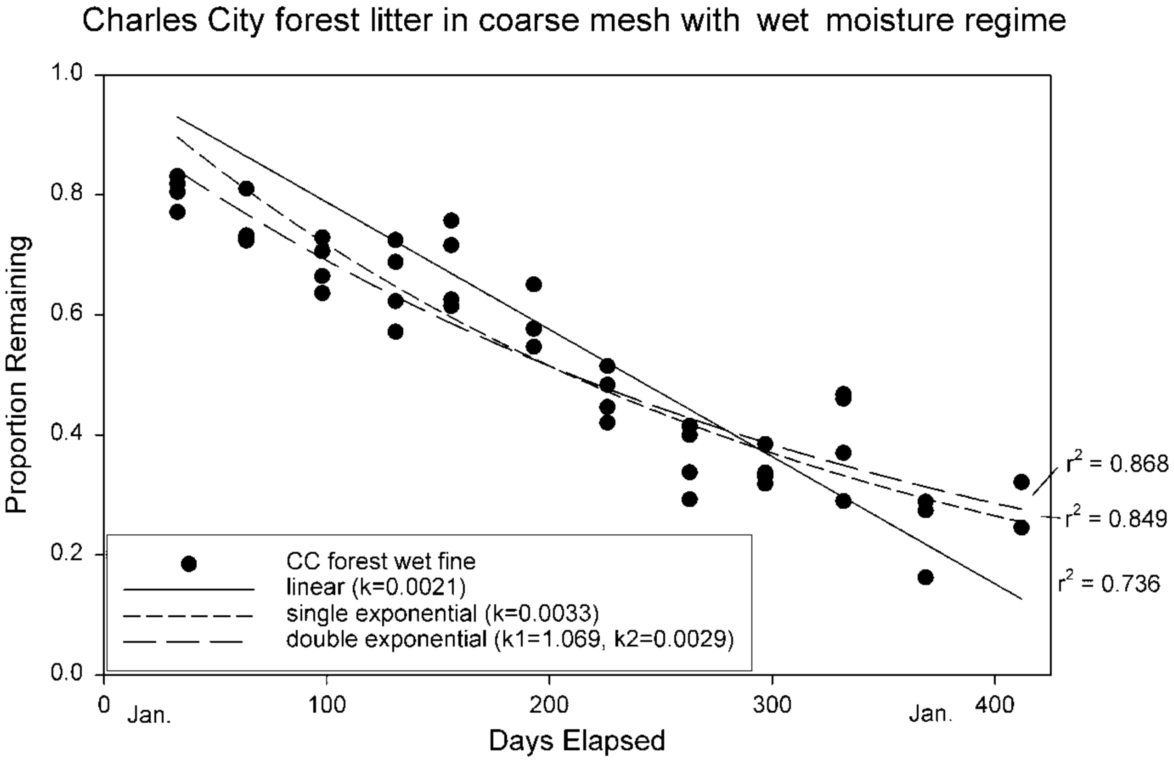

Figure 9b. Decomposition models for forest litter in coarse mesh litterbags with a wet moisture regime in the Charles City created wetland

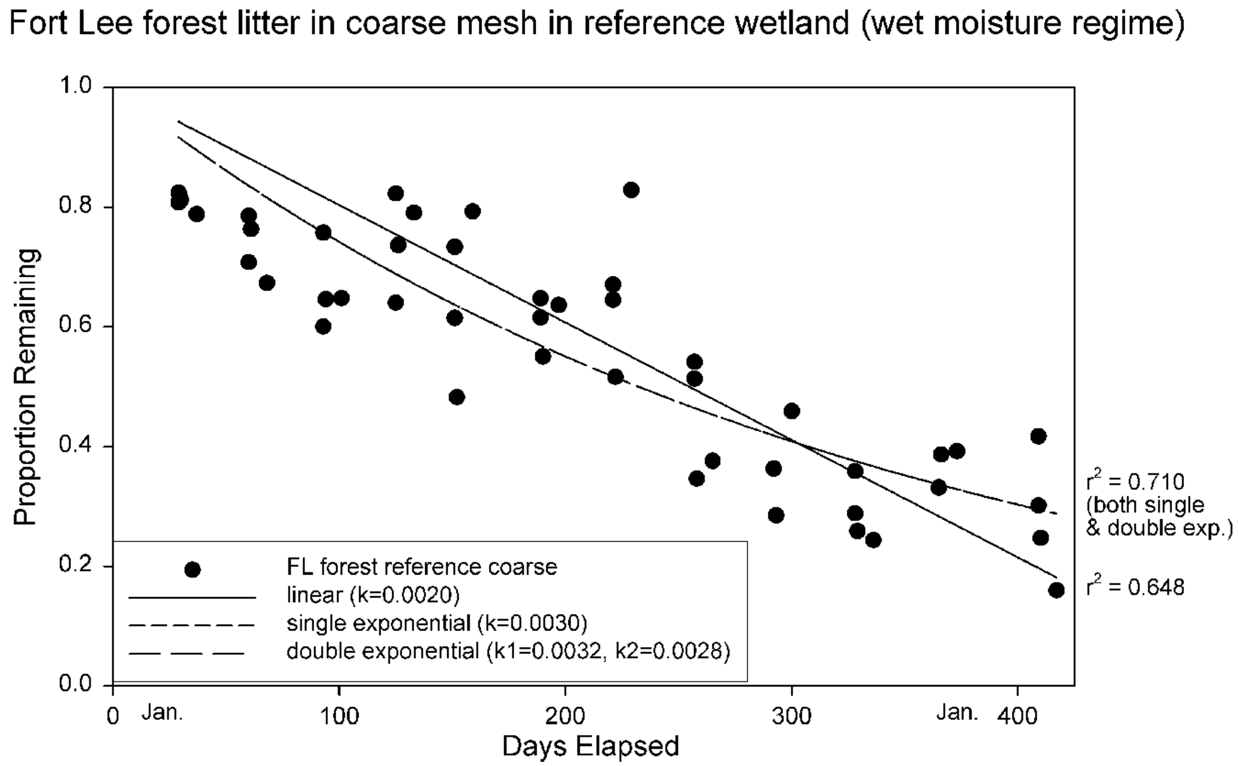
Fort Lee forest litter in coarse mesh in reference wetland (wet moisture regime)

Figure 10a. Decomposition models for forest litter in coarse mesh litterbags in the Fort Lee adjacent natural wetland (moisture regime similar to wet in created wetland).

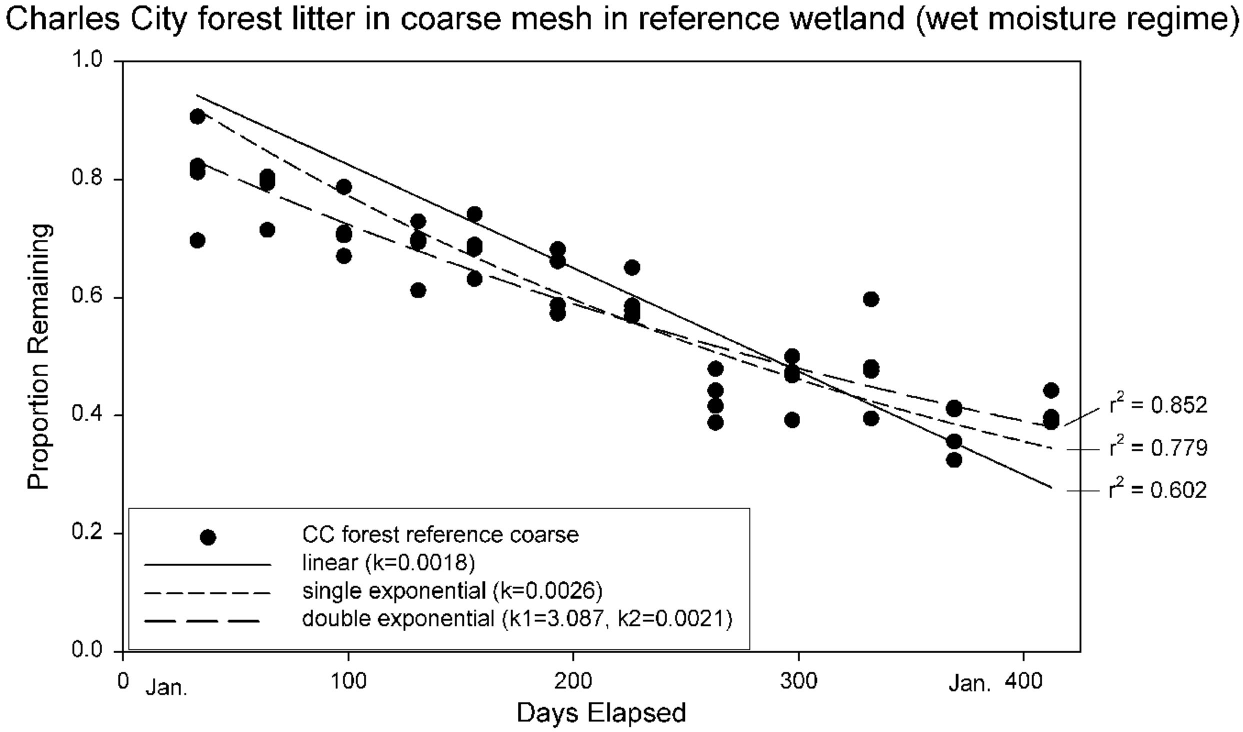
Charles City forest litter in coarse mesh in reference wetland (wet moisture regime)

Figure 10b. Decomposition models for forest litter in coarse mesh litterbags in the Charles City adjacent natural wetland (similar moisture regime as wet in created wetland).

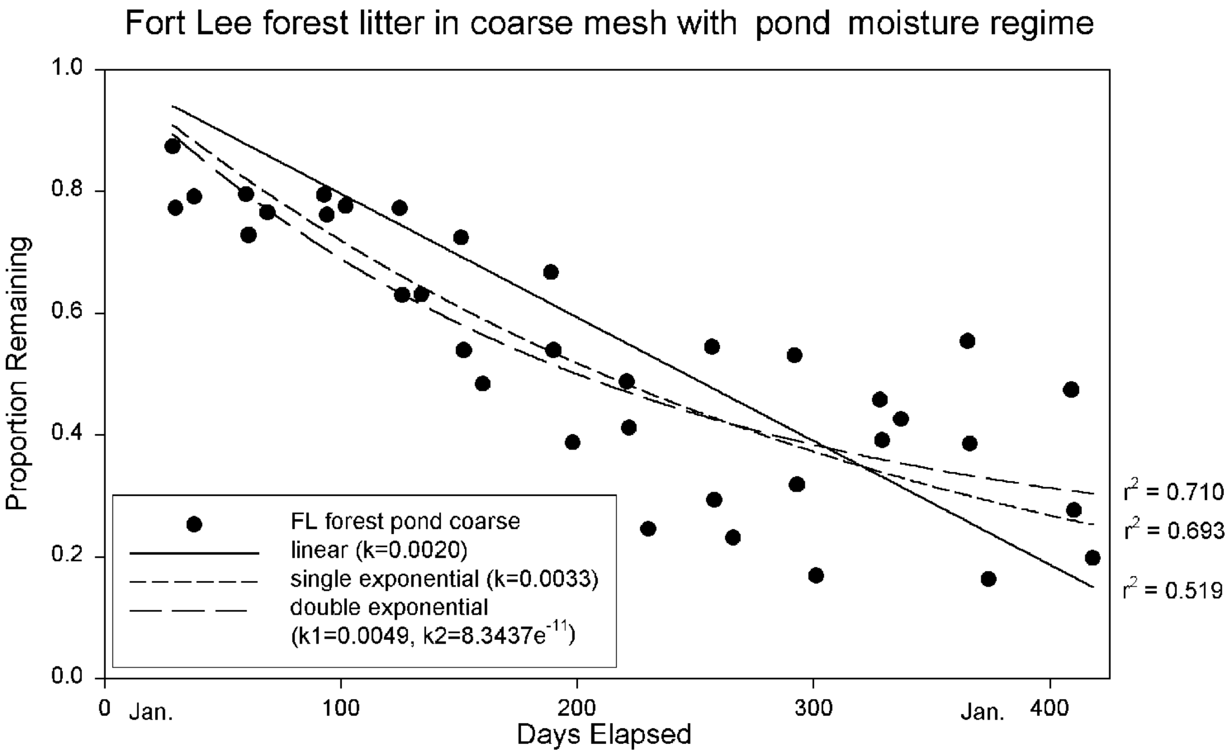

Figure 11a. Decomposition models for forest litter in coarse mesh litterbags with pond moisture regime in the Fort Lee created wetland.

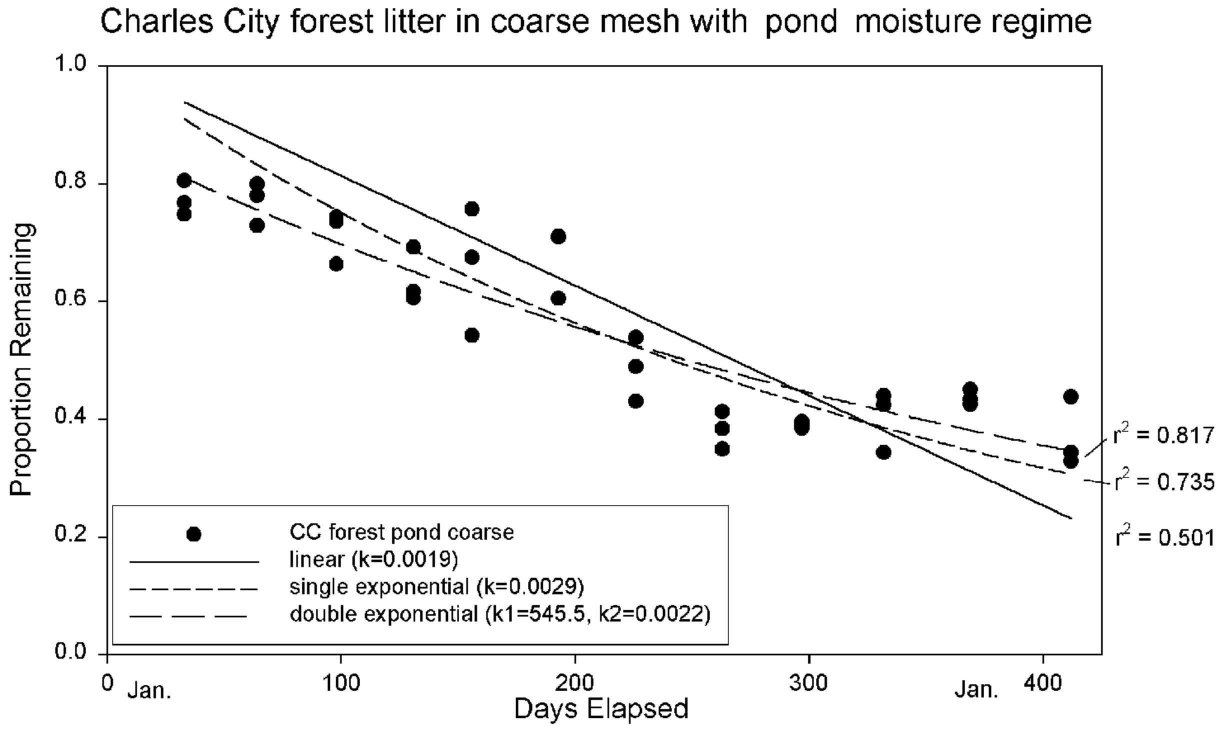

Figure 11b. Decomposition models for forest litter in coarse mesh litterbags with pond moisture regime in the Charles City created wetland

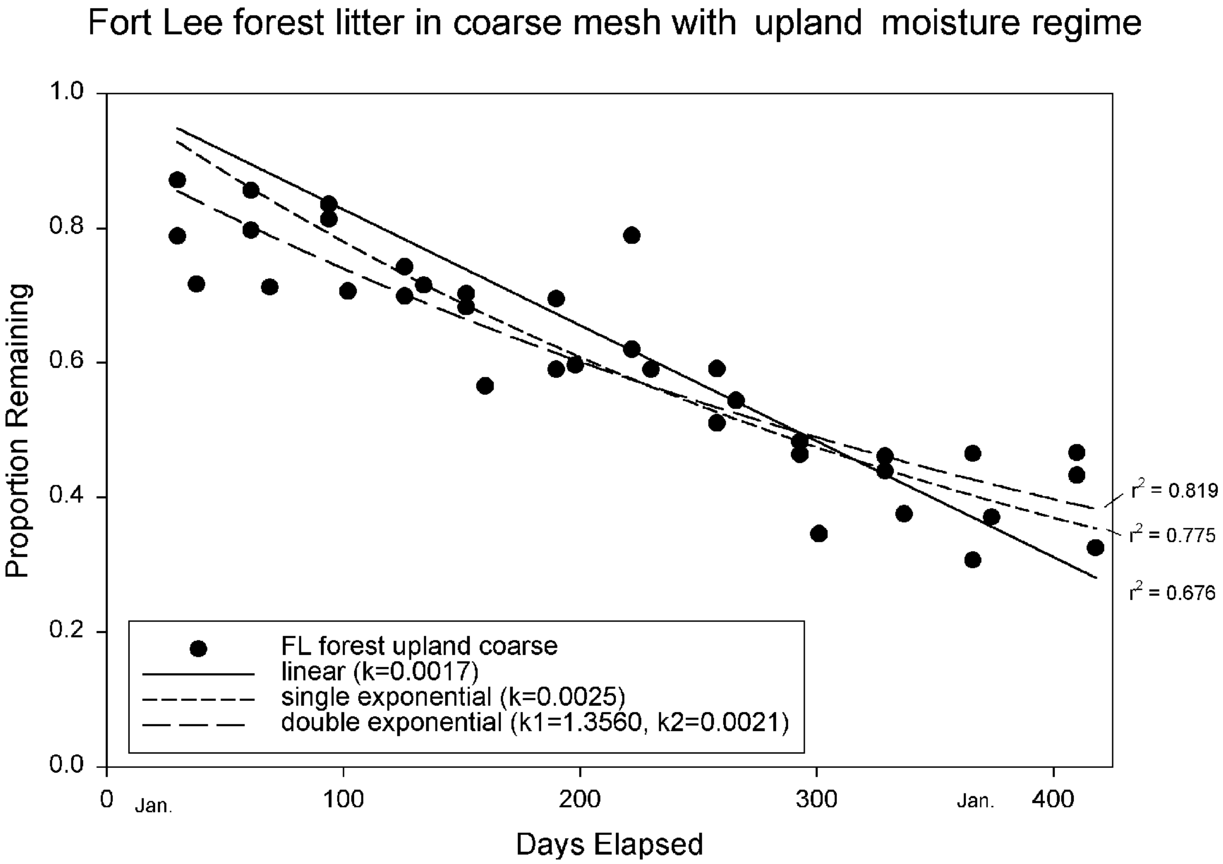

Figure 12. Decomposition models for coarse mesh litterbags with upland moisture regime in the Fort Lee created wetland.

of often 20-30% during the first month of decomposition due to leaching and loss of labile material from the litter (Fig. 9-12). Double exponential models produced as good or better fits based on r^2 values than single exponential models for all litterbags containing forest litter (Table 4).

The decay rates at both the FL and CC wetlands showed similar patterns along the moisture gradient for forest litter decomposition. The wet sites showed the highest rates, while the upland regime at FL exhibited the lowest. The reference and pond were intermediate, with the pond treatments generating higher rates for the coarse mesh litterbags and the reference sites for the fine mesh litterbags. The decay rates at FL were faster than at the CC wetland for each moisture regime. This difference could be due to a number of factors including differences in the created wetland ages, seasonal climatic variations, or more likely, differences in moisture levels between the FL wetland which remained wetter due to ground-water inputs and the CC wet flat wetlands which relied on precipitation and runoff. This second suggestion is supported by the pattern of decomposition. After the initial leaching loss, decomposition at FL followed a relatively smooth, although variable, exponential decay pattern (Figure 9a, 10a, 11a, 12). The pattern of decomposition at CC showed a second sharp increase in weight loss at about 200 (6-7 mo.) days for the created wetland (Figure 9b and 11b) or at 250 (8-9 mo.) days for the adjacent natural wetland (Figure 10b) and a plateau between 100 and 200 days (3-6 mo.) (Figure 9b, 10b, 11b). These plateaus correspond to periods with little to no rainfall and dry conditions within the CC wetland. The marked increase in weight loss corresponded to the end of the drought and higher water levels within the wetland. The lag of the moisture effect in the reference wetland is likely due to the higher water demands of the forest relative to the young emergent created wetland.

While care was taken to select similar site conditions for each of the moisture gradient replicates, the high variability of the results for the pond regime at the FL created wetland (Figure 11b) indicates differences among replicates. The 2nd replicate, while also permanently ponded with similar surrounding vegetation, was located slightly deeper (approx. 0.25m) and in a larger water body than the 1st and 3rd replicate (Figure 13a and 13b). The cause of the faster decay observed in the 2nd replicate is unknown, but was likely related to dissolved oxygen or biota. Since the fine mesh litterbags did not show a similar difference among replicates, the differences are probably due to macrofauna within the larger pond and not found in the smaller shallower ponds of the other two replicates.

Marsh Litter Decomposition

Linear and single exponential models had similar r^2 values for marsh litter (Table 4). Double exponential models did not have any better fit than single exponential models, and in most cases were essentially equivalent to the single exponential models. The marsh litter did not exhibit the characteristic initial rapid weight loss of soluble and labile constituents, and did not show decreases in decomposition rate until after almost 12 months had elapsed (Figure 14-17). The marsh litter was collected as senesced standing litter from quadrats within the FL created wetland. With no annual leaf-fall event as in the forest system, much of the litter collected may have been pre-leached of soluble and readily labile elements as the litter stood prior to collection. Additionally, marsh litter, dominated by *Typha* spp. in this case, is more recalcitrant than tree litter and may have less readily leachable/labile elements (see Chapter 1, Table 2). For these reasons, linear models fit the decomposition data well and often showed slightly higher r^2 values than the single exponential model. Wieder and Lang (1982) noted similar results and suggested

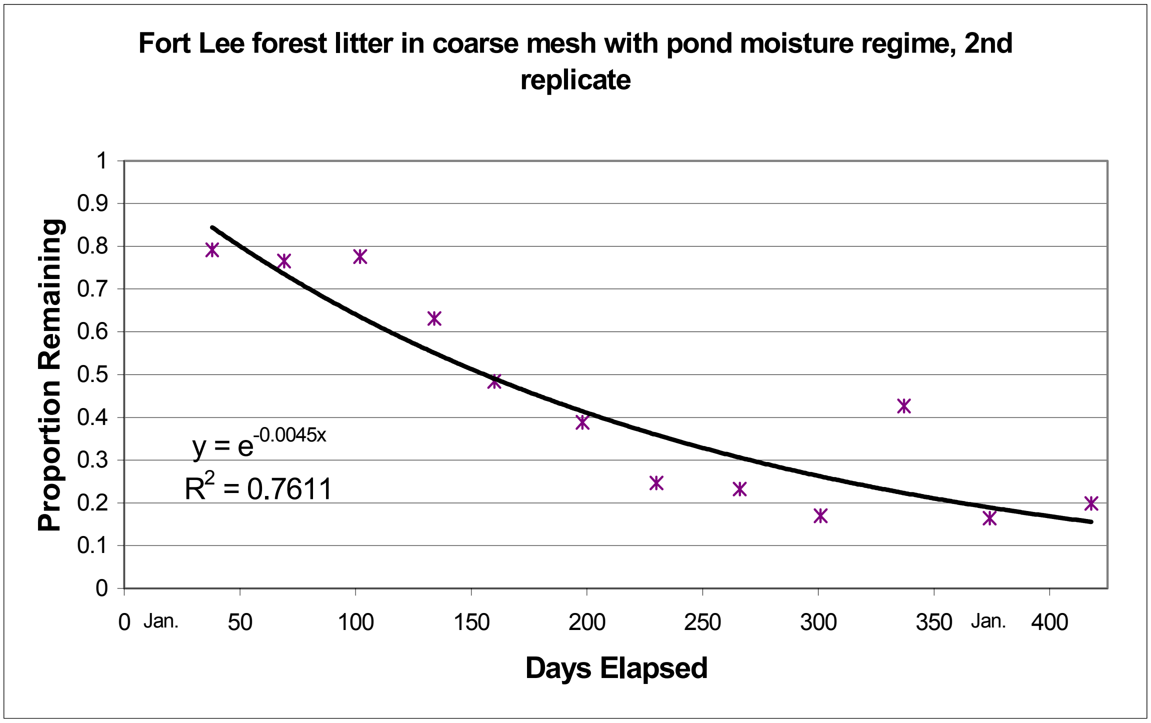

Figure 13a. Decomposition of forest litter in coarse mesh litterbags in the Fort Lee created wetland with a pond moisture regime, 2nd replicate.

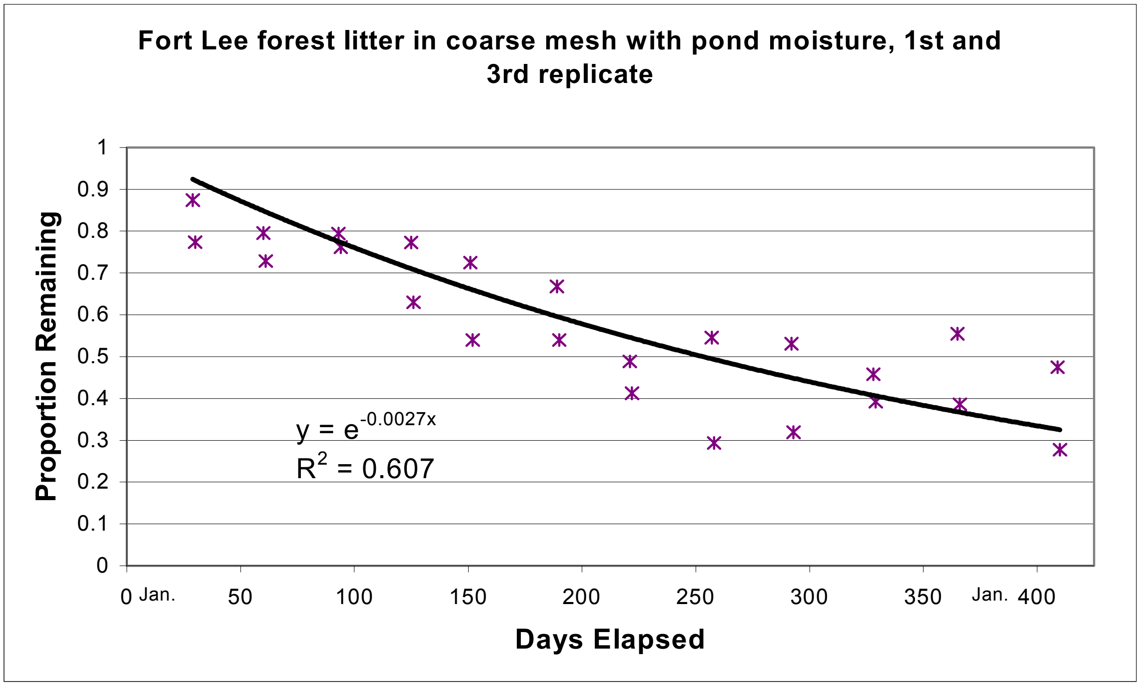

Figure 13b. Decomposition of forest litter in coarse mesh litterbags in the Fort Lee created wetland with a pond moisture regime, 1st and 3rd replicate.

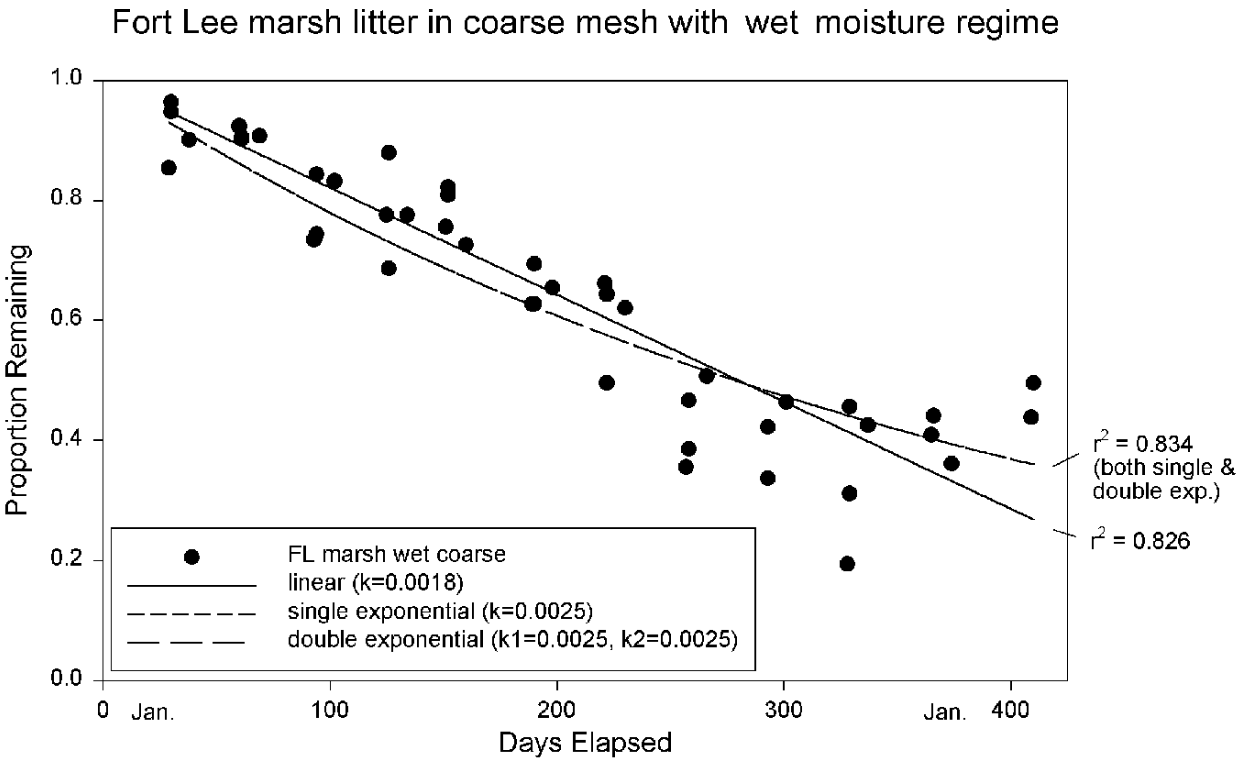
Fort Lee marsh litter in coarse mesh with wet moisture regime

Figure 14a. Decomposition models of marsh litter in coarse mesh litterbags with a wet moisture regime in the Fort Lee created wetland.

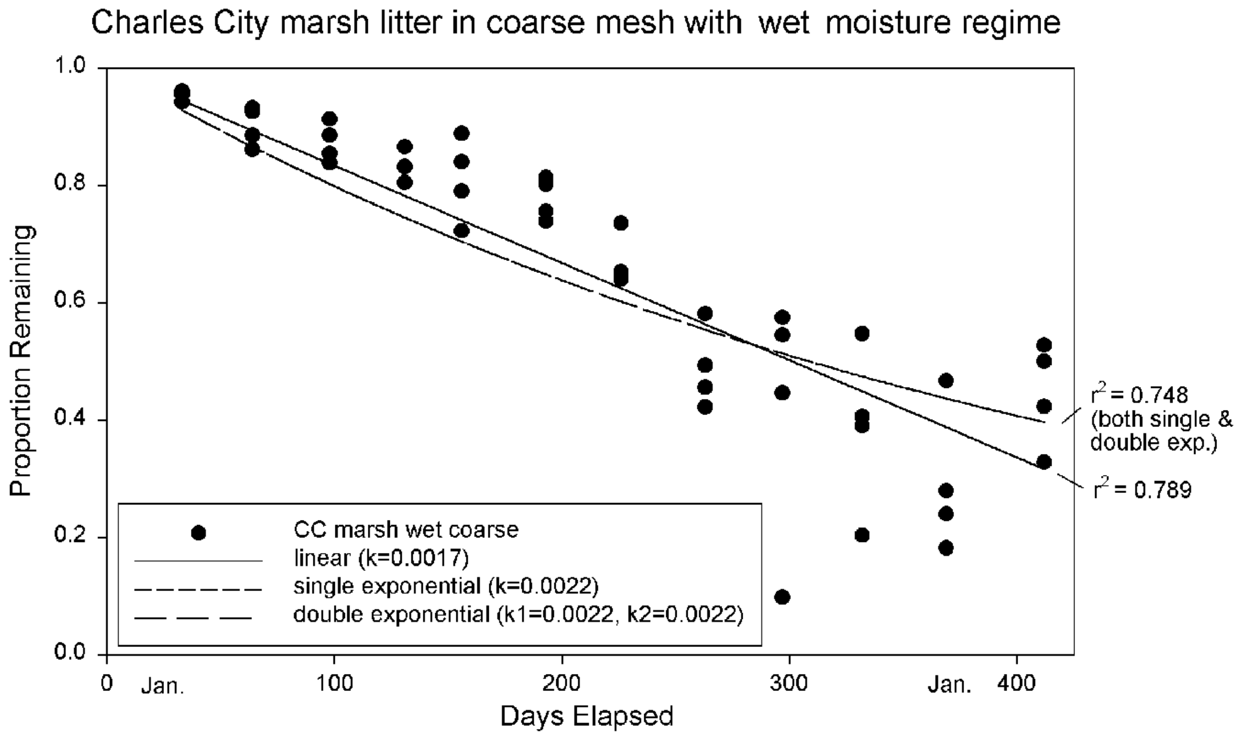
Charles City marsh litter in coarse mesh with wet moisture regime

Figure 14b. Decomposition models of marsh litter in coarse mesh litterbags with a wet moisture regime in the Charles City created wetland.

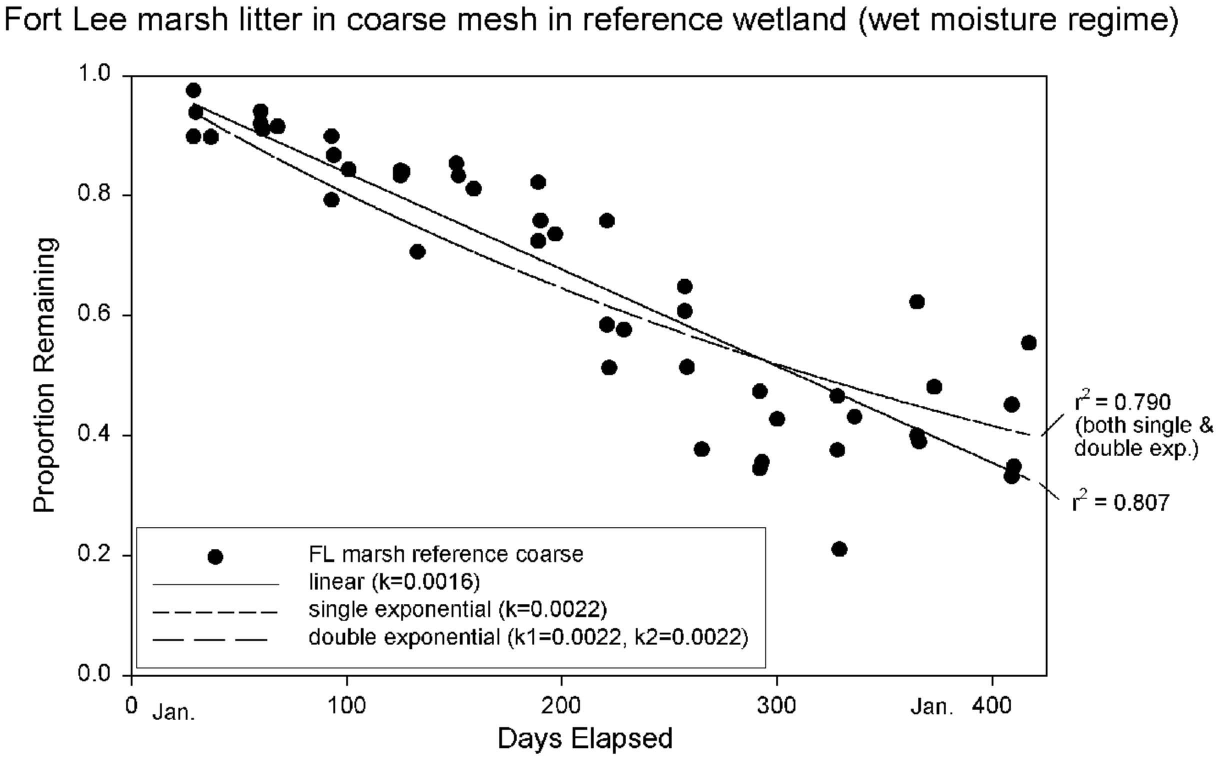

Figure 15a. Decomposition models of marsh litter in coarse mesh litterbags in the Fort Lee adjacent natural wetland (similar moisture regime to wet in created wetland).

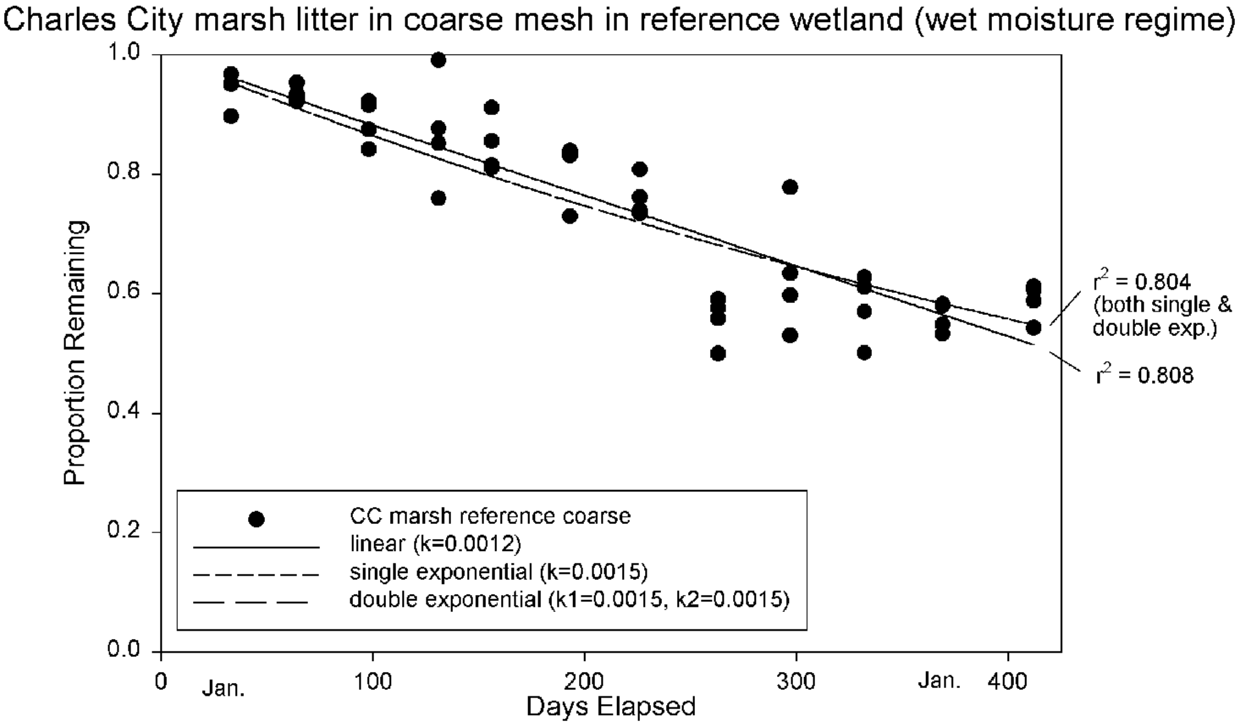

Figure 15b. Decomposition models of marsh litter in coarse mesh litterbags in the Charles City adjacent natural wetland (similar moisture regime to wet in created wetland).

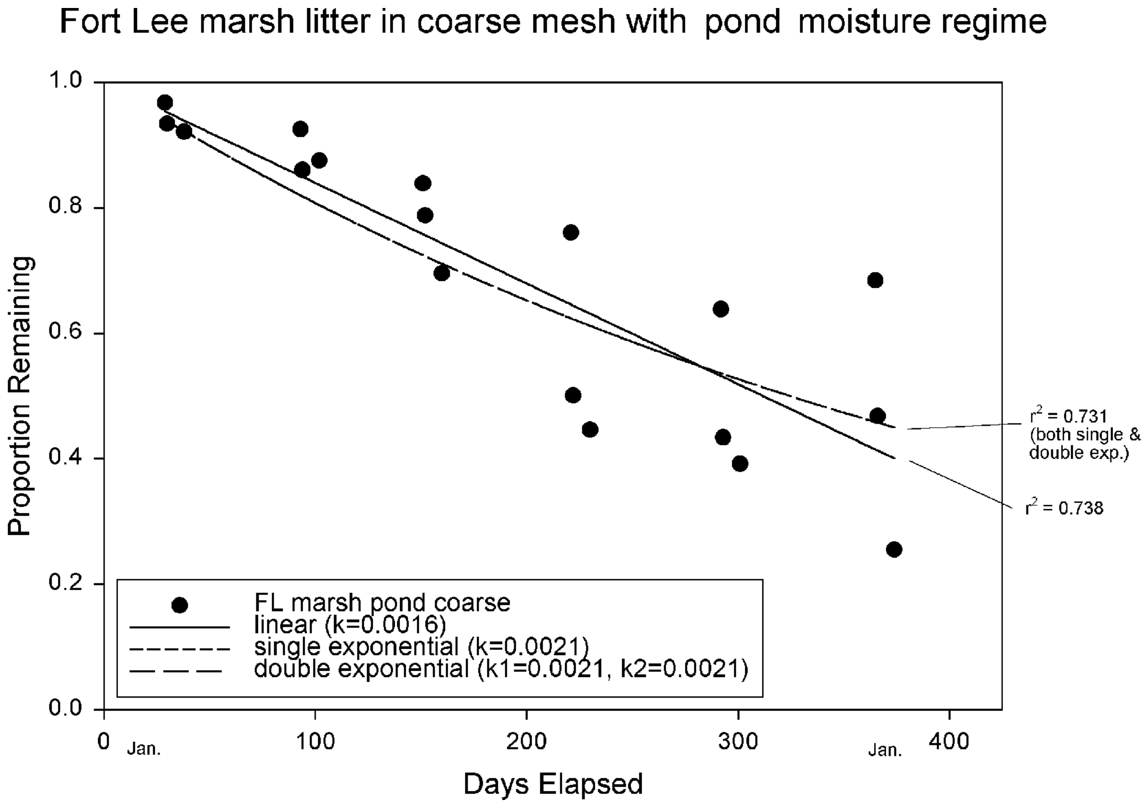

Figure 16. Decomposition models of marsh litter in coarse mesh litterbags with a pond moisture regime in the Fort Lee created wetland.

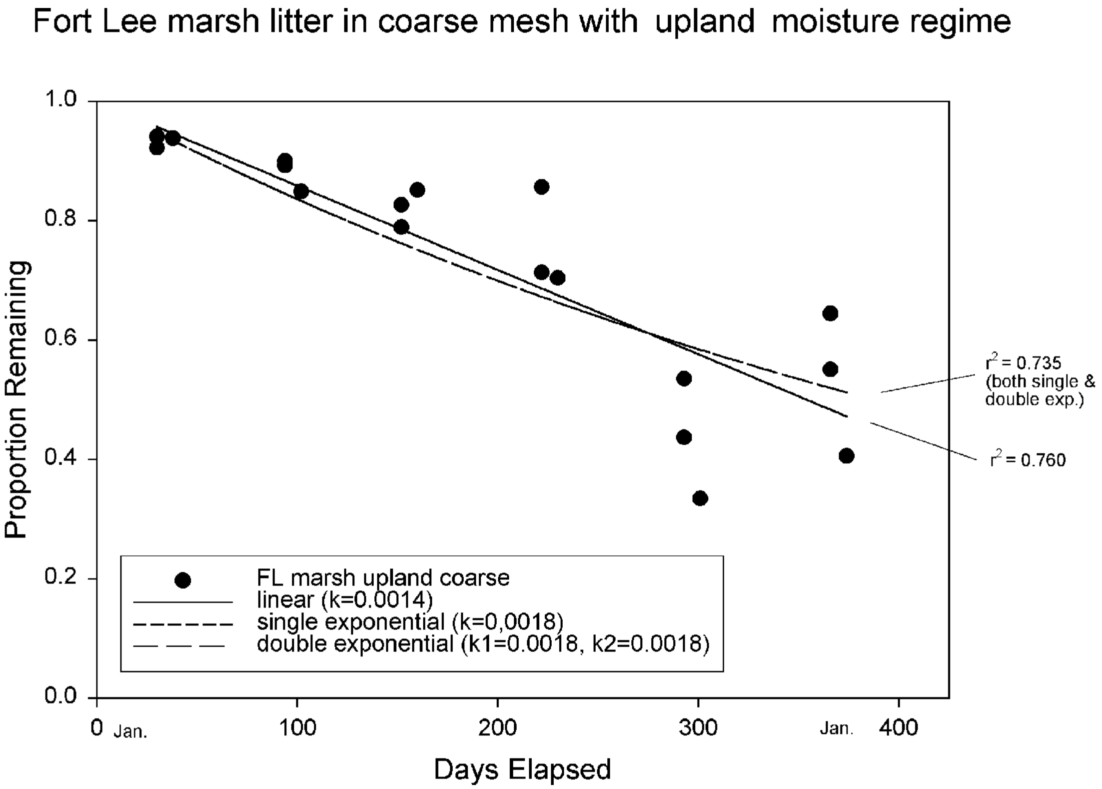

Figure 17. Decomposition models of marsh litter in coarse mesh litterbags with an upland moisture regime in the Fort Lee created wetland.

that for some recalcitrant litters it may take a year or more for the more typical exponential decay pattern to develop. Since the single exponential model better fits the theoretical understanding of decomposition and the decay rates seem to be decreasing by the end of the period examined (i.e. 350+ days), single exponential are considered better models than linear despite the improved r^2 values (Table 4, Figure 14-17). With the majority of the decomposition results falling within a relatively linear portion of the exponential decay curve, however, care should be exercised in extrapolating estimates from outside the time range examined or in comparing decay constants for the marsh litter.

Similar weight loss patterns were exhibited between moisture regimes, wetlands and litterbag mesh sizes with the marsh litter and the forest litter. Wet litter decomposed at the faster rate, upland litter decayed the slowest and reference and pond were intermediate (Table 4). The older created wetland, FL, showed higher decay rates than the CC wetland, although this may be due to differences in the types of wetlands and water sources instead of simple age. Coarse meshed litterbags showed a higher decay rate than fine mesh litterbags given the same moisture regime and wetland (Table 4). The differences between different mesh sizes is often attributed to the action of macrodetritivores which are excluded from the fine mesh litterbags, but also may be due to a bag effect where some small fragments of litter are retained by the fine mesh, yet fall through the coarse mesh.

Comparisons of Treatments – Analysis of Variance and Paired Treatment Effects

Forest Litter Decomposition

The overall moisture gradient patterns described by the decomposition models (Table 4) were supported by the statistical differences noted among treatments at various sampling dates.

Overall weight loss was greatest for the wet moisture regime and lowest for the upland moisture regime in the FL created and adjacent natural wetlands (Fig. 18a). The pattern was the same in the CC wetlands, with the wet regime exhibiting greater weight loss than the reference or pond regimes (Figure 18b). This pattern of highest decomposition in the areas with intermediate moisture levels coupled with slower rates in wetter and drier areas is consistent with the literature-based theory of decomposition (Table 2). The greater weight loss in the wet mitigation regime versus the reference area is surprising, however, since the moisture regimes were similar (i.e. 0-4 cm standing water during winter). With the relatively intact litter layer and associated detritivores, it was expected that litter in the natural adjacent wetlands would decompose more rapidly. The cause of the more rapid decomposition in the created wetland is unclear, but possible mechanisms are discussed later.

The fine and coarse mesh size litterbags in the FL and CC wetlands exhibited some differences in weight loss over time (Fig. 19a & b). The coarse mesh, as expected, showed greater weight loss than the fine mesh, especially later in the study. While this difference is often attributed to the action of macrofauna which are excluded from the fine mesh litterbags, this comparison is potentially confounded with bag effects from the loss of litter fragments or moisture differences, and by possible ecological effects such as exclusion of macropredators and enhancement of the meso-fauna such as mites. While there was not a significant overall difference observed between mesh sizes in the CC wetland, differences were significant for two of the moisture gradient/mesh size combinations (Figure 20 a-c). The two moisture regimes within the created CC wetland, wet and pond, showed greater weight loss for coarse mesh litterbags while there was not a significant relationship in the adjacent natural wetland. This suggests either a difference in macrodetritivores between the natural and created wetlands and/or

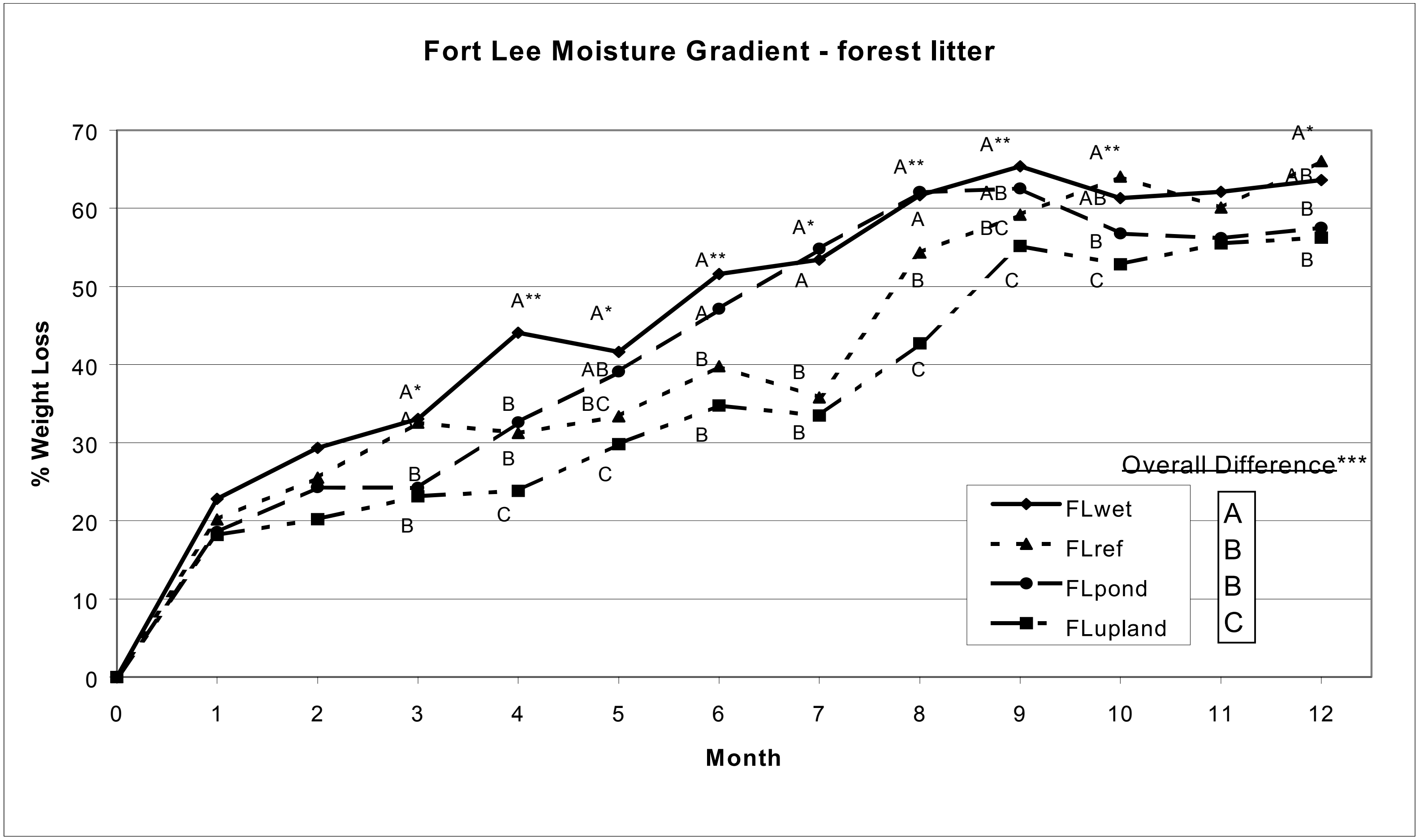

Figure 18a. Percent weight loss in the Fort Lee created and adjacent natural wetland by moisture gradient.

* Average values at a given date with the same letter are not significantly different (p=0.05).

** Average values at a given date with the same letter are not significantly different (p=0.10).

*** Overall moisture gradient treatment differences; regimes with the same letter are not significantly different (p=0.05).

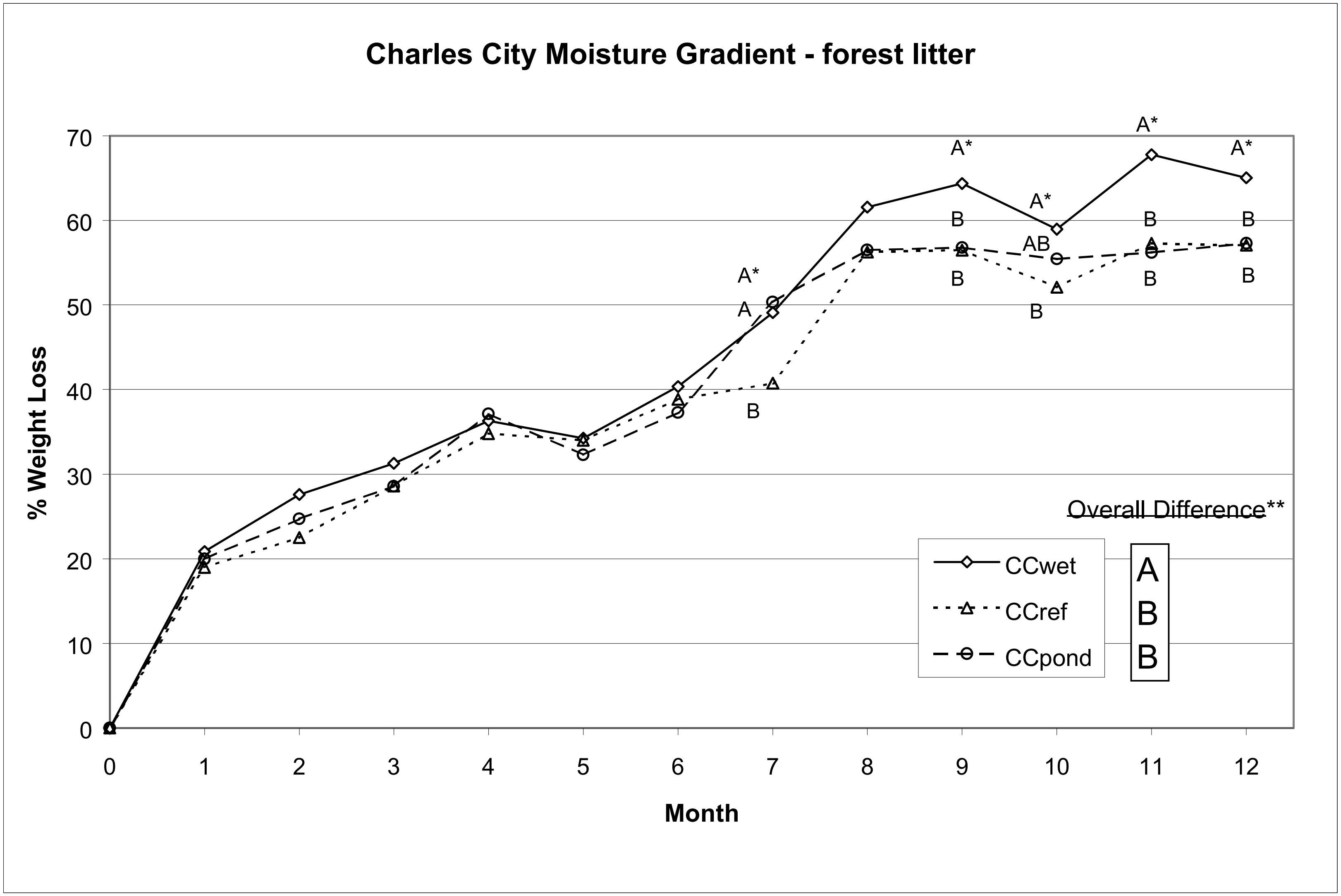

Figure 18b. Percent weight loss in the Charles City created and adjacent natural wetlands by moisture gradient.

* Average values at a given data with the same letter are not significantly different (p=0.05)

** Overall moisture gradient treatment differences; regimes with the same letter are not significantly different (p=0.05)

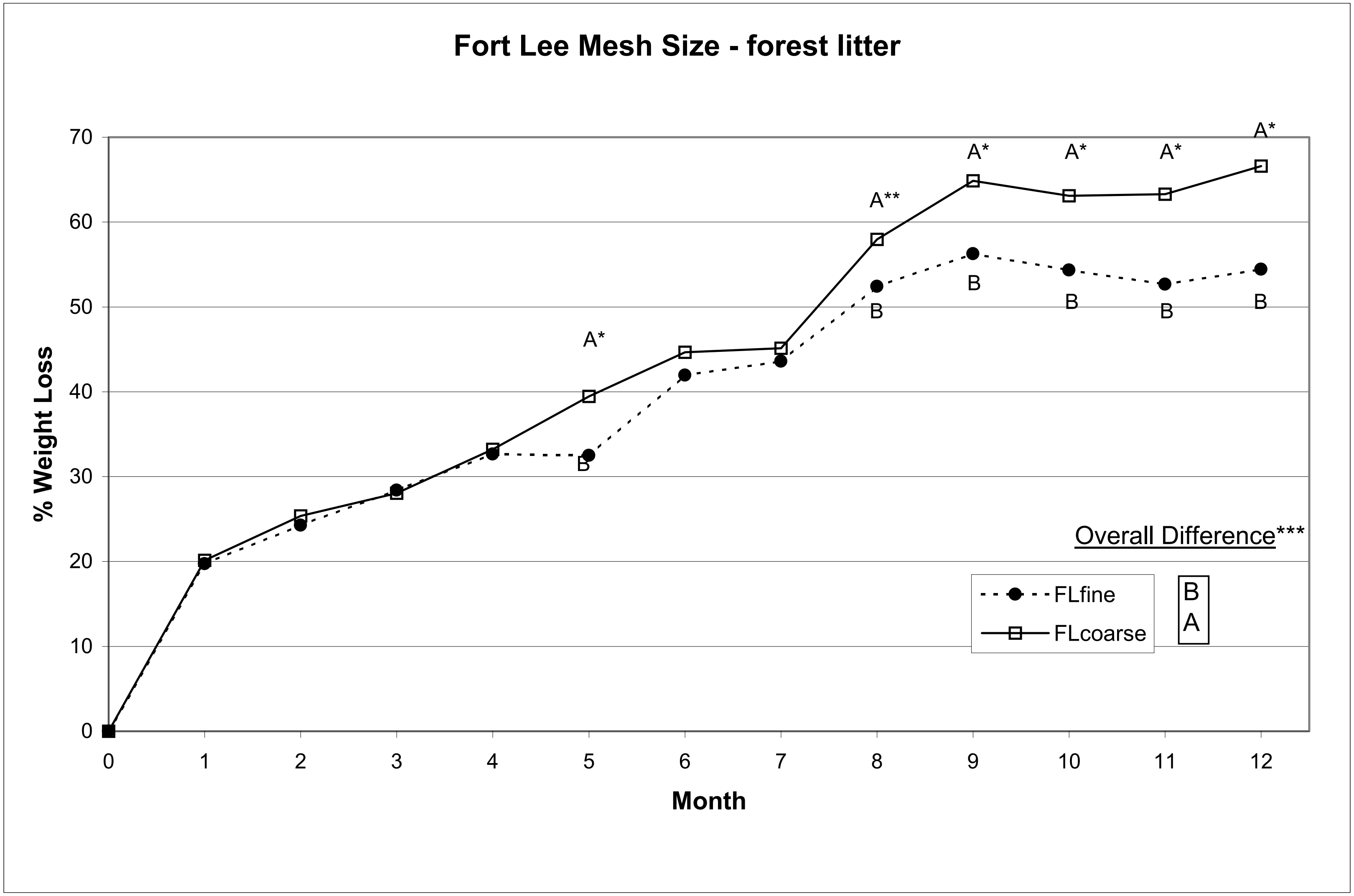

Figure 19a. Percent weight loss in the Fort Lee created and natural adjacent wetlands for fine and coarse mesh size litterbags.
* Average values at a given date with the same letter are not significantly different (p=0.05), ** (p=0.10).
*** Overall mesh size treatment differences; mesh sizes with the same letter are not significantly different (p=0.05).

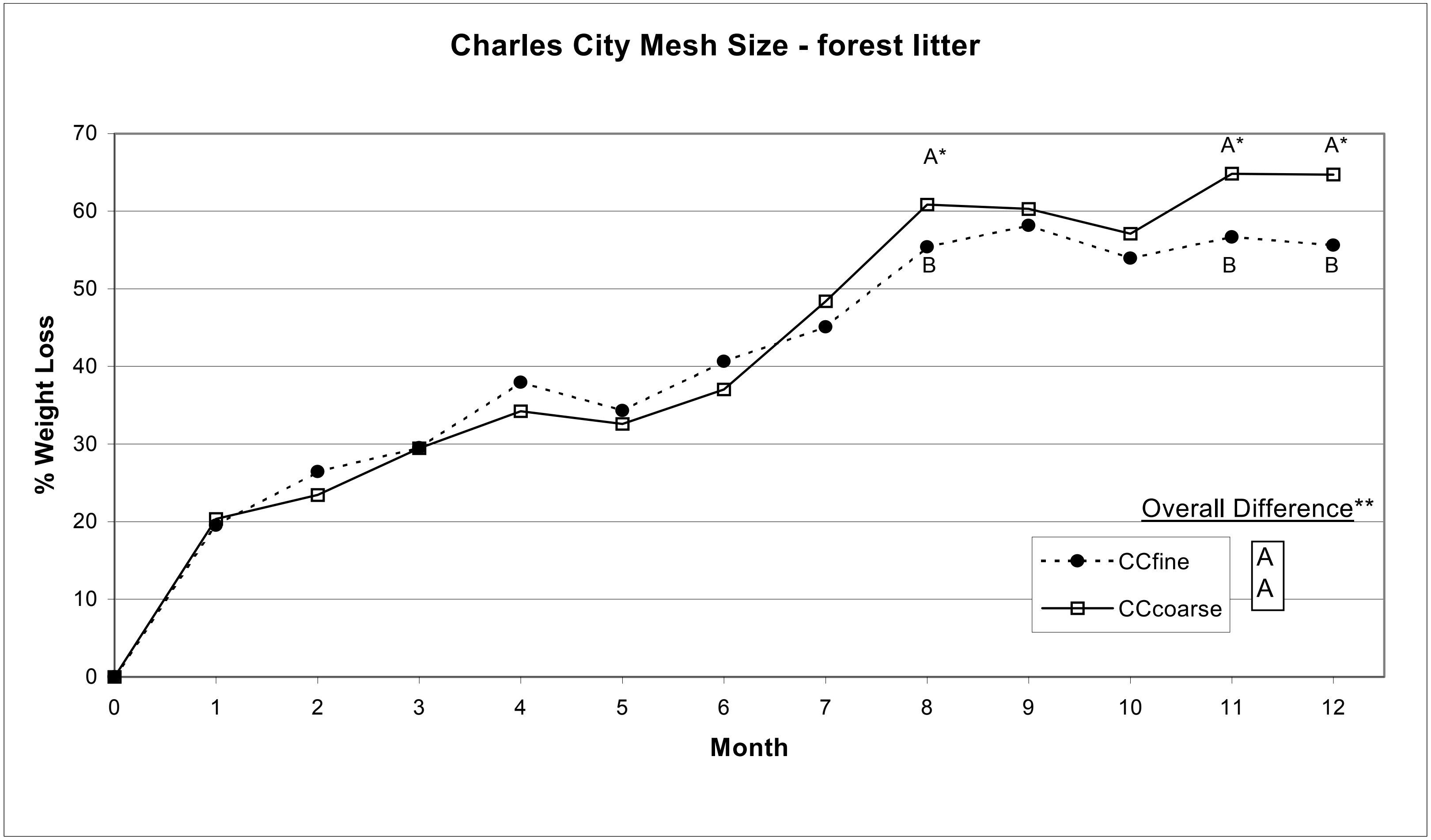

Figure 19b. Percent weight loss in the Charles City created and natural adjacent wetlands for fine and coarse mesh size litterbags.

* Average values at a given date with the same letter are not significantly different (p=0.05).

** Overall mesh size treatment differences; mesh sizes with the same letter are not significantly different (p=0.05).

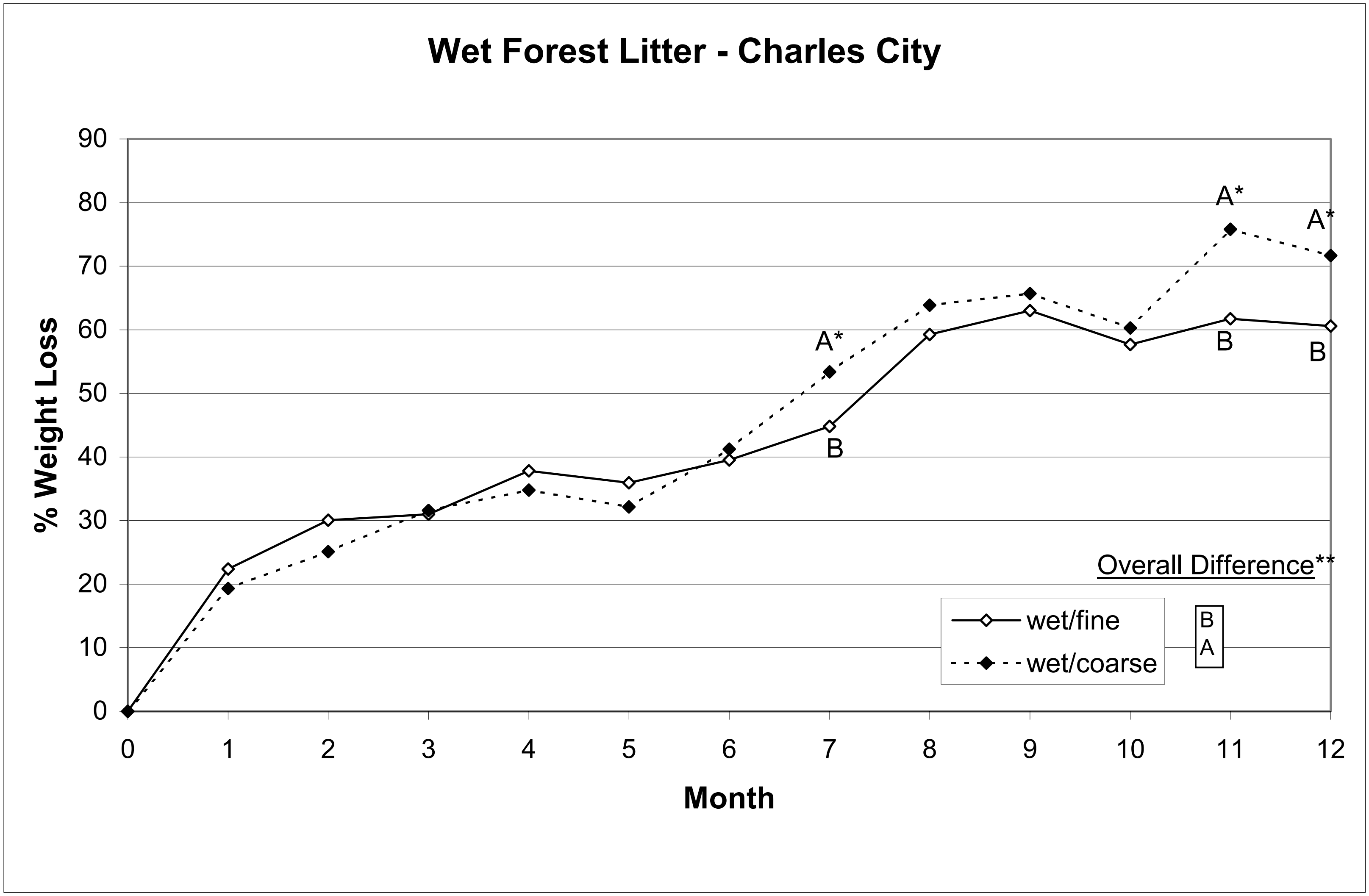

Figure 20a. Percent weight loss of forest litter in fine or coarse mesh litterbags in the Charles City wetland with wet moisture regime.
* Average mesh size values with the same letter are not significantly different for that month (p=0.05).
** Overall mesh size treatment differences; mesh sizes with the same letter are not significantly different (p=0.05).

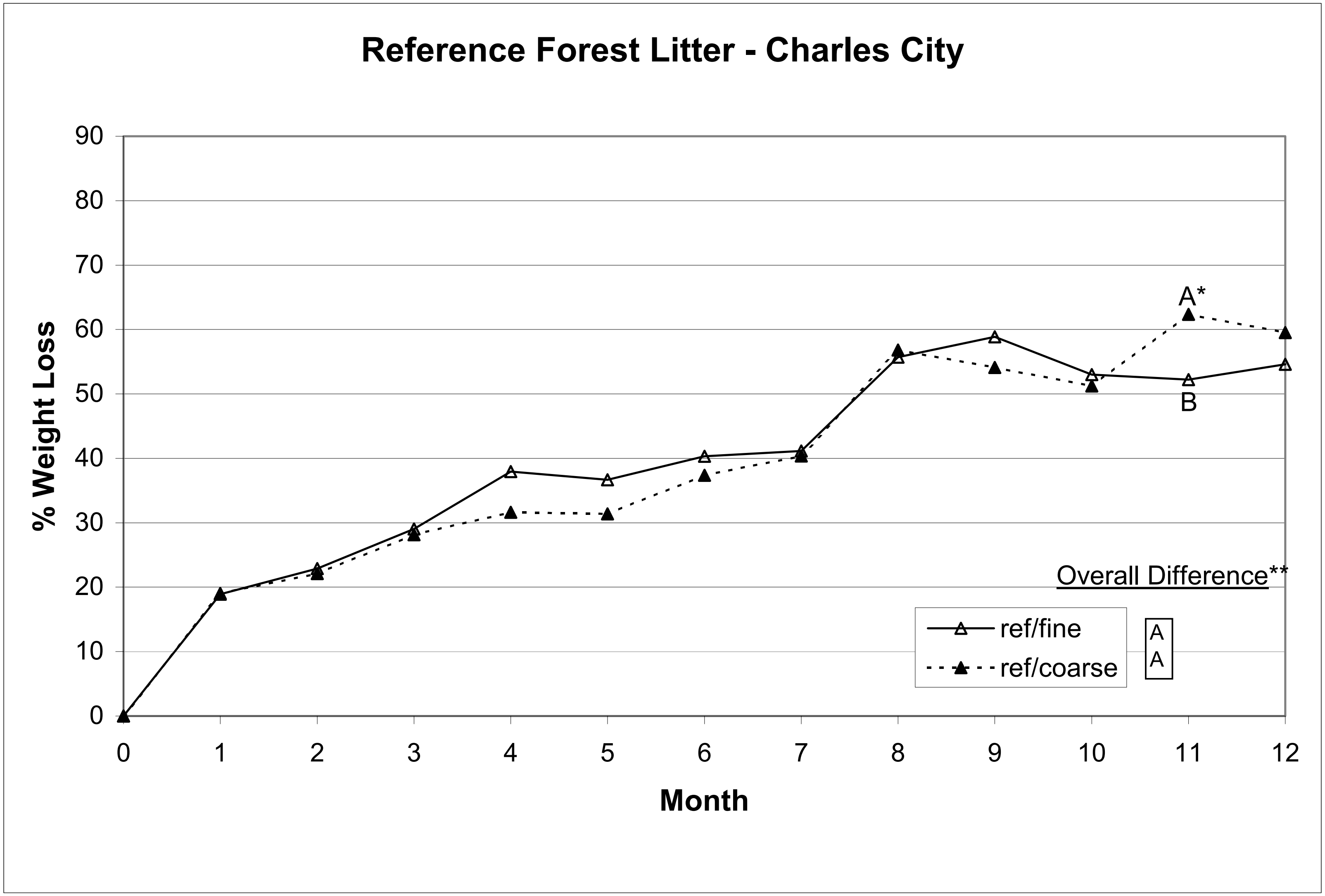

Figure 20b. Percent weight loss of forest litter in fine or coarse mesh litterbags in the Charles City adjacent natural wetland.
* Average mesh size values with the same letter are not significantly different for a given month (p=0.05).
** Overall mesh size treatment differences; mesh sizes with the same letter are not significantly different (p=0.05).

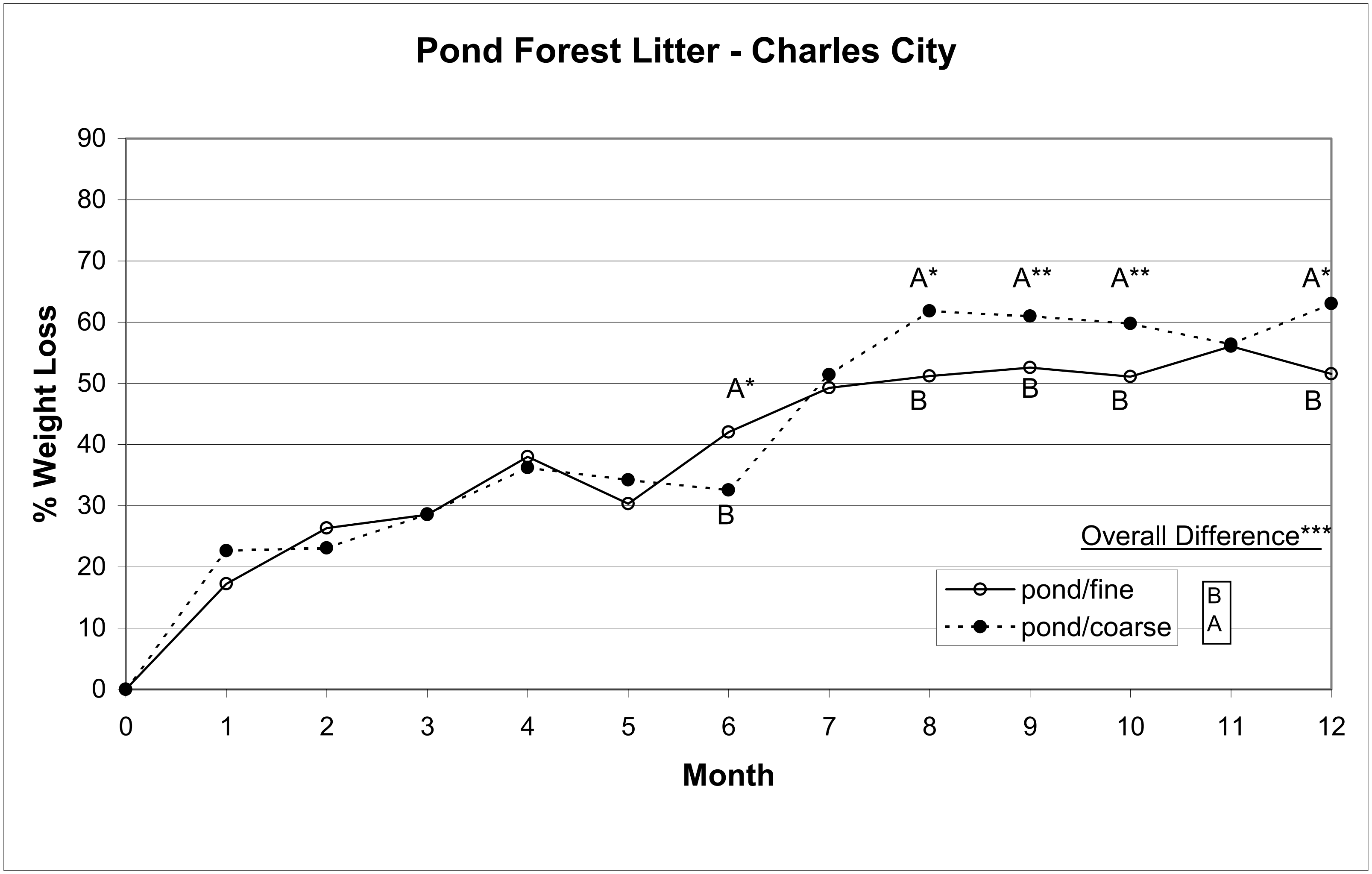

Figure 20c. Percent weight loss of forest litter in fine or coarse mesh litterbags in the Charles City created wetland with pond moisture regime.

* Average mesh size values with the same letter are not significantly different for a given month (p=0.05); ** (p=0.10).

*** Overall mesh size treatment difference; mesh sizes with the same letter are not significantly different (p=0.05) another factor that increased litter fragmentation within the created wetland. Litterbags became incorporated into the clay surface soil especially in the pond moisture regime and subsequently were dried and re-wetted during the study, perhaps increasing physical fragmentation.

Marsh Litter Decomposition

The relatively recalcitrant marsh litter generated fewer treatment effects than the forest litter. While a similar effect of moisture regime was observed with the marsh litter and the forest litter in the FL and CC wetlands, there were some important differences (Figure 21a-b). While the wet regime exhibited greater weight loss than the reference treatment for the CC created and natural wetlands, no difference was found between the FL created and adjacent natural wetlands. It appears that biotic or physical forces, which could have increased fragmentation within the wet regime relative the reference, found the marsh litter less palatable and/or more resistant. The wetter pond and drier upland regimes in the created FL wetland produced lower weight losses for marsh litter than the intermediate wet regime; similar to the pattern for forest litter.

Coarse mesh litterbags lost more marsh litter weight than fine mesh litterbags in the FL wetland, similar to the results for the forest litter (Figure 22). Litterbag mesh size effects were more complicated for the CC created and natural wetlands (Figure 23). Marsh litter in coarse mesh lost more weight than litter in fine mesh in the wet regime of the created wetland, while there was no mesh size effects in the adjacent natural wetland (Figure 23). Except for the lack of marsh litter being examined in the pond moisture regime, this is the same pattern seen in the forest litter (Figure 20 a-c). Again, it is unclear whether this difference is due to variation in biotic or physical forces.

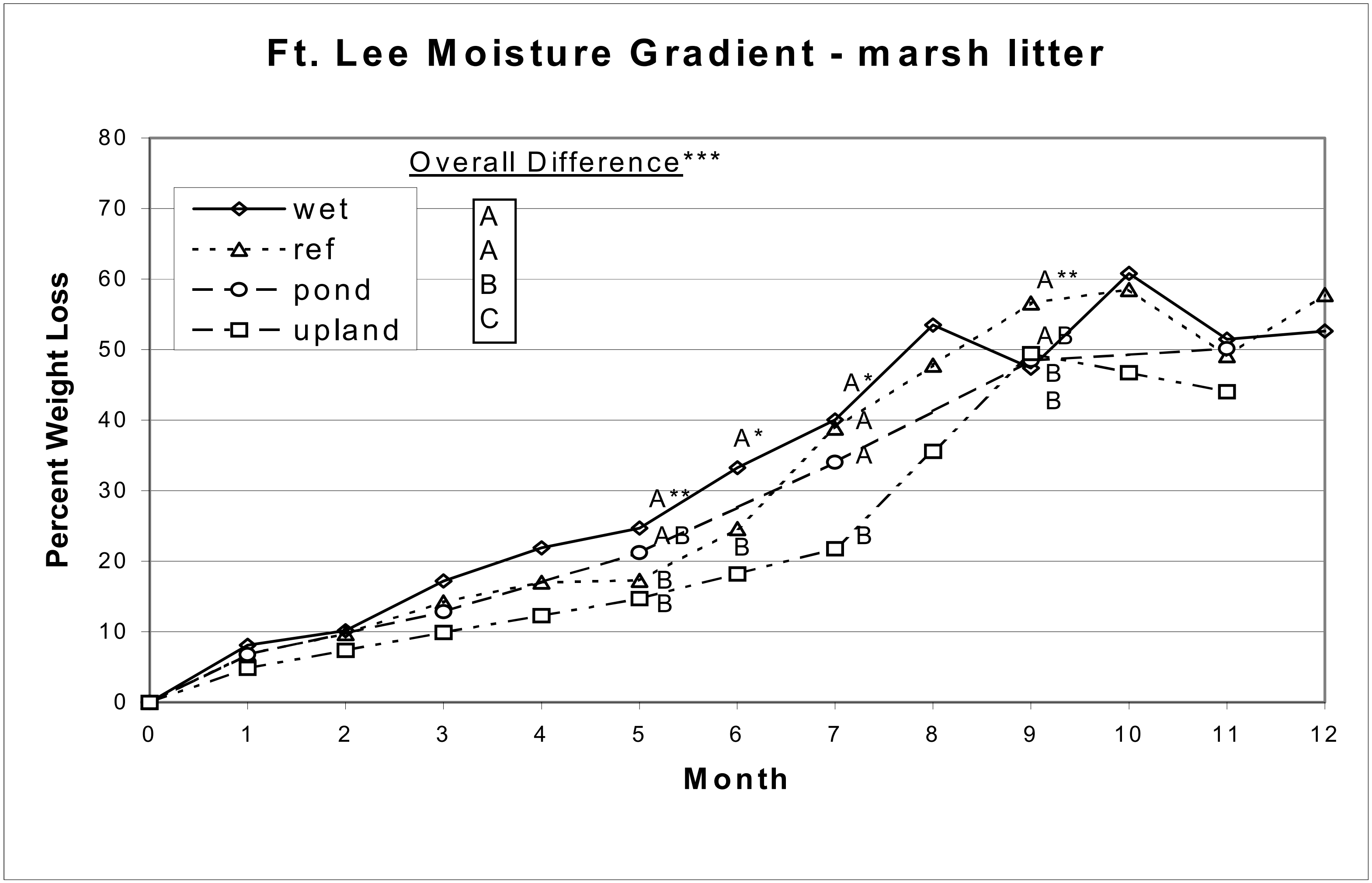

Figure 21a. Percent weight loss of marsh litter in the Fort Lee created and adjacent natural wetlands by moisture gradient.
* Average moisture regime values with the same letter are not significantly different (p=0.05); ** (p=0.10).
*** Overall moisture gradient treatment differences; regimes with the same letter are not significantly different (p=0.05).
Note: Marsh litterbags were only collected from the upland and pond moisture regimes on odd numbered months.

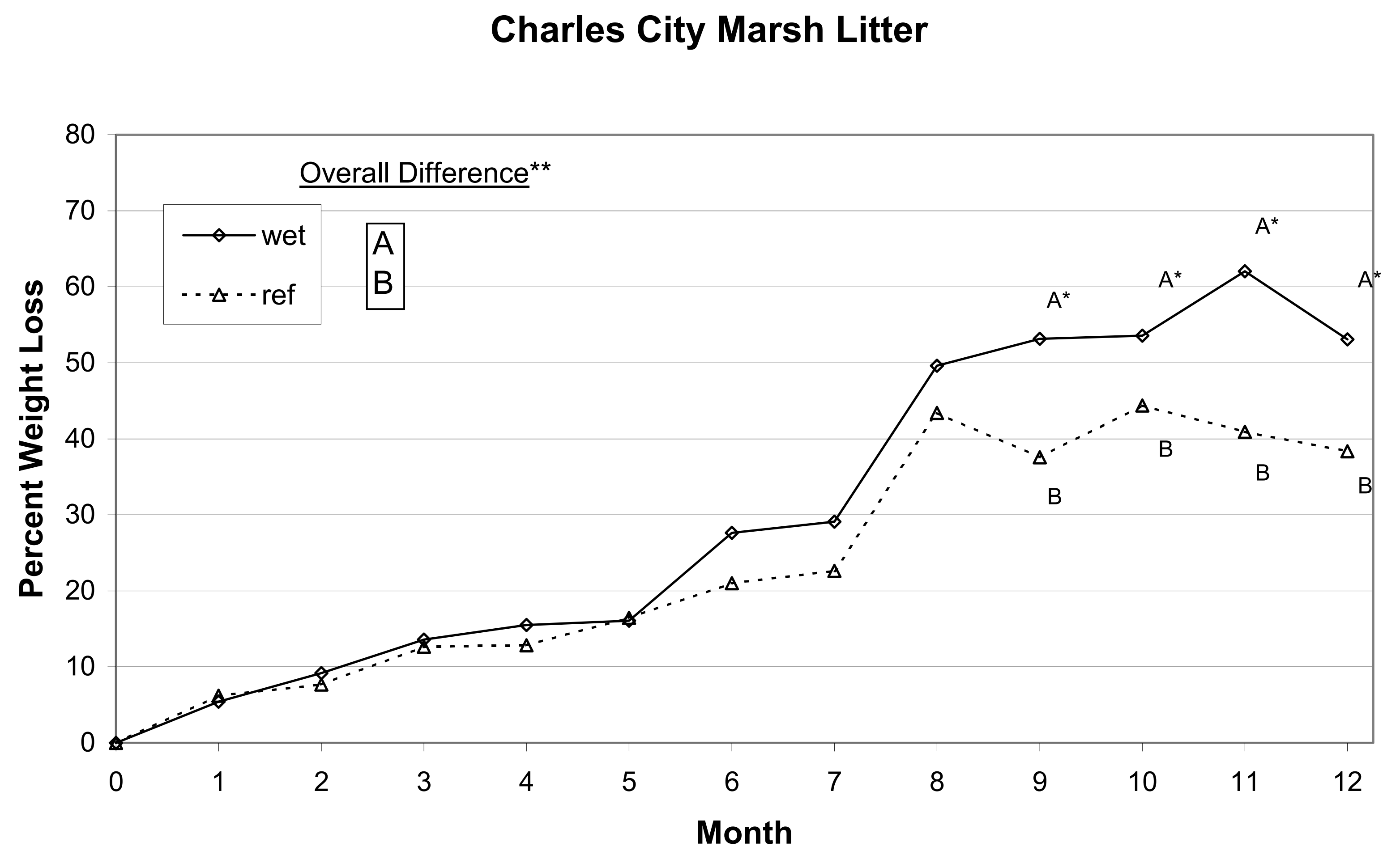

Figure 21b. Percent weight loss of marsh litter in the Charles City created and natural adjacent wetlands by moisture gradient.
* Average values at a given date with the same letter are not significantly different (p=0.05).
** Overall moisture regime treatment differences; regimes with the same letter are not significantly different (p=0.05).

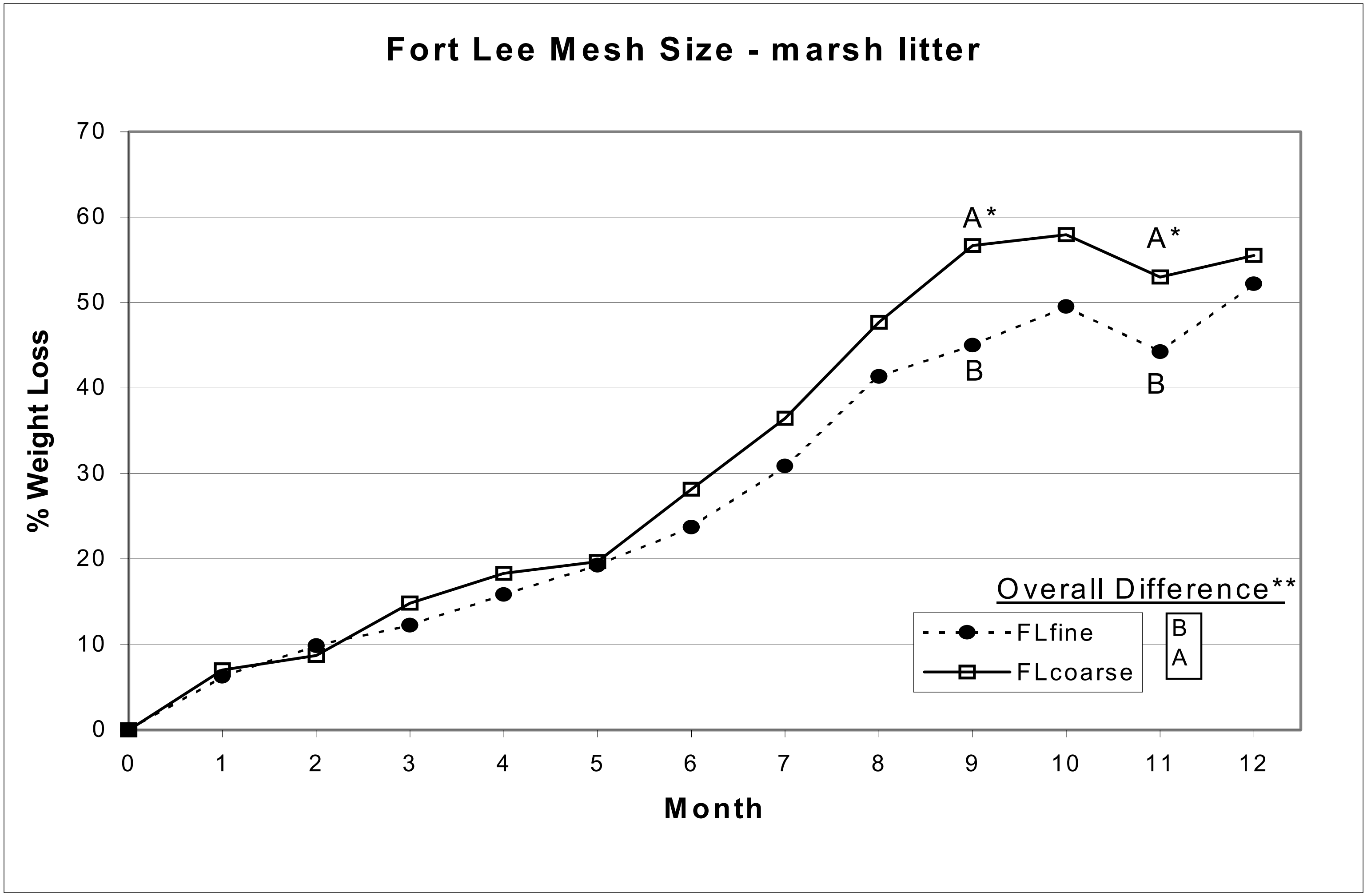

Figure 22. Percent weight loss for fine and coarse mesh litterbags in the Fort Lee created and natural adjacent wetlands.
* Average mesh size values with the same letter are not significantly different (p=0.05).
** Overall mesh size treatment difference; mesh sizes with the same letter are not significantly different (p=0.05).
Note: Due to incomplete experimental design for marsh litter, statistical comparisons were only possible for odd numbered months

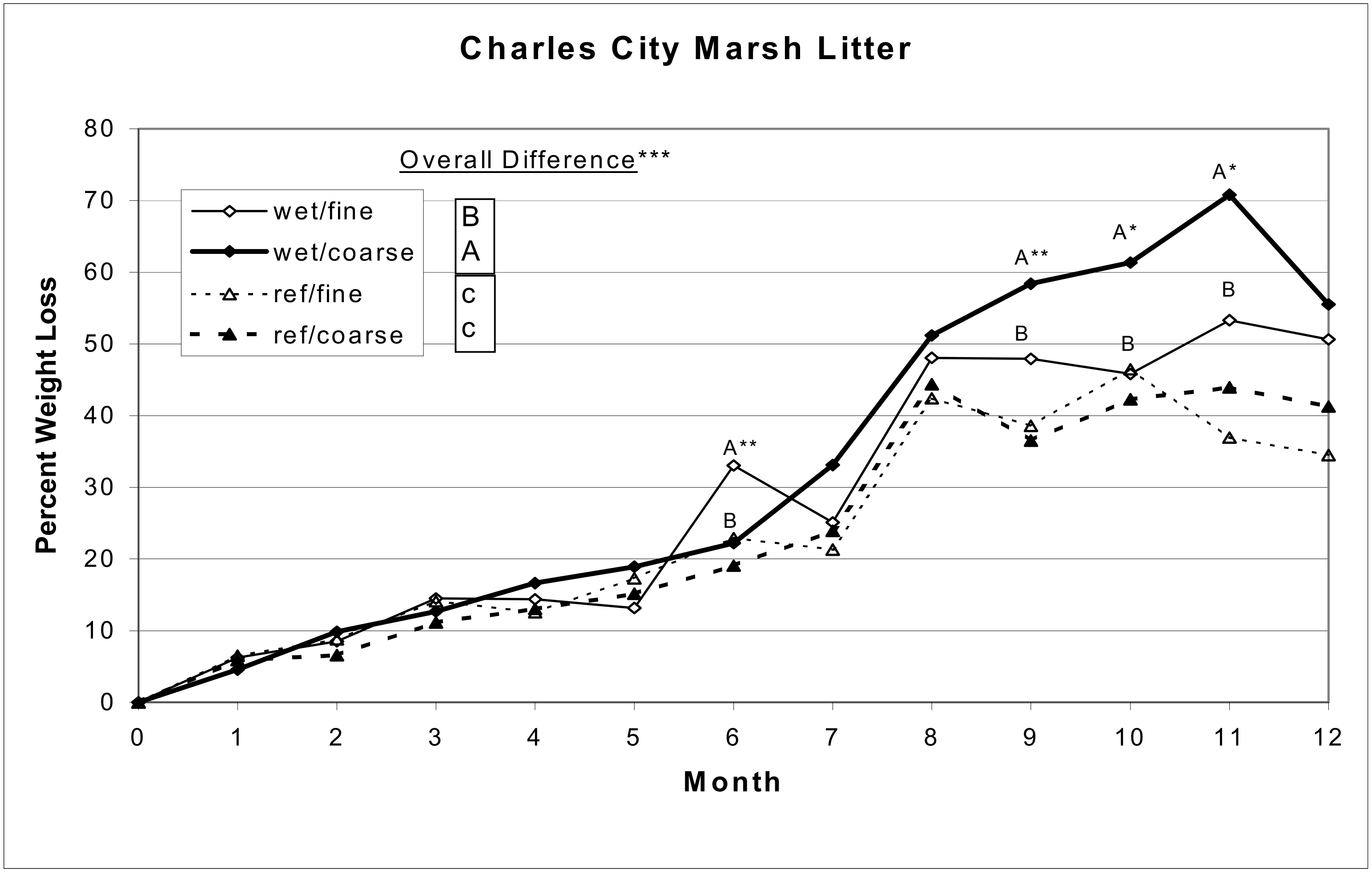

Figure 23. Percent weight loss for mesh size/moisture regime combinations within the Charles City created and natural adjacent wetlands.

* Average mesh size values by moisture regime with the same letter are not significantly different for a given month (p=0.05); ** (p=0.10)

*** Overall moisture regime/mesh size treatment differences; treatments with the same (upper or lower case for wet and reference respectively) letter are not significantly different (p=0.05).

During the final month of the study, some treatments occasionally exhibited an apparent increase in weight remaining (e.g. wet/coarse in Fig. 23). Since any missing or damaged litterbags were accumulated in this final collection, sample sizes were smaller and average values were less reliable (i.e. the pattern reflects variability, not an increase in weight). Accumulation of sediment with high organic matter contents or small pieces of extraneous litter would not be corrected for through the ash-free weight procedure and would explain the apparent increase in litter weight.

Carbon to Nitrogen (C:N) Ratios

The ratio of C:N in litter is an indicator of litter quality or decomposability, and can be examined to assess the relative degree of decomposition over time. Relatively low initial C:N ratio values suggest a high quality litter, which is more palatable and typically decomposes faster (see Chapter 1). In this study, forest litter had a lower C:N ratio than marsh litter and would have been expected to decompose faster due to C:N values of 62 (range of 52-76) and 72 (range of 45-94), respectively. This prediction was correct, as decay rates and mean comparisons of weight loss indicated faster decomposition for forest litter in all of the wetlands examined. As decomposition progressed, the C:N ratio of litter decreased as microbes gained energy and evolved gaseous C from the litter, typically approaching a value close to the C:N ratio of stable soil organic matter (12-20 for O and A horizons of CC adjacent natural wetland). After over one year of decomposition, forest litter C:N ranged between 20-30, while marsh litter remained higher (30-40) (Fig. 24 & 25). Coupled with the slower weight loss, these higher C:N values indicate that the marsh litter is more recalcitrant than the forest litter.

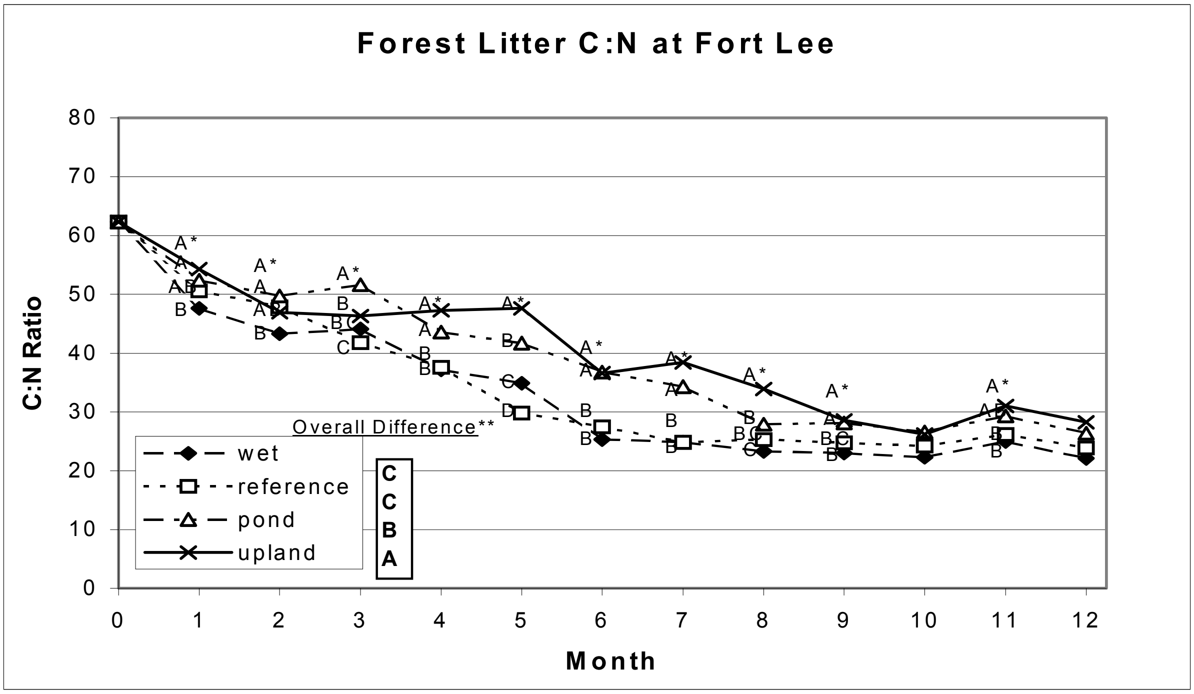

Figure 24a. C:N ratio of forest litter by moisture regime in the Fort Lee created and adjacent natural wetlands.

* Average values at a given date with the same letter are not significantly different (p=0.05)

** Overall moisture gradient treatment differences; regimes with the same letter are not significantly different. (p=0.05).

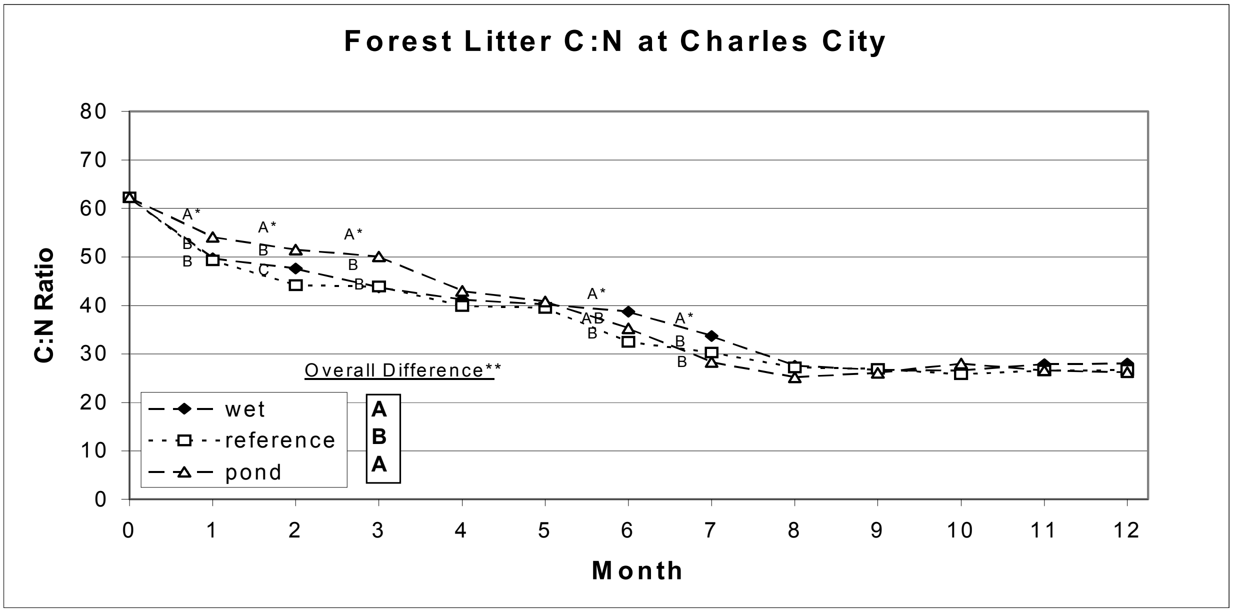

Figure 24b. C:N ratio of forest litter by moisture regime in the Charles City created and adjacent natural wetlands.

* Average values at a given date with the same letter are not significantly different (p=0.05)

** Overall moisture gradient treatment differences; regimes with the same letter are not significantly different (p=0.05)

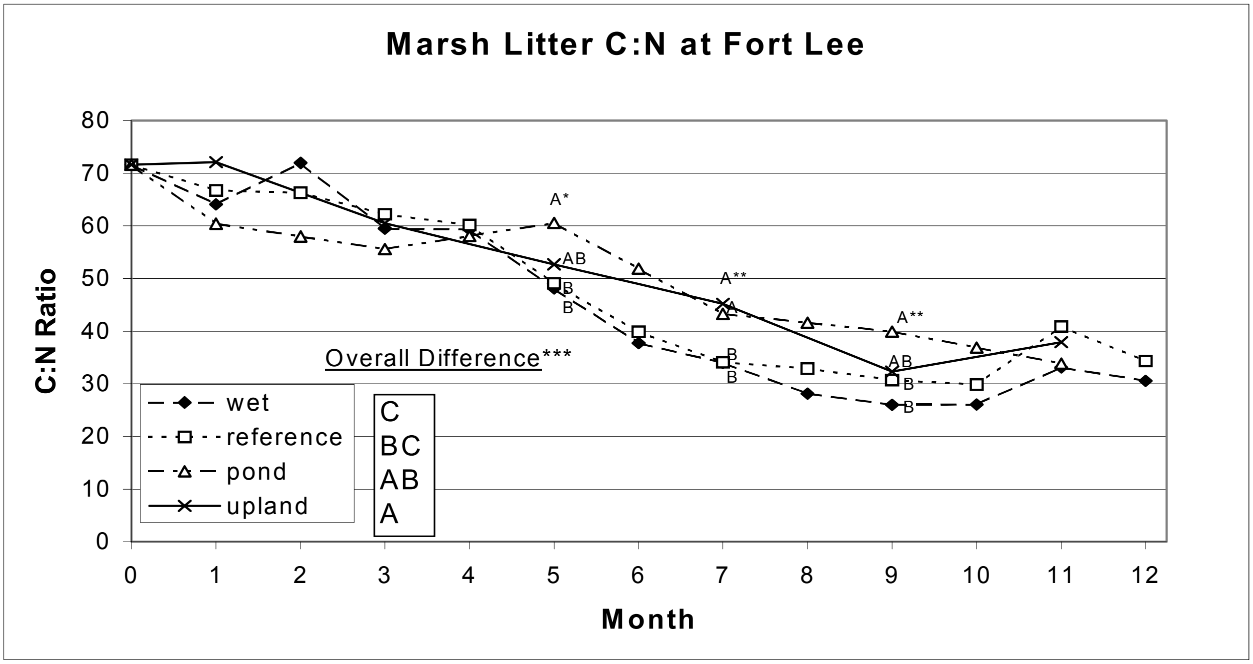

Figure 25a. C:N ratio of marsh litter by moisture regime in the Fort Lee wetlands.
* Average monthly moisture regime values, regimes with the same letter are not significantly different (p=0.05); ** (p=0.10).
*** Overall moisture gradient treatment differences; regimes with the same letter are not significantly different (p=0.05).

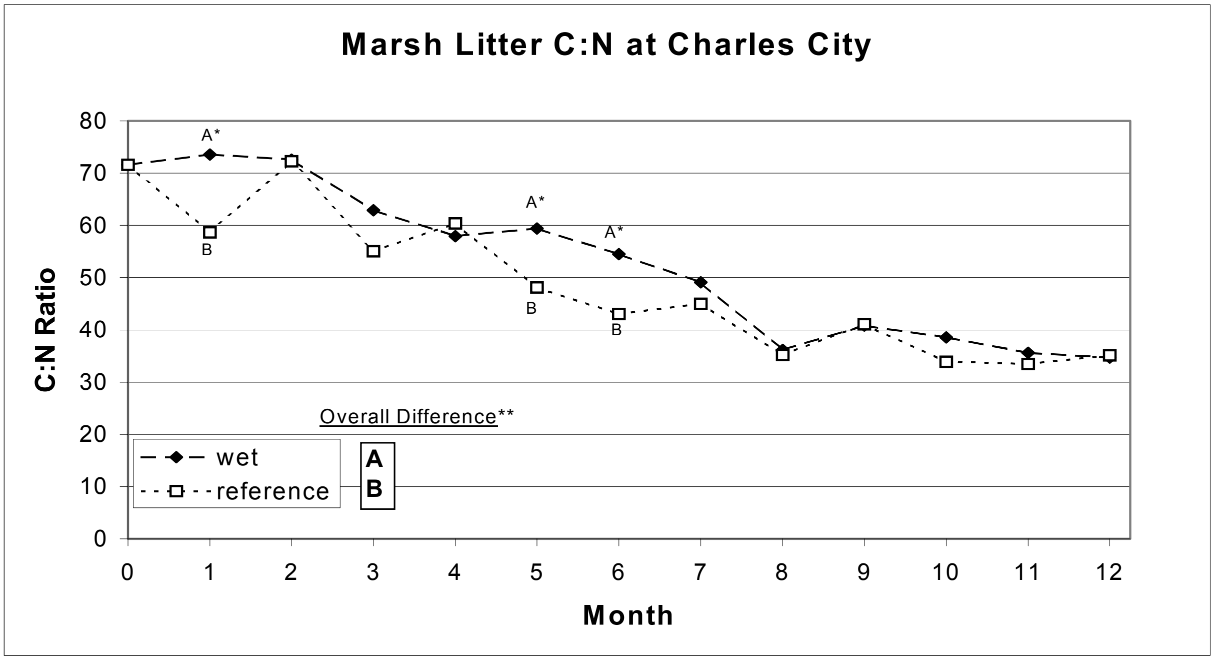

Figure 25b. C:N ratio of marsh litter by moisture regime in the Charles City wetlands.
* Average monthly moisture regime values with the same letter are not significantly different month (p=0.05).
** Overall moisture regime treatment differences; regimes with the same letter are not significantly different (p=0.05)

Since C:N values decrease as litter decomposes, they can also be used to compare the relative decomposition of litter among different treatments. Moisture gradient C:N comparison for both the forest and marsh litter corresponded well in the FL wetland; faster rates of weight loss for the wet regime and slower rates for the upland corresponded to low and high C:N values, respectively (Fig. 24a. & 25a.). C:N values were not different between the FL created (wet) and adjacent natural wetland (reference), while weight loss rates were typically faster in the created wetland (wet). C:N values were higher in the CC created (wet) and natural adjacent (reference) wetlands for forest and marsh litter (Fig. 24b. & 25b.), contrary to the more rapid weight loss in the created wetland. The higher C:N values for the created wetland may be due to the young age of the CC wetland, and they may eventually approach the reference values as the soil and litter layer develops. The different trends between the FL and CC created and adjacent natural wetlands may indicate different factors controlling decomposition between the older and younger created wetlands. Biotic functions affecting C:N ratios (see Chapter 4) may be better developed in the older FL wetland.

Forest and marsh litter exhibited different C:N patterns between fine and coarse mesh litterbags (Table 5). Forest litter exhibited lower C:N values in the coarse mesh litterbags at FL and CC, presumably associated with macroinvertebrate activity. Macroinvertebrates have important indirect effects on litter decomposition such as microbial inoculation and increasing litter surface area trough fragmentation (Crossley, 1976), which may enhance microbial activity and lower C:N values. Marsh litter showed the opposite trend, with lower C:N values in fine mesh litterbags, suggesting macroinvertebrates are less important in the decomposition of the low quality, relatively recalcitrant marsh litter. The lower C:N values in the CC marsh litterbags could also be due to a bag effect such as fine mesh collecting dew and retaining moisture longer

Table 5. Overall differences and average C:N values for fine and coarse mesh litterbags by type of litter (forest or marsh) and wetland (Charles City or Fort Lee).

Litterbag Mesh Size	Forest Litter		Marsh Litter	
	Fort Lee	Charles City	Fort Lee	Charles City
fine	35.9 A*	36.6 A*	45.1 A*	45.7 B*
coarse	33.5 B	34.6 B	47.5 A	52.6 A

* average C:N values with the same letter in the same column are not significantly different (p=0.05)

than the coarse mesh litterbags, or perhaps a loss of smaller partially decomposed litter fragments from the coarse mesh bags. These possible bag effects may have been masked by the overall macroinvertebrate shredding and processing effects with the more palatable forest litter.

Conclusions

The single exponential decay rates for the forest and marsh litter were consistent with rates found in other studies and ranged from 0.73-1.46 and 0.47-0.91 yr^{-1}, respectively (Table 2). Litter species composition played a dominant role in the decomposition rates. Emergent marsh litter decomposed at a much slower rate than deciduous forested wetland litter, and at rates consistent with the wide range of values seen in the literature (Table 2). Differences in the litter properties also affected which decomposition model produced the best fit to the data sets. The leaf litter from the forested wetland exhibited a rapid initial loss of often 20-30% followed by an exponential decay pattern. To model these two components, a double exponential model was most effective, although the single exponential decay constants are more useful for comparison with other decomposition studies. The relatively recalcitrant marsh litter did not exhibit a rapid initial loss, and therefore exhibited a relatively linear pattern consistently to one year after placement. While linear models fit the data as well as the single exponential models, the single exponential models are considered more theoretically realistic. As decomposition progresses, single exponential models approach an asymptote of 0% weight remaining, while linear models intersect and predict negative % weight remaining. While decomposition rates were faster in the older created wetland at FL than the CC created wetland, this difference cannot be attributed to age alone. Since the types of wetland and water sources were different, the FL created wetland remained wetter longer than the CC wet flat type wetland, confounding the comparison.

The most surprising result is that both marsh and forest litter decomposed more quickly in the created wetlands than in the adjacent natural wetlands in areas with similar moisture regimes. I hypothesized that the natural wetlands with intact litter layers and relatively undisturbed conditions would have enhanced biological litter processing and decomposition when compared with the created wetlands. The observed results could have been caused by several different factors. Shade from forest canopies has been shown to reduce the summer temperatures in natural forested wetlands relative to adjacent created wetlands (Stolt et al., 2000). The higher spring and early summer temperature in the created wetlands may account for the increased litter decomposition. Differences in the detritivore communities or scarceness of litter in the created wetlands may also have played a part (see Chapter 4). There is also a possibility that physical stressors on the litter were different between the created and adjacent natural forested wetlands. Litterbags often became incorporated into the soil either via shrink/swell of soils during wet/dry cycles or the rapid growth of cattails in the CC (pond sites especially) and FL created wetlands respectively. However, a difference such as soil incorporation should have been more pronounced in the coarse mesh bags than the fine mesh bags. The higher rate of decomposition in the created wetlands is consistent with the soil organic matter levels remaining constant or showing slight decreases over time in the FL created wetland as reported by Cummings (1999). This poses a more important question: Whether the decay rates in the created wetlands will decrease over time as a canopy develops, and if they do not, whether sufficient organic matter will accumulate in the created wetland soils over time?

Moisture had an important effect on litter decomposition in the created wetlands. As suggested by Baker et al. (2001) and Battle and Golladay (2001), there appears to be an intermediate amount of moisture along a gradient from upland to permanently inundated which allows for faster rates of decomposition (Table 2). Within the created wetlands, the wet areas showed the highest rates of decomposition relative to the wetter pond areas and drier upland areas. Presumably, lack of moisture limited decay in the upland areas, while long to permanent periods of flooding in the pond areas created anoxic conditions, which limited decomposition. These moisture effects were supported by the low and high C:N ratios for the wet and upland moisture regimes respectively.

By the final months of the study, coarse mesh litterbags showed greater weight loss than fine mesh litterbags in both the FL and CC wetlands. While some portion of this mesh size effect is likely due to the action of macrodetritivores which were excluded from the fine mesh litterbags, there may also be "bag effects" such as physical loss of fragments (Valiela et al., 1985) or ecological predator exclusion (Crossley and Hoglund, 1962). Differences in C:N litter patterns between created and adjacent natural wetlands at CC and FL, and for marsh and forest litter in fine and coarse mesh litterbags further indicate the need for resolution of macroinvertebrate and bag effects. Without more information on the detritivore communities (see Chapter 4) it is difficult to determine the relative importance of the macrodetritivore exclusion and bag effects.

Chapter 3. Forest Litter Area and Perimeter Patterns

Introduction

The litterbag method (see Chapter 2) is the most commonly used method to estimate decomposition in terrestrial and aquatic sites, although unconfined leaf packs have gained popularity in aquatic environments. Typically, the loss of litter weight is followed over a period of a year or more through collection of replicates after different periods of time. Different mesh sizes are often used for the litterbags to assess the relative importance of different size classes of detritivores. In addition to the insight gained by varying the litterbag fabric mesh size, measuring litter area along with litter mass should reveal additional information about the process of decomposition. By tracking the litter area and density on a weight per area basis, the relative prevalence of processes like leaching and skeletonization by detritivores (low density, high area) can be compared to processes which result in the disappearance of whole fragments or leaves.

Bocock and Gilbert (1957) and Bocock et al. (1960) were among the first investigators to use the litterbag method to track weight loss as a measure of decomposition. In addition to analyzing the litter for loss of mass, they tracked the loss of whole leaves from the litterbags. The combination of these two data sets provided additional insight into the decomposition process and the role of marcoinvertebrates such as earthworms, which remove whole leaves to their burrows for consumption. The weight per leaf statistic they developed was the precursor and analog to future studies that measured leaf area loss (Heath et al., 1966; Edwards and Heath, 1975) and mass loss simultaneously (this study).

Bocock and Gilbert (1957) and Bocock et al. (1960) recorded the number of leaves along with the litter weight of birch (*Betula verrucosa*), linden (*Tilia cordata*), oak (*Quercus robur*) or ash (*Fraxinus excelsior*) depending on the experiment. When the bags were collected, the contents were sorted, with visible animals and extraneous mineral matter being removed, and the number of remaining leaves counted. When leaves had been significantly fragmented, the number of leaves remaining was estimated by the number of recognizable midribs and petioles. After counting, each litter sample was dried and weighed. Depending on the forest stand examined and litter species, losses from both skeletonization and removal of whole leaves were observed. Ash leaflets were lost as whole leaves more often than oak leaves with the conclusion that earthworms, the dominant macrodetritivore, seemed to prefer N-rich ash leaflets to the less palatable oak leaves (Bocock and Gilbert, 1957). Even examining mass remaining on a per leaf basis, ash leaflets (<25% per leaf) decomposed more quickly than oak leaves (approx. 45% per leaf).

Heath et al. (1966) and Edwards and Heath (1975) were the first researchers to examine the loss of leaf area, which they assumed would follow a similar pattern to weight loss. Comparing decomposition with two different mesh sizes on a woodland and fallow agricultural field, they assessed area loss visually (Heath et al., 1966) or with a photometer (Edwards and Heath, 1975) for the 50 2.5-cm diameter leaf disks and reported it as "percentage disappearance." Heath et al. (1966) did not record mass losses, so their results are analogous to the results from traditional litterbag studies with multiple mesh sizes examining weight loss instead of measuring both simultaneously (this study). Mass was not measured because the litter was measured for loss of area, then returned to the site for further study instead of replicates being removed. While Heath et al. (1966) were able to assess the relative contribution of leaching/microbes and macroinvertebrates from multiple mesh sizes, they didn't have the added insight of mass per area that Bocock and Gilbert (1957) and Bocock et al. (1960) approximated with mass per leaf.

Besides a trial of a new decomposition method, which combines the traditional multiple mesh-size litterbag weight loss technique with area and perimeter measurements of the litter, this study examines decomposition along a moisture gradient in created and adjacent natural wetlands. There are relatively good literature derived estimates of the rates of decomposition in floodplain forests and swamps of the southeast United States (see Chapter 1, Table 2). Differences in decomposition rates have been examined along gradients from stream-bank to upland forest, between different forest types, with mixtures and single species litter and with various human disturbances (Chapter 1, Table 2). Even within similar ecosystems in the same geographic area, there is considerable variation with decay rates ranging from 0.242 to 2.081 yr^{-1} (2.86 and 0.33 yr. $T_{1/2}$ respectively) for mixed litter. As would be expected, single species litter showed greater variation and ranged from 0.146 to 9.770 yr^{-1} or $T_{1/2}$ of 4.74 and 0.07 yr. respectively. The overall average of 78 litter/site combinations examined was 1.17 yr^{-1} and is consistent with that calculated by Lockaby and Walbridge (1998) of 1.01 yr^{-1} which together represent half-lives of between 0.59 and 0.69 yr.

In contrast, there is little information available on decomposition in wetlands created for replacement of freshwater non-tidal forests (Table 2). In this study, similar moisture regimes (i.e. 2-4 cm standing water in winter) were examined in paired created and reference wetlands, and in wetter and drier locations within the created systems. This moisture gradient from upland to permanently flooded was expected to generate the same patterns of decomposition as seen in the forested wetland systems, with slower rates in the uplands, and in flooded locations if they become anaerobic.

There were two main objectives for this portion of the study, (1) to evaluate the usefulness of measuring litter area and perimeter along with weight loss for litterbag decomposition studies, and (2) to compare the decomposition of created wetlands of two different ages and adjacent natural forested wetlands. It was hypothesized that the degree of fragmentation and percent litter area lost would lag behind the loss of weight as the initial leaching and decomposition of relatively labile compounds weakened the litter while improving the palatability for detritivores. Combining the information from the litter area and perimeter measurements using two mesh sizes of litterbags allows assessment of the relative importance of leaching and microbial activity alone versus these actions along with the effects of macroinvertebrate consumption and fragmentation of the litter. It was thought that the intact litter layer and associated biota of the adjacent natural wetlands would result in faster decomposition than in created areas with similar moisture regimes. A secondary objective was to examine the effects of moisture along a gradient in the created wetlands, from areas that supported upland vegetation down to permanently flooded areas. From information in the literature, it appeared that the intermediate moisture regimes (i.e. areas than flood and dry periodically) should decompose most rapidly, with the lack of moisture and anoxic conditions reducing relative decomposition in the upland and permanently flooded areas respectively.

Methods and Materials

Site Description and overall litterbag methods are given in Chapter 2, with the exception that only forest litter area was analyzed here. Table 6 provides the revised experimental design for the area loss portion of this study.

Table 6. Experimental Design for litterbag litter area study

Moisture Regime	Litter Type	Fort Lee			Charles City		
		# replicates	# collections	description	# replicates	# collections	description
wet	forest	4	12	2-10 cm standing water in winter cattails dominated emergent veg.	4	12	2-10 cm standing water in winter cattails dominated emergent veg.
reference	forest	4	12	2-10 cm standing water in winter deciduous wetland tree species	4	12	2-10 cm standing water in winter deciduous wetland tree species
pond	forest	3	12	20-40 cm permanent standing water no emergent vegetation	3	12	15-30 cm standing water in ruts during winter (not permanent) no emergent vegetation
upland	forest	3	12	saturated at soil surface in winter tall fescue, sericea lespedeza veg.	0	0	n/a

Litterbag Collection, Preparation and Analysis

Litterbags were collected from each location once a month for a year. After removing the landscape staples, bags were placed into separate plastic bags to prevent the escape of arthropods. Upon return to the lab, any debris adhering to the outside of the bag was carefully removed. Each bag was opened and any macroinvertebrates were picked from the litter and preserved in ethanol for later identification. The litter was then rinsed in distilled water to remove both sediments and any remaining arthropods.

After removing the arthropods, litter was dried at 55 °C for 72 hours and then weighed to determine gross decomposition rates. Prior to grinding the litter for ash, C and N determination, litter area and perimeter were measured. Litter from each litterbag (Chapter 2, Figure 4) and quality control samples (to estimate initial values) were spread on a known area (30 x 40 cm). Care was taken to unfold any leaves and make sure they did not overlap. Occasionally, a litter sample was split for this reason and two area measurements were made which were subsequently combined. Using a copy-stand and an Olympus D-400 ZOOM 1.3 Megapixel digital camera, digital images of the each litterbag sample were taken (Figure 26). Images were downloaded to a PC and cropped to the 30 x 40 cm size using Paint Shop Pro™ 6. After adjusting contrast and brightness to ensure proper conversion, images were converted to black and white and area was measured by the number of black pixels using the histogram function, and was subsequently converted to cm^2 (Figure 27). Litter perimeter was measured by using the software to trace the contour of the litter, measure the number of contour pixels and convert this to cm based on the known 30 and 40 cm dimensions of the image (Figure 27). The ratio of litter area to litter perimeter was calculated to estimate average litter particle size.

Figure 26. Digital image of forest litter prior to manipulation.

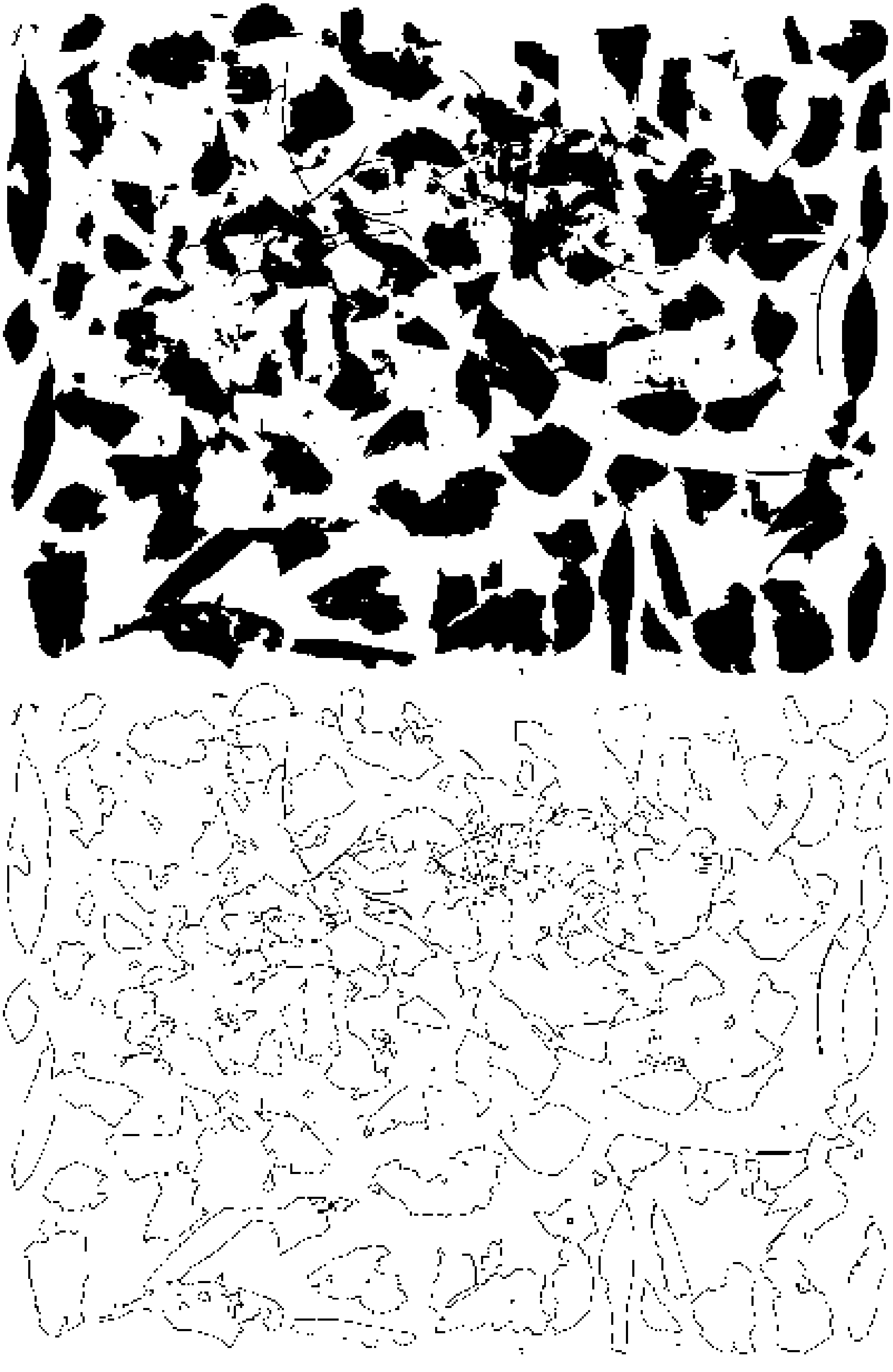

Figure 27. Image of forest litter used to calculate litter area (top) and perimeter (bottom).

After taking the digital photographs, litter from each litterbag was ground and a litter sub-sample was ashed at 500 ° C to determine ash-free weight. Sub-samples from the quality control litterbags were ashed to estimate the initial ash content and all decomposition rates and weight were expressed on an ash-free basis. By combining information on the loss of litter weight and area over time, new comparisons like weight to litter area ratios (analogous to density) were calculated.

Decay models and other regressions were made using the software Sigmaplot^{TM} or Microsoft Excel. An overall analysis of variance was produced using the PROC GLM procedure on the SAS System, Version 7 (1998). LSD mean separations were used to test overall treatment effects, and, where significant, differences at a given date. A 95% probability level was used for statistical tests unless otherwise noted.

Results and Discussion

Decay Rates and Models of Litter Decomposition

Single exponential decay models were used to describe the pattern of litter area loss over time. These decay constants were compared by moisture gradient/mesh size combinations with the decay constants for the loss of litter weight (Table 7). The time required to lose 50% and 95% of initial weight or area was also calculated for comparison (Table 7). The fit of the models was similar and as discussed in Chapter 2; a double exponential model may have modeled the results slightly closer. A single exponential model was utilized for simplicity and ease of comparison with other litter decomposition studies which predominately use single exponential models.

Table 7. Single exponential models and r^2 values for litter weight and area loss with half-life and 95% decomposition time estimates.

Site	Litter Type	Mesh Size	Moisture Regime	Weight Loss Single Exponential Model $y=e^{-kt}$			Area Loss Single Exponential Model $y=e^{-kt}$			Weight Loss (yr)	Area Loss (yr)	Weight Loss (yr)	Area Loss (yr)
				k (d^{-1})	k (yr^{-1})	r^2	k (d^{-1})	k (yr^{-1})	r^2	$T_{1/2}$	$T_{1/2}$	$T_{0.95}$	$T_{0.95}$
Fort Lee	Forest	fine	wet	0.0031	1.13	0.512	0.0025	0.91	0.738	0.61	0.76	2.65	3.28
			reference	0.0027	0.99	0.654	0.0023	0.84	0.801	0.70	0.83	3.04	3.57
			pond	0.0027	0.99	0.454	0.0023	0.84	0.318	0.70	0.83	3.04	3.57
			upland	0.0020	0.73	0.733	0.0016	0.58	0.693	0.95	1.19	4.10	5.13
		coarse	wet	0.0040	1.46	0.731	0.0031	1.13	0.629	0.47	0.61	2.05	2.65
			reference	0.0030	1.10	0.710	0.0028	1.02	0.714	0.63	0.68	2.73	2.93
			pond	0.0033	1.21	0.693	0.0030	1.10	0.427	0.58	0.63	2.49	2.73
			upland	0.0025	0.91	0.775	0.0020	0.73	0.737	0.76	0.95	3.28	4.10
Charles City	Forest	fine	wet	0.0030	1.10	0.603	0.0028	1.02	0.615	0.63	0.68	2.73	2.93
			reference	0.0026	0.95	0.641	0.0024	0.88	0.598	0.73	0.79	3.15	3.42
			pond	0.0025	0.91	0.593	0.0024	0.88	0.555	0.76	0.79	3.28	3.42
		coarse	wet	0.0033	1.21	0.849	0.0034	1.24	0.833	0.58	0.56	2.49	2.41
			reference	0.0026	0.95	0.779	0.0025	0.91	0.791	0.73	0.76	3.15	3.28
			pond	0.0029	1.06	0.735	0.0028	1.02	0.733	0.65	0.68	2.83	2.93

In all but one case, decay rates were lower for litter area than weight indicating slower decomposition as exhibited by the $T_{0.50}$ and $T_{0.95}$ values (Table 7). These results support the assumption that the initial rapid loss of weight as litter decomposes is attributed to leaching and microbial decomposition of labile compounds, and fragmentation and consumption by detritivores are less important. It seems that the loss of litter area lags behind the traditional measure of litter decomposition, loss of weight, as litter weakens and becomes more palatable to detritivores over time.

Despite the lag in decomposition of litter area relative to weight, the moisture gradient and mesh size differences were similar for both statistics. The intermediate wet moisture regime in the created wetlands exhibited the fastest decay rates, while the drier upland regime was the slowest. When adjacent natural and created wetlands with the same moisture regimes were compared (i.e. wet and reference), the created wetlands exhibited faster rates of decomposition (Table 7), similar to the results of the weight loss models (Chapter 2). As with litter weight loss, area loss was faster for coarse mesh size litterbags. While this result was expected, it is unclear what proportion of the difference can be attributed to the action of macrodetritivores versus litter fragments lost through the coarse mesh.

Comparisons of Treatments – Analysis of Variance

Litter Area

Similar to the decay models, litter area and weight loss exhibited similar moisture gradient responses and treatment differences. Decomposition at the Fort Lee (FL) created and adjacent natural wetland showed a relatively consistent pattern of litter area loss, while area loss at Charles City (CC) was less consistent, with a relatively rapid loss between months 6-8 and plateaus of little change during months 1-6 and 8-12 (Figure 28a & b). Within the created wetlands, the wet and pond regimes showed greater litter area loss than the drier upland regime at FL (Figure 28a & b). Litter area decomposition with similar moisture regimes was greater in the created than the adjacent natural wetlands for both the FL and CC wetlands (Figure 28a & b). It is uncertain whether this difference was due to a physical factor, such as higher temperatures, more sunlight, or soil mixing, or a biotic factor such different vegetative structure or differing plant species and associated detritivores. Mesh size differences do not explain which factor is responsible. While coarse mesh litterbags showed greater area loss at the FL wetland, which is typically attributed to the action of macrodetritivores, the CC wetland did not exhibit significant differences. A difference in soil attributes, or the CC wetland being younger than FL, could also explain the lack of a significant difference.

Area and weight loss relationships: Percent litter weight vs. area loss and "Litter Density"

A useful method for comparing the litter area and weight loss percentages is to graph their relationship for each moisture gradient and mesh size combination (Figure 29a & b). By fitting a regression line to the relationship, the relative importance of weight and area loss as decomposition progresses can be assessed. A slope of 1.0 indicates weight loss and area loss are occurring at the same rate, > 1 that weight loss increases relative to area as decomposition proceeds and <1 that area loss increases relative to weight. All slopes were less than one, indicating that area loss increased relative to weight loss as decomposition moved forward (Table 8). This observation is consistent with the typical pattern of litter decomposition, characterized by relatively rapid initial decomposition. This initial weight loss is also supported by the positive intercepts of between 4.06 and 23.6%. During the later stages of decomposition,

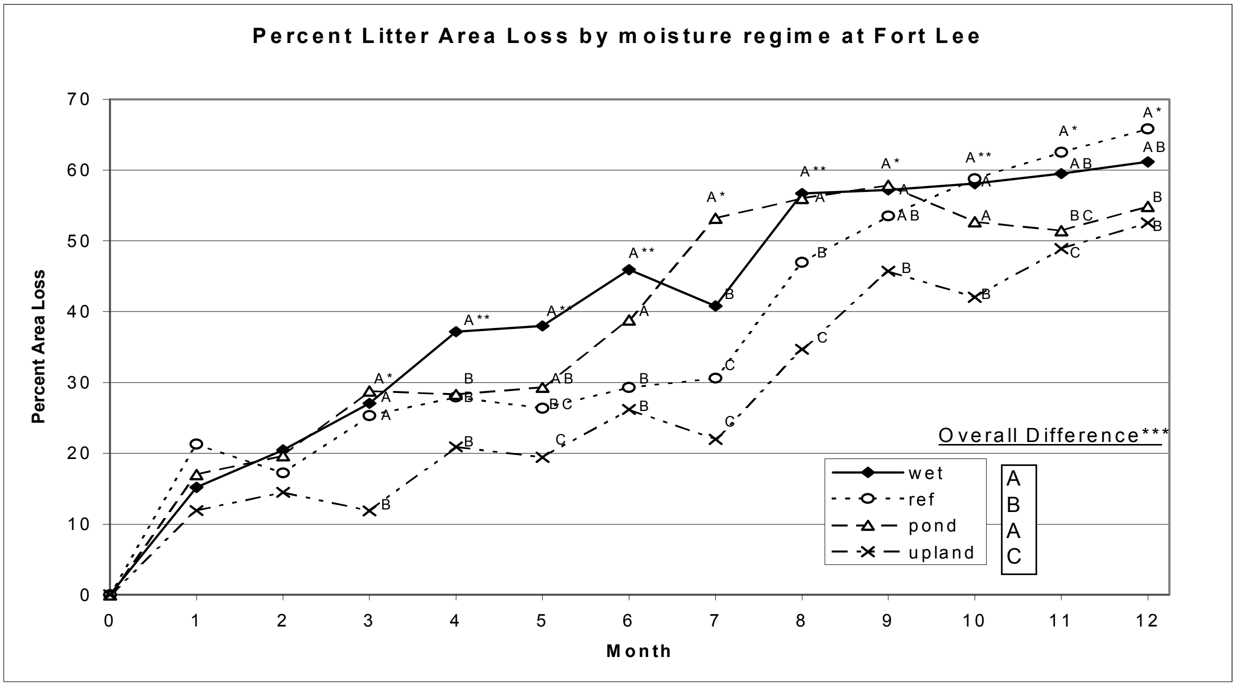

Figure 28a. Percent litter area loss by moisture regime at Fort Lee
* Average monthly moisture regime values with the same letter are not significantly different (p=0.05); ** (p=0.10).
*** Overall moisture regime treatment differences; regimes with the same letter are not significantly different (p=0.05).

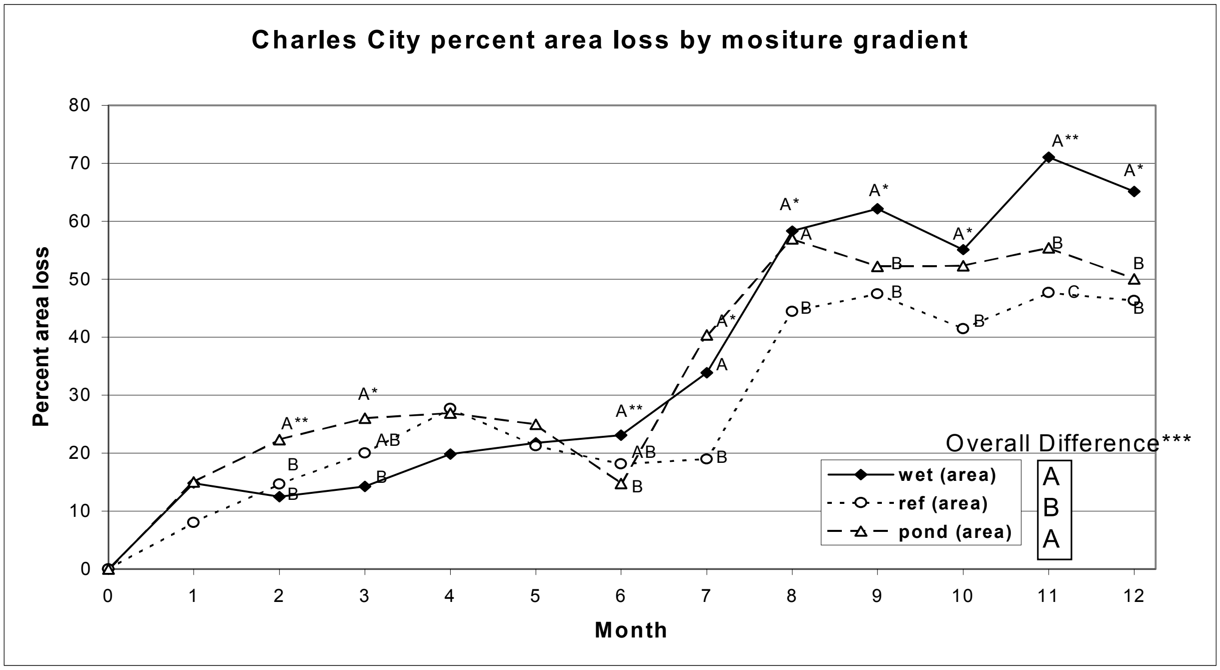

Figure 28b. Percent litter area loss by moisture gradient at Charles City.
* Average monthly values with the same letter are not significantly different (p=0.05); ** (p=0.10).
*** Overall moisture regime treatment differences; regimes with the same letter are not significantly different (p=0.05).

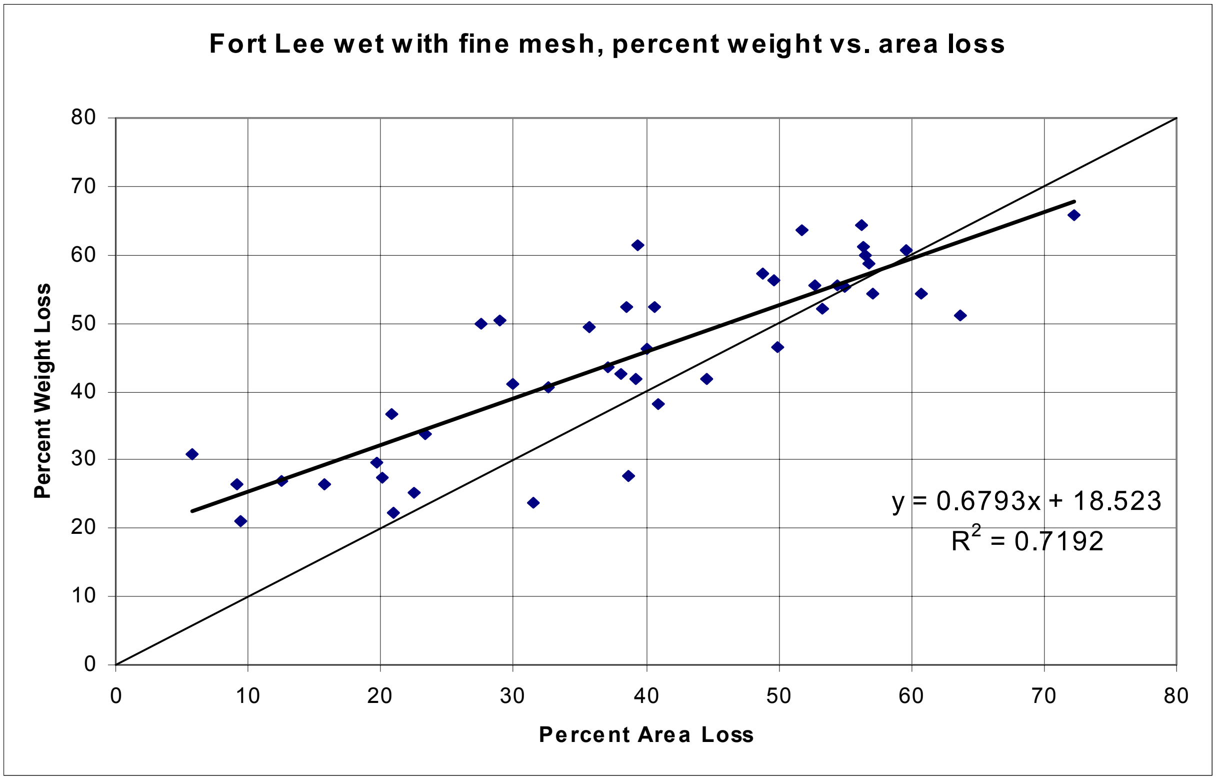

Figure 29a. Percent weight loss vs. percent area loss for fine mesh litterbags at wet moisture regime of Fort Lee created wetland.

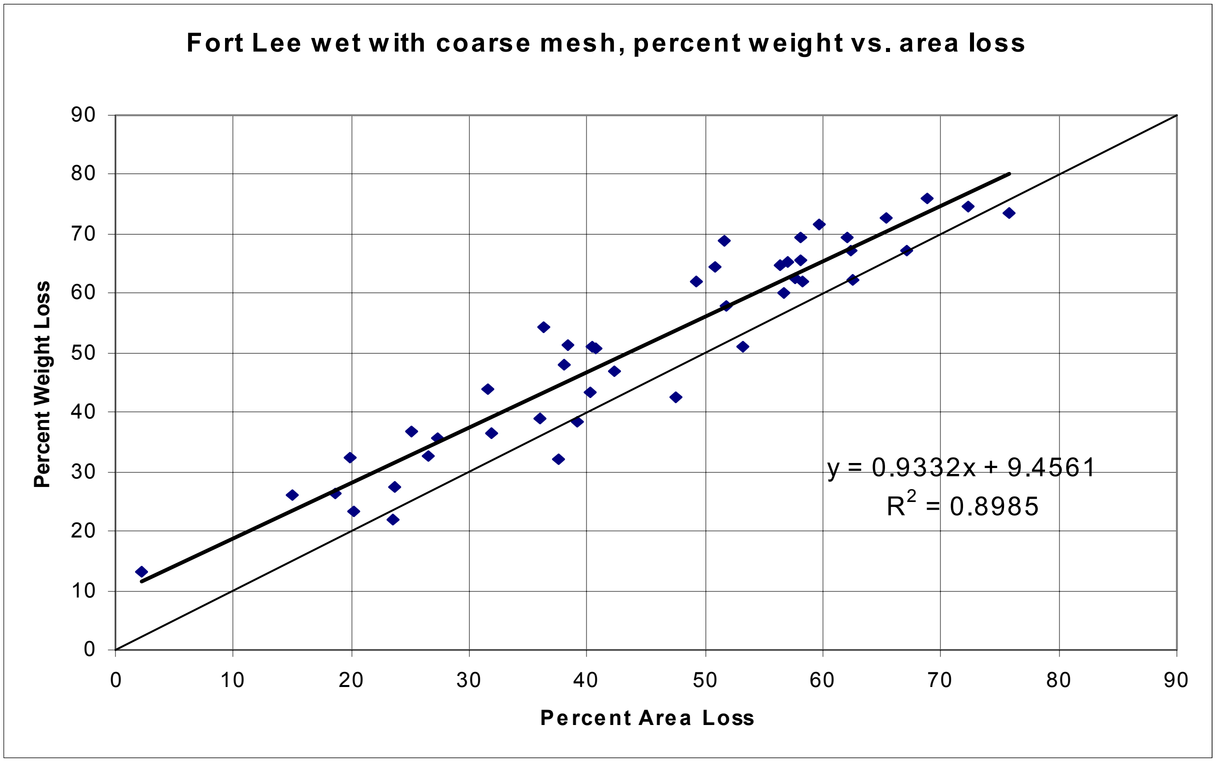

Figure 29b. Percent weight loss vs. percent area loss for coarse mesh litterbags at wet moisture regime of Fort Lee created wetland.

Table 8. Linear Model constants for relationship between percent litter area and weight loss for each moisture regime / mesh size combination.

Site	Litter Type	Mesh Size	Moisture Regime	Linear Model of weight vs. area loss relationship (% wt. loss) = (k) x (% area loss) + b		
				k	b	r^2
Fort Lee	Forest	fine	wet	0.679	18.5	0.719
			reference	0.692	17.0	0.723
			pond	0.739	13.7	0.731
			upland	0.854	11.2	0.756
		coarse	wet	0.933	9.46	0.899
			reference	0.990	4.06	0.897
			pond	0.897	9.02	0.848
			upland	0.873	11.8	0.847
Charles City	Forest	fine	wet	0.605	23.6	0.798
			reference	0.769	19.2	0.760
			pond	0.670	16.9	0.708
		coarse	wet	0.716	19.8	0.855
			reference	0.885	14.5	0.815
			pond	0.763	16.3	0.729

detritivore consumption and loss of litter fragments increase the rate of area loss relative to weight loss. Litter from coarse mesh litterbags consistently provided higher slopes than fine mesh size litterbags of the same moisture gradient/site combination, often approaching 1.0, suggesting similar area and weight losses throughout decomposition (Table 8, Figure 29 a & b). This pattern could be due to a macroinvertebrate or bag effect, where fragments of litter were lost throughout the process of decomposition (either consumed or simply falling through the mesh) in the coarse mesh litterbags, while they were retained in the fine mesh.

Analogous to vegetation density, the ratio of mass to surface area (2-D), or "litter density" is calculated as the ratio of weight and area of litter during the decomposition process (Figure 30 a & b). Litter density ranged from 65-100 g/m^2 for the FL and CC wetlands throughout the study. While there were no significant differences between mesh sizes, there were slight differences between moisture regimes (Figure 30a & b). At the FL wetland, the pond regime (83.8 g/m^2) maintained higher weight to area ratios than the wet and upland regimes (80.3 and 79.5 g/m^2 respectively), with the reference regime intermediate (82.5 g/m^2). Results from the CC wetland contradicted the FL pattern, with the reference regime (74.4 g/m^2) lower than the pond and wet regimes (80.9 and 79.0 g/m^2 respectively). A similar contradictory comparison between the created (wet) and adjacent natural wetlands (reference) at FL and CC was observed in the C:N results (see Chapter 2). These results further suggest that although decomposition rates appear to be higher in the created wetlands (wet) at both sites, the difference may not be due to the same forces.

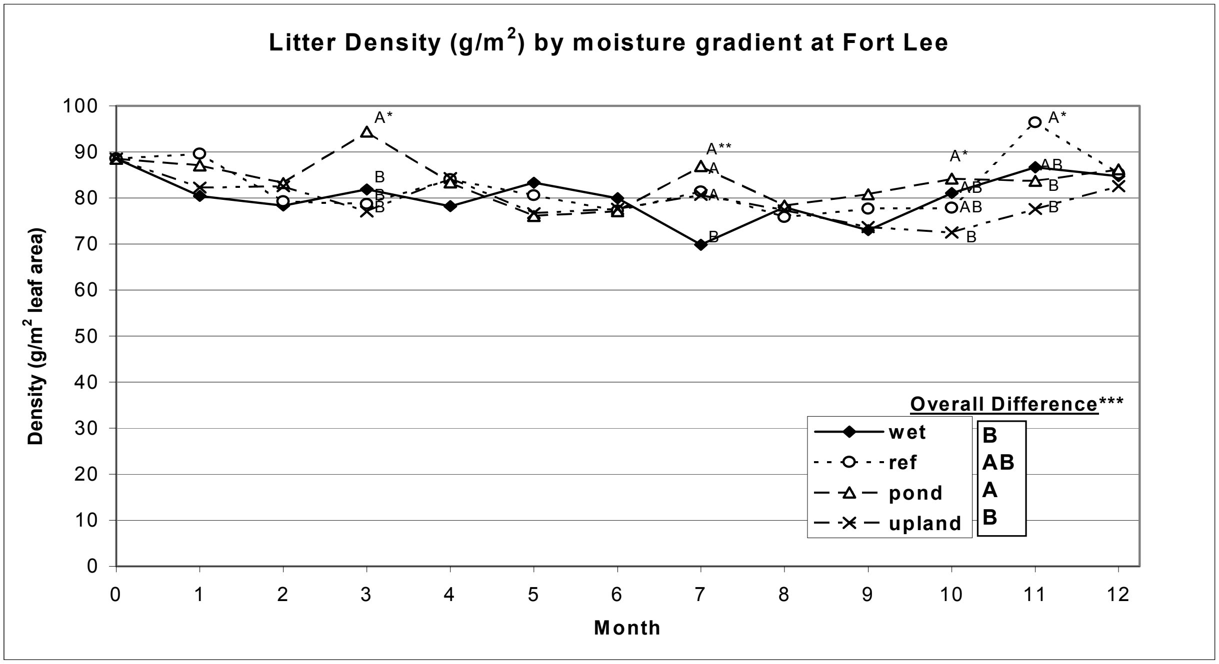

Figure 30a. Litter Density by moisture regime in the Fort Lee wetland.
* Average monthly values with the same letter are not significantly different (p=0.05); ** (p=0.10).
*** Overall moisture regime treatment differences; regimes with the same letter are not significantly different (p=0.05).

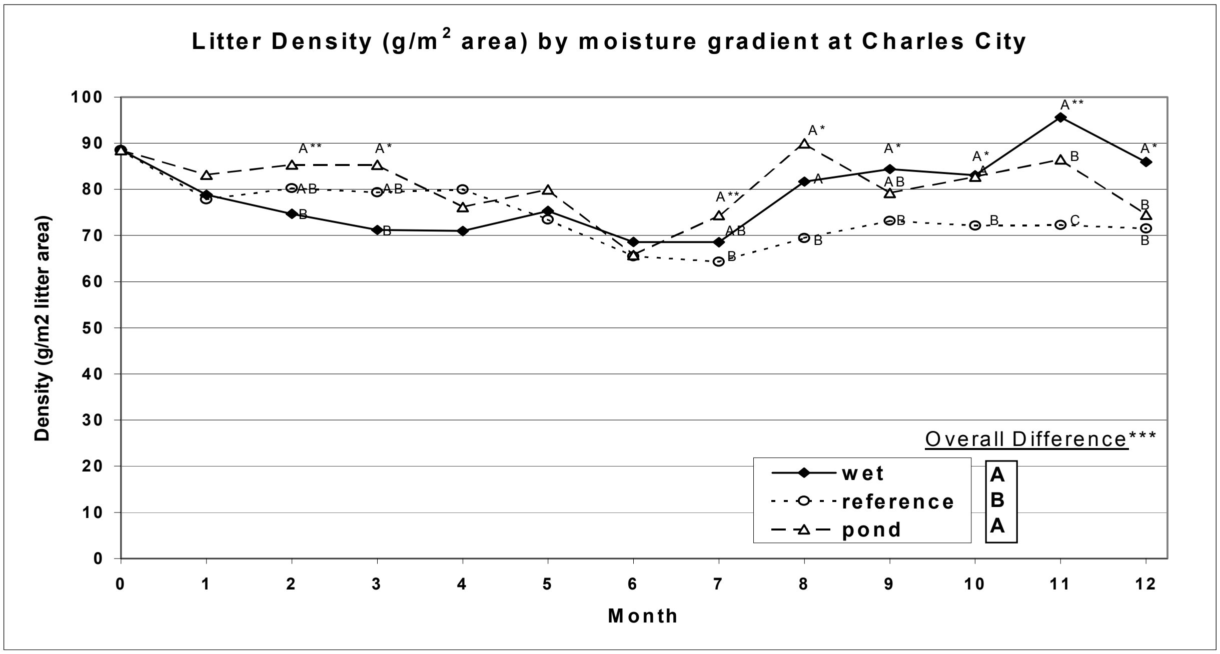

Figure 30b. Litter Density by moisture regime in the Charles City wetland.
* Average monthly values with the same letter are not significantly different (p=0.05); ** (p=0.10).
*** Overall moisture regime treatment differences; regimes with the same letter are not significantly different (p=0.05).

Litter Area to Perimeter Ratio

The ratio of litter area to perimeter can be thought of as an estimate of the average fragment size, although many fragments of the same size and a few whole leaves with many small fragments may give the same value. As would be expected, area:perimeter ratios decreased consistently throughout the study with plateaus between 0.1 and 0.2 cm^2/cm after 8 or 9 months (Figure 31a & b). There was an initial rapid decrease in area:perimeter ratio of approximately 0.1 cm^2/cm during the first month similar to the decreases in litter area and weight. This decrease in average fragment size suggests rapid fragmentation along with the more typically reported loss of soluble and labile compounds. Perhaps as the litter gets matted down and incorporated into the litter layer, it is disproportionately fragmented, while in succeeding months the mat of leaves is less affected by physical forces and detritivores.

The upland moisture regime had an overall larger area:perimeter ratio than all other treatments; the pond regime also produced a larger area:perimeter ratio than the wet and reference regimes in the FL wetland (Figure 31a). This result is consistent with the weight and area loss results. The drier upland conditions generated the slowest decomposition, likely due to physical (less wetting and drying and soil incorporation) and biological factors (different detritivores and vegetation). The CC wetland did not exhibit any overall moisture gradient differences for area:perimeter ratios, although there were difference for particular months (Figure 31b). During the 5th and 6th months, the area:perimeter ratio of the pond regime was high, but this pattern changed between the 6th and 7th months. During the later months (8-12) the area:perimeter ratio of the reference litter was largest (Figure 31b). This switch in patterns seemed to be related to the rapid decomposition during the seventh month, which was also observed in the area and weight loss results (Figure 31b). The rapid decomposition during

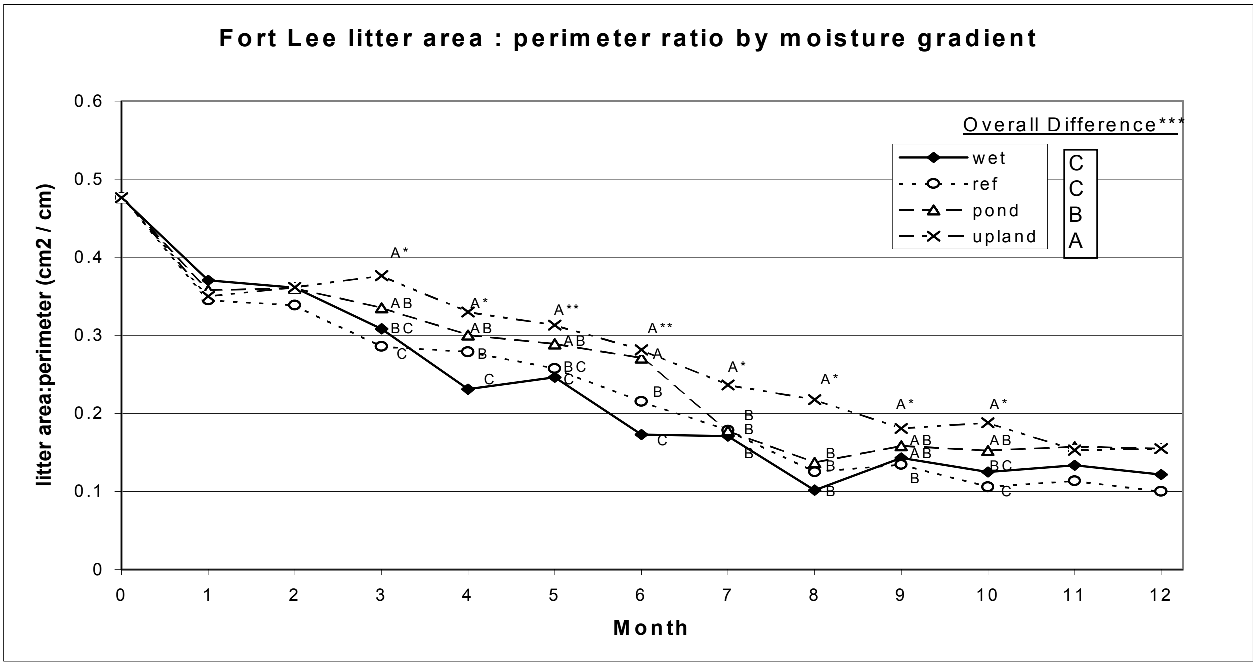

Figure 31a. Litter area:perimeter ratio for each moisture regime at Fort Lee.
* Average moisture regime values with the same letter are not significantly different for a given month (p=0.05); ** (p=0.10).
*** Overall moisture regime treatment differences; regimes with the same letter are not significantly different (p=0.05).

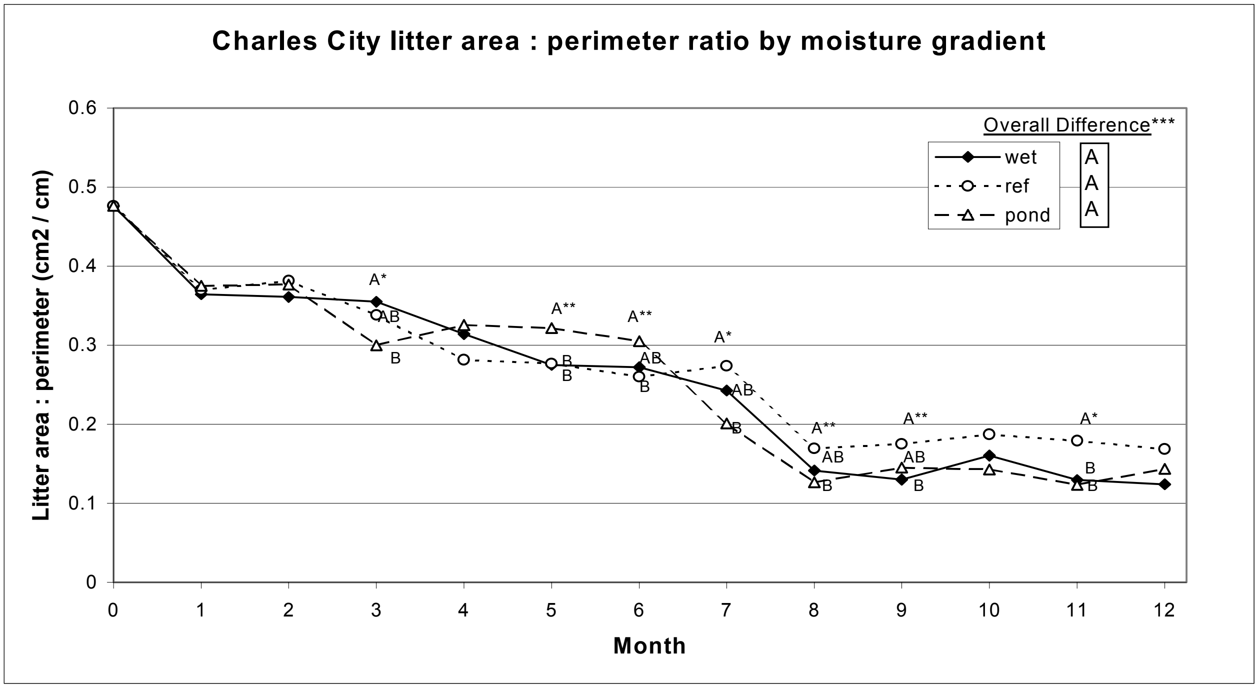

Figure 31b. Litter area:perimeter ratio for each moisture regime at Charles City.
* Average monthly values with the same letter are not significantly different (p=0.05); ** (p=0.10).
*** Overall moisture regime treatment differences; regimes with the same letter are not significantly different (p=0.05).

month 7 at CC coincided with the end of a drought, with the intervening plateau being a period when moisture limited decomposition. The FL wetland moisture levels were less affected by the drought as it received significant groundwater inputs while the CC wetland relied exclusively on precipitation and local run-off. Coarse mesh litterbags had larger area:perimeter ratios than fine mesh litterbags in the CC wetland, but there was no difference at FL. This result at CC could easily be attributed to the larger mesh allowing fragments to fall from the coarse litterbag, which would otherwise remain contained in the fine mesh.

Conclusions

The overall conclusions based on the litter area and perimeter, and their various combinations with traditional weight loss measurements were consistent with those found in Chapter 2 on litter weight loss. When litter areas of created and adjacent natural wetlands with similar moisture regimes are compared, litter area decomposition was slower in the natural wetlands. While this difference may not be surprising considering the many differences between the secondary forest of the natural wetland and the less than 10 year-old marsh of the created wetlands, the reverse relationship may have been easier to explain with a relatively intact litter layer and the associated biota. While the increased temperature of the unshaded created wetland could explain some difference in weight loss, other physical or biological factors must also be important, as area loss is also greater in the created system. Perhaps the detritivore communities are different with different feeding behaviors (i.e. consuming whole leaf fragments vs. consuming the inter-veinal portions and leaving the leaf structure relatively intact). At the CC wetland, direct contact with the shrink-swell soil during wet/dry cycles could have increased fragmentation. At FL, the vigorous cattail roots buried and incorporated some litterbags deeper into the soil within the wet moisture regime areas. Perhaps with additional information on the invertebrate detritivore communities (see Chapter 4), better inferences can be made on whether differences in physical or biological factors are more important.

The secondary objective of comparing decomposition across a moisture gradient from the upland/wetland fringe to permanently inundated parts of created wetlands generated expected results. The drier upland area of the created wetland produced slower rates of litter area loss along with larger area:perimeter ratios than the intermediate wet and wettest pond areas, consistent with the weight loss results. The moisture gradient differences in litter weight and area are likely attributable to similar factors, although weight loss may be explained more directly than area, considering the rapid weight loss from leaching. As the litter loses weight via leaching and microbial action it becomes structurally weaker and easier to fragment along with becoming more palatable to detritivores, explaining similar area loss patterns, yet lagging behind weight loss.

Since this was the first trial of this litterbag method variation (measuring litter area and weight loss over time), another objective was to assess the usefulness of the technique. Combining the area and weight loss data gave added insight into the process of decomposition and method of the loss of material (i.e. fragmentation/consumption of litter pieces vs. removing portions of the litter via leaching or consumption that leaves the litter structurally intact). Often, the initial rapid loss of litter weight is attributed to leaching and microbial decomposition, but litter area and fragment size (i.e. area:perimeter ratio) also showed similar rapid losses. This result suggests that physical forces fragmenting the litter as it becomes incorporated into the litter layer or detritivores may also play an important initial role. Along with using different mesh sizes, chemical litter analysis, and identifying detritivore communities from litterbags, information from digital images of litterbag litter can be a useful tool for better understanding the combination of chemical, physical, and biological forces that effect decomposition. Which litterbag assessment technique to use depends on whether you want to compare decomposition rates between locations or understand the decomposition process itself.

Chapter 4. Macroinvertebrates Collected from Litterbags: Detritivores and Associated Decomposition Rates

Introduction

The importance of macroinvertebrate detritivores has long been recognized as an important factor in litter decomposition. Charles Darwin even wrote a volume in 1881 on the behavior and effects of earthworms processing litter into "vegetable mould" (Darwin, 1881). While it is perhaps the most obvious effect, direct consumption of litter is not the only effect of invertebrates, which also shred the litter into smaller pieces and inoculate the litter with microbes, which encourage further decomposition. While many ecosystems depend on the action of invertebrate detritivores, in other systems they are not as important to litter processing as other physical and biological factors.

A common method for estimating the influence of detritivores on litter decomposition is to vary the mesh size of litterbags (see Chapter 2). By choosing different mesh sizes, certain size classes of organisms can be excluded or allowed access to the litter. Assuming there are no "bag effects" from loss of undecomposed litter through the mesh, the relative importance of certain invertebrate size classes can then be assessed with the finest mesh litterbag assumed to represent the portion of decomposition due primarily to leaching and microbes. Bocock (1964) conducted one of the earliest examinations of the effect of mesh size in using the litterbag method to assess the effects of macroinvertebrates on decomposition. Bocock compared decomposition of ash litter (*Fraxinus excelsior*) in two woodlands with both coarse meshed nylon hairnets (1-cm mesh) and 15 x 15 cm litterbags with 1-mm diameter circular apertures. The technique assumed fine mesh bags represented decomposition from leaching, microbes and soil fauna smaller than 1 mm, while large mesh bags also included the effects of macroinvertebrates on decomposition. Between 10 and 40% of the decomposition was attributed to the action of macroinvertebrates based upon fine vs. coarse mesh comparisons, although the specific detritivores were not identified (Bocock, 1964).

As the litterbag technique developed, three and sometimes four mesh sizes were employed to further explore the relative contributions of different sized animals. Anderson (1973) utilized three mesh sizes (7 mm, 1 mm and 0.175 mm) and "aerial bags" to analyze the relative importance of leaching, microbes, mesofauna and macrofauna during decomposition in a woodland. Aerial bags, which were suspended above the ground with cord, were used along with laboratory analyses for water-soluble components to estimate leaching separately from microbial activity. The assumption was that bacterial and fungal activity would be inhibited by the low moisture content of the suspended bags. The progressively coarser bags would allow access to the litter by either mesofauna or meso- and macrofauna along with the background microbial and leaching losses from the fine mesh bags. Anderson found that the relative importance of biotic and abiotic factors were site-dependant, with biota playing a more important role in beech (*Fagus sylvatica* L.) rather than sweet chestnut (*Castanea sativa* Mill.) forests.

Many authors have used multiple mesh sizes for litterbags as an important tool for understanding the role of meso and macroinvertebrates in decomposition in forests (Bocock, 1964; Anderson, 1973; Herlitzius, 1983; Gustafson, 1943), agroecosystems (House and Stinner, 1987; Tian et al., 1992) swamps, marshes (Mason and Bryant, 1975), bogs (Coulson and Butterfield, 1978), streams (Kirby, 1992), rivers (Mathews and Kowalczewski, 1969) and lakes (Brock et al., 1982; Danell and Anderson, 1982) throughout the world. While many studies have shown differences in decomposition rates between large and small mesh, some environments and treatments exhibit no difference in decomposition (House and Stinner, 1987). Clearly, different abiotic and biotic factors have varying importance for determining decomposition in different ecosystems.

A study of microarthropod numbers suggests that the comparison between litterbags with different mesh sizes may not be as simple as subtraction (Crossley and Hoglund, 1962). They found that mite numbers (*Tydeus* sp.) in litterbags reached 300 per dm^2, while adjacent core samples collected the same day showed 30-50 per dm^2. Apparently, either due to a more stable microclimate or exclusion of predators larger than 2 mm, the bags dramatically increased mite numbers. Further investigation with 1 mm and 2 mm mesh sizes confirmed this effect, but showed no difference between the mesh sizes. While the effect of increased microarthropod numbers may not have had a significant effect on litter weight loss, it suggests the possibility of confounding “bag effects” from differences in temperature, moisture or other ecological factors.

There have been a few reported studies of macroinvertebrate communities in constructed or restored wetlands (without corresponding litter decomposition results). Spieles and Mitsch (2000) compared macroinvertebrate communities between constructed wetlands receiving secondary treated domestic wastewater and lower-nutrient river water in Ohio. Invertebrate communities close to the wastewater inflow were less diverse than other locations. Dissolved oxygen levels during a 24 hour period explained 65.4% of the variation in the invertebrate community metrics (Spieles and Mitsch, 2000). There are a few reported comparisons of invertebrate communities between natural and created or restored wetlands in Florida emergent wetlands (Streever et al., 1996), California salt marshes (Scatolini and Zedler, 1996), and coastal plain wetlands in New York (Brown et al., 1997). Streever et al. (1996) found no significant difference between 20 dipteran taxa between 10 natural and 10 constructed wetlands. Brown et al. (1997) found good colonization in three years of restored wetlands by most invertebrate taxa, however, restored wetlands had lower numbers of some non-aerial, less mobile taxa than natural wetlands. A 4-year old constructed salt marsh had lower invertebrate abundance collected from litterbags than an adjacent natural salt marsh (Scatolini and Zedler, 1996). It is difficult to make any predictions based on these studies relative to my study of created and natural forested wetlands in Virginia, other than to say there is no clear pattern of whether invertebrate communities are different in mitigation wetlands.

Litterbags have also been used either with natural or artificial substrates to collect invertebrates (Blair and Crossley, 1988; Crossley and Hoglund, 1962; Danell and Andersson, 1982; Maloney and Lambert, 1995; Scatolini and Zedler, 1996; Smith, 1986; Wiegert, 1974). Despite this, only a few reported studies have collected and identified invertebrates from litterbags during decomposition studies in terrestrial systems (Anderson, 1975; Blair et al., 1990; Curry, 1969b; Takeda, 1988; Thomas, 1968), and none were reported for wetlands. Several studies in forests only examined micro- and meso-arthropods extracted from fine mesh litterbags with variations on the Tullgren funnel (Blair et al., 1990; Takeda, 1988; Thomas, 1968). Anderson (1975) examined invertebrate communities in three different mesh size litterbags (48 µm, 1 mm, 7 mm) in a sweet chestnut stand in England and found the highest abundance of invertebrates in the medium mesh size. Anderson suggested the fine mesh excluded many invertebrates, while medium mesh retained larger amounts of fine litter particles than the coarse mesh for the invertebrates to inhabit. Another possibility is a bag effect, where predation by macroinvertebrates on meso-invertebrates was excluded by the medium mesh size as observed by Crossley and Hoglund (1962). Curry (1969b) found differences seasonally, and between buried and surface litterbags, of invertebrate communities in decomposing grassland vegetation in Ireland. Combined entomological and decomposition or litter processing studies are more common in litterbag and leaf pack studies of aquatic systems (Anderson and Sedell, 1979). With the availability of aquatic macroinvertebrate keys for identification and life history knowledge, it is now even possible to classify the taxa based on what and how they feed (e.g. shredder or collector-gatherer).

In this study, macroinvertebrates were collected, preserved and classified along with the weight and area loss measurements of their litter substrates. When possible, taxa that were commonly detritivores were identified and analyzed. Besides providing additional knowledge on which taxa are important detritivores in the natural and created wetlands and whether invertebrate communities vary by moisture regime or between created and natural wetlands, the detritivore taxonomic results may help corroborate differences in mass loss observed between mesh sizes (see Chapter 2). The decomposition supposedly attributed to the action of invertebrates is likely validated if greater weight or area litter loss from larger mesh size litterbags corresponds with a larger detritivore community.

Methods and Materials

Site Description and Experimental Design

Please refer to the Methods and Materials of Chapter 2 for experimental design, site descriptions and details of litter bag construction.

Invertebrates

Litterbags were immediately placed in sealed plastic bags upon collection to prevent mobile invertebrates from escaping. Once in the laboratory, invertebrates were collected from the litterbags by rinsing with distilled water. Invertebrates were separated from the litter and preserved in 80% ethanol for later classification (Figure 32). Various field guides, textbooks and classification guides were used to identify each organism and when possible their trophic relationships (e.g. predator, detritivore, etc) (Dorit et al., 1991; Merritt and Cummins, 1996; Milne and Milne, 1980; Thorp and Covich, 1991). Typically, invertebrates were identified to class or order level. Some aquatic and semi-aquatic families of coleoptera, diptera, hemiptera, and trichoptera were also identified (Merrit and Cummins, 1996; Thorp and Covich, 1991).

While the majority of invertebrates were collected from within coarse-mesh size litterbags, some invertebrates were found inside fine-mesh litterbags. This observation was particularly common for chironomidae larvae, which likely entered as small instars and grew within the bag, although in some cases rips were found in the bags. Occasionally, when exuvia or only a portion of an invertebrate were found with the litter and could be identified, they were counted. Coarse and fine mesh invertebrate numbers were pooled for statistical comparisons (i.e. one sample for each litter type, moisture regime, and month combination). Invertebrate abundance, number of taxa (richness), and abundance for common taxonomic categories (e.g. *oligochaeta*) were compared.

Statistical analysis was conducted using 'proc glm' of the SAS software program on essentially the coarse mesh invertebrate data. Selected mean separations were conducted among moisture regimes and litter types in each wetland and among taxa within each moisture regime using the protected LSD procedure.

Figure 32. Example of a macroinvertebrate found in the wetlands (*Tipulidae* larvae).

Results and Discussion

Due to the limited scope of this study, invertebrates collected from the litterbags were not identified to the genus or species level. While some aquatic and semi-aquatic taxa were identified to family, order or class was more common (Table 9). While all taxa were examined to compare moisture regimes and sites, four taxa that typically consist of detritivores were examined more closely. These taxa consisted of the class *oligochaeta* or segmented worms, the class *malacostraca* which consists of the orders *amphipoda*, *decapoda* and *isopoda* or scuds, crayfish and sow bugs respectively, and two diptera larvae families, *chironomidae* or midges and *tipulidae* or crane flies.

Litter Type

Consistently marsh litter contained more invertebrates and taxa than the forest litter in all moisture regimes and in both the Fort Lee (FL) and Charles City (CC) wetland (Table 10). Additionally, it does not appear that there were any taxonomic preferences for certain litter since overall moisture regime differences and moisture regime differences for marsh and forest litter were all similar. The larger abundance and richness for marsh litter, therefore appears to be related to larger amount of marsh litter per litterbag (12.5 g vs. 5 g for forest litter). While litterbag volumes were initially similar for marsh and forest litter, forest litter quickly became matted together while the marsh litter largely retained its shape. For this reason, typically only overall moisture regime and wetland differences are reported instead of giving litter type/moisture regime combinations.

Table 9. Taxa, common names and type of invertebrates identified from litterbags.

phylum	**class**	**order**	**family**	**common name**	**nutrition (typically)**
Annelida	Hirudinea			leeches	predator/parasite
	Oligochaeta			segmented worms	detritivores
Arthropoda	Arachnida	Araneae/Acarina		spiders/mites	predators
	Chilopoda			centipedes	predators
	Diplopoda			millipedes	detritivores
	Insecta	Coleoptera	Dytiscidae	predacious diving beetle	predators
			Hydrophilidae	water scavenger beetle	predator/scavenger
			other	beetles	predator/scavenger/herbivore/ few detritivores
		Collembola		springtails	detritivore/herbivore
		Diptera	Chironomidae	midges	detritivore (shredders, gatherers or filterers)
			Tipulidae	crane flies	detritivore (many shredders)
			other	flies	varies
		Hemiptera		true bugs	predator or herbivore-piercers
		Hymenoptera	Formicidae	ants	predator/scavenger
		Lepidoptera		butterflies and moths	herbivore (larvae)
		Trichoptera		caddisflies	predators/herbivores/detritivores (collector gatherers or filterers)
		other		insects	varies
	Malacostraca	Amphipoda		scuds	usually detritivores (some grazers, predators, scavengers)
		Decapoda	Cambaridae	crayfish	omnivores/scavengers
		Isopoda		sow bugs/woodlice	usually detritivores (some grazers, predators, scavengers)
Mollusca	Bivalvia			clams and mussels	detritivore/planktonivore (filter feeders)
	Gastropoda	Stylommatophora		slugs	herbivore - grazers
		other		snails	herbivore - grazers
Nematoda				nematodes	micro-predators/parasites

Table 10. Average Abundance and Number of Taxa per replicate collected from Fort Lee (n=300) and Charles City (n=228) wetlands.

Site	**Litter type**	**Invertebrate Abundance**	**Number of Taxa**
Fort Lee - Average per Replicate	marsh litter forest litter	7.96 A 4.48 B	2.08 A 1.26 B
Charles City - Average per Replicate	marsh litter forest litter	3.18 A 1.78 B	1.24 A 0.74 B

Fort Lee

Overall, invertebrate numbers were higher in the spring and fall, and lower during the summer dry-down period (Figure 33). Invertebrate abundance was typically below 20 invertebrates each month, with spikes of > 50 in the second and ninth months for the wet and upland moisture regimes respectively. The large increase in the upland value in the ninth month is anomalous because it was due to 598 *formicidae*, or ants, collected in one litterbag. For this reason, abundance values are typically shown without this litterbag's invertebrate data. The spike in the wet moisture regime was due to a moderate number of *isopoda*, especially young nymphs, in several litterbags and therefore likely was not an aberrant observation.

Over the 12-month period, the wet moisture regime in the FL wetland had a higher abundance of invertebrates than the upland or pond regimes in the created wetland and the adjacent natural wetland (Figure 33). Similarly, greater abundances were noted in the 2nd and 9th month for the wet moisture regime in the created wetland. During the 5th, month as the wetland dried out in the wet and upland moisture regime, the permanently ponded moisture regime exhibited greater invertebrate abundance. While invertebrate numbers tended to increase during the fall, there were no differences between moisture regimes after the 5th month. This pattern of greater abundance, especially in the wet moisture regime during the early stages of decomposition may be due to seasonal variation or greater numbers of detritivores in the fresh litter.

The number of taxa per replicate was similar to the invertebrate abundance results; the wet moisture regime in the created wetland had greater taxa richness than the pond regime or adjacent natural wetland (Figure 34). While comparisons by specific taxa are discussed below, this higher macroinvertebrate abundance and richness in the created wetland relative to the

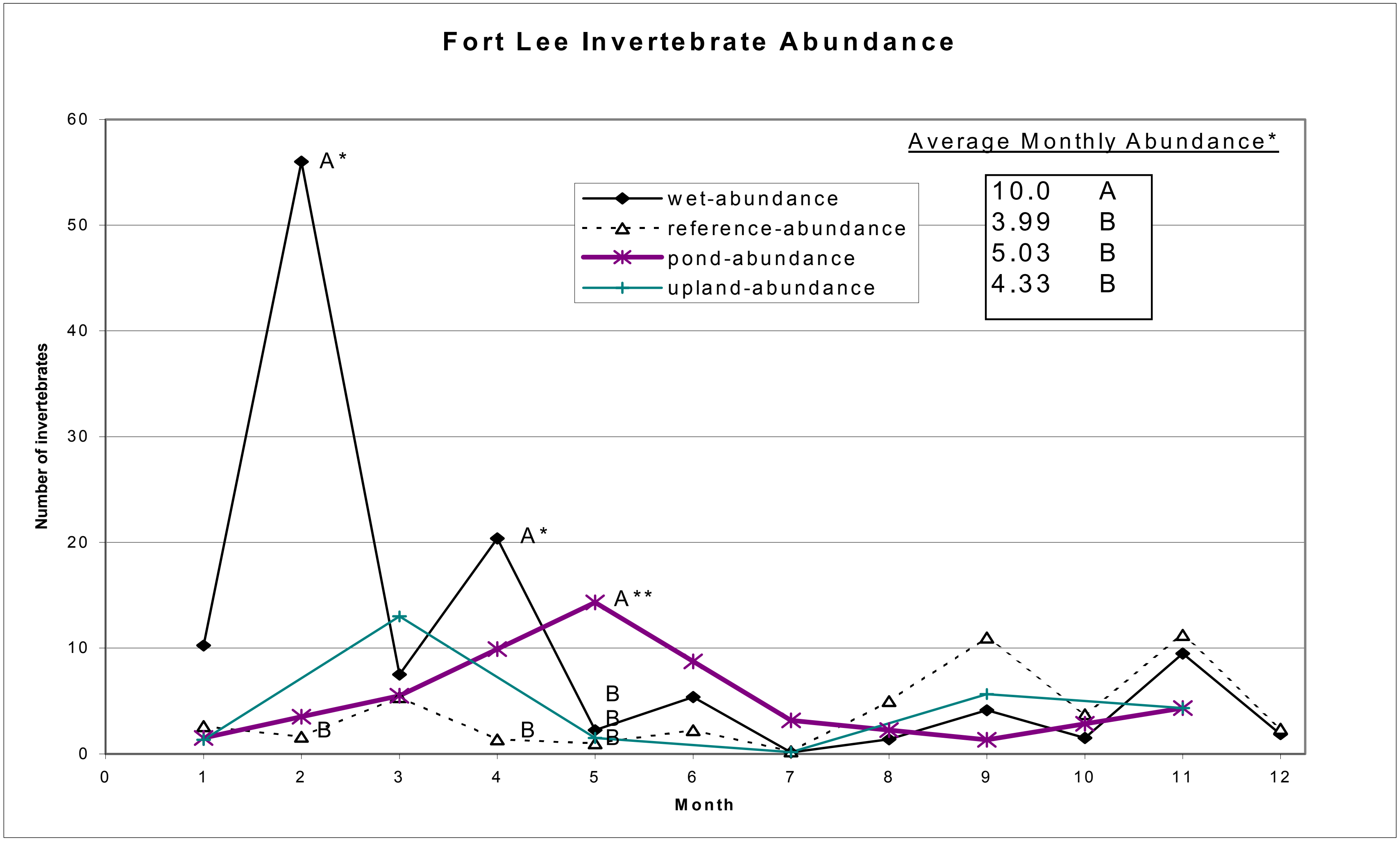

Figure 33. Invertebrate abundance by moisture regime and month at the Fort Lee wetland.
* Monthly and overall moisture gradient differences for 12 month period, regimes with the same letter are not significantly different (p=0.05), ** (p=0.10).
Note: only wet vs. reference contrasts could be calculated for even months because of the incomplete design (i.e. no marsh litterbags for pond and upland); Does not include 598 *formicidae* found in one litterbag during the 9th month.

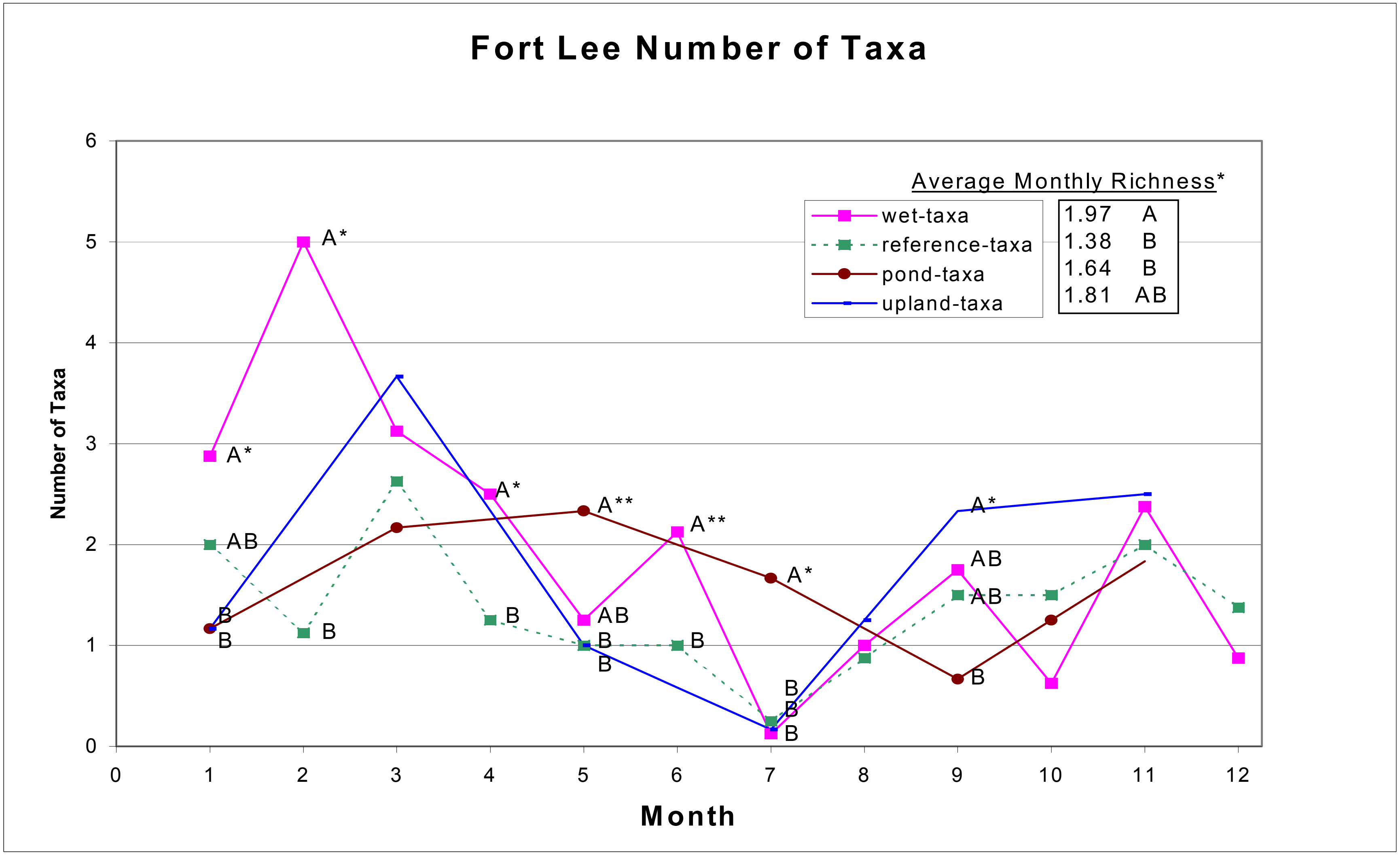

Figure 34. Number of invertebrate taxa by month and moisture regime at the Fort Lee wetlands.
* Overall moisture gradient differences, regimes with the same letter are not significantly different (p=0.05).
Note: only wet vs. reference contrasts could be calculated for even months because of the incomplete design (i.e. no marsh litterbags for pond and upland)

adjacent natural wetland may explain the corresponding faster rates of decomposition in the created wetland (see Chapter 2).

The common taxa (O*ligochaeta, Arachnida, Coleoptera, Chironomidae, Tipulidae*, and M*alacostraca*) collected from the litterbags were compared for each moisture regime and between moisture regimes (Table 11, Figure 35). During the first few months of decomposition, the wet moisture regime in the created wetland had large numbers of *Malacostraca* relative to other taxa and moisture regimes (Table 11, Figure 35d). The adjacent forested wetland had a different pattern of common taxa abundance, with higher numbers of *Chironomidae* (month 9, 11 and overall) and *Malacostraca* (month 11) during the later stages of decomposition (Figure 35). Except for one spike in *Malacostraca* during the 5th month in the ponded moisture regime of the created wetland, the pond and upland moisture regimes exhibited few differences among taxa (Table 11).

Even without considering statistical analyses, different taxa were obviously dominant along the moisture gradient from pond to wet to upland in the created wetland (*Chironomidae*, *Isopoda*, and *Araneae* respectively), and between the created and adjacent natural wetland (*Isopoda* and *Chironomidae* respectively) (Table 12 & 13). The pond moisture regime, as expected, did not contain terrestrial taxa such as ants (*Formicidae*) or butterflies/moths (*Lepidoptera*) and was dominated by midge larvae (*Chironomidae*) and scuds (*Amphipoda*). Conversely, the upland moisture regime produced terrestrial taxa such as centipedes, ants and caterpillars, yet lacked aquatic taxa such as midge larvae (*Chironomidae*) (Table 12 &13). Dominant taxa for the upland moisture regime included spiders (*Araneae*), and ants (*Formicidae*). The intermediate moisture regimes (reference and wet) had corresponding mixtures of taxa. Despite these similarities, the wet regime in the created wetland contained

Table 11. Abundance per replicate for *Oligochaeta, Arachnida, Coleoptera, Chironomidae, Tipulidae* and *Malacostraca* by moisture regime in the Fort Lee created and natural adjacent wetland.

Wetland	**Moisture Regime**	**taxa**	**month**												
			1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**average**
Fort Lee	**wet (created)**	Oligochaeta	2.00AB*	3.88B*	2.13	0.25B*	0.00	0.00	0.00	0.00	1.13	0.25	3.63	0.00	1.10B*
		Arachnida	0.50B	0.88B	0.38	0.38B	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.19B
		Coleoptera	0.13B	0.38B	0.38	0.88B	1.00	1.00	0.00	0.25	0.00	0.00	0.13	0.00	0.34B
		Chironomidae	0.00B	0.50B	0.38	0.00B	0.25	0.00	0.00	0.13	2.38	1.25	3.88	1.38	0.84B
		Tipulidae	0.50B	1.38B	1.00	0.00B	0.25	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.27B
		Malacostraca	6.13A	46.8A	3.13	18.5A	0.25	3.88	0.00	0.88	0.00	0.00	1.63	0.25	6.79A
	wet (forested)	Oligochaeta	0.38	0.13	0.75	0.00	0.00	0.63	0.00	0.25	0.00B*	0.00	0.13B**	0.00	0.19B*
		Arachnida	0.75	0.63	1.38	0.25	0.63	0.13	0.25	0.00	0.00B	0.00	0.00B	0.00	0.33B
		Coleoptera	0.13	0.00	0.63	0.75	0.00	0.13	0.00	0.13	0.13B	0.00	0.13B	0.00	0.17B
		Chironomidae	0.00	0.00	0.13	0.00	0.00	1.13	0.00	4.25	8.25A	2.50	4.75A	1.13	1.84A
		Tipulidae	0.38	0.25	1.13	0.13	0.00	0.00	0.00	0.38	0.00B	0.00	0.13B	0.00	0.20B
		Malacostraca	0.88	0.00	1.25	0.00	0.00	0.00	0.00	0.00	1.25B	1.13	6.00A	1.00	0.96AB
	pond	Oligochaeta	0.00	0.00	0.00	0.00	0.00B*	0.00	0.83	0.00	0.00	0.00	1.50	0.00	0.39
		Arachnida	0.00	0.00	0.00	0.00	0.00B	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Coleoptera	0.67	0.00	0.50	1.00	0.33B	0.00	0.33	0.00	0.00	0.00	0.17	0.00	0.33
		Chironomidae	0.00	3.33	3.67	4.67	2.50B	4.67	0.33	1.00	0.83	0.00	1.50	2.00	1.47
		Tipulidae	0.00	0.00	0.00	0.00	0.17B	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
		Malacostraca	0.50	0.33	1.00	1.67	10.8A	0.00	1.17	0.00	0.00	0.00	0.00	0.00	2.25
	upland	Oligochaeta	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.33	0.08
		Arachnida	0.50	1.00	3.50	1.00	0.00	8.67	0.00	0.67	0.33	0.00	0.83	0.00	0.86
		Coleoptera	0.33	0.00	1.50	0.00	0.17	0.00	0.33	0.00	0.67	0.00	0.67	0.33	0.61
		Chironomidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Tipulidae	0.00	0.33	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.17	0.00	0.03
		Malacostraca	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.03

* monthly and overall differences by moisture regime, taxa with the same letter for the same moisture regime are not significantly different (p=0.05), ** (p=0.010).

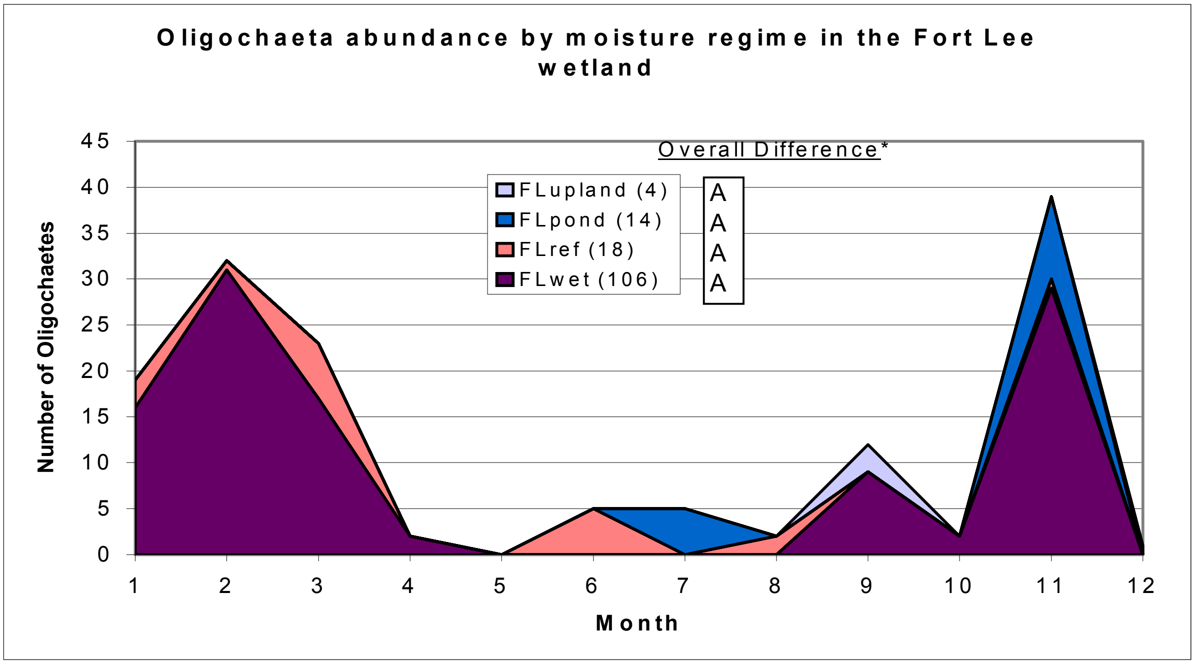

Figure 35a. *Oligochaeta* abundance by moisture regime and month.
* Overall moisture regime treatment differences; regimes with the same letter are not significantly different (p=0.05).

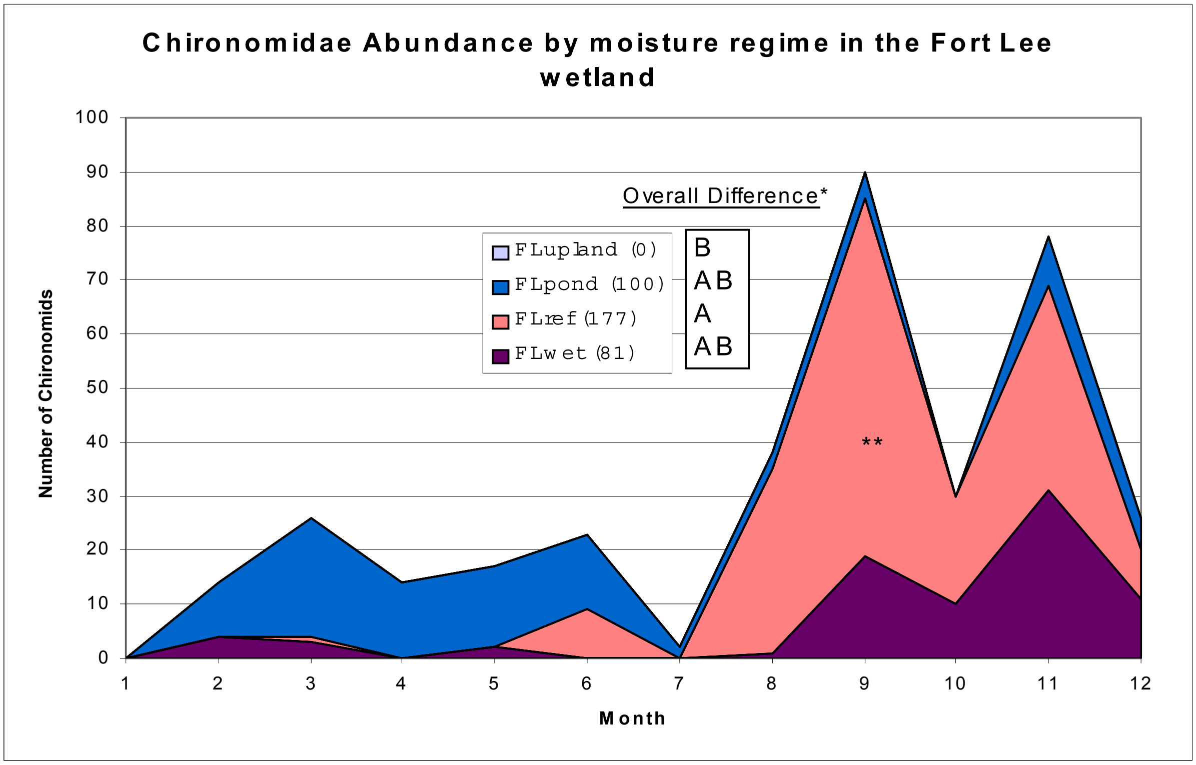

Figure 35b. *Chironomidae* abundance by moisture regime and month.
* Overall moisture regime treatment differences; regimes with the same letter are not significantly different (p=0.05).
** Moisture regime with ** is significantly greater than other regimes during given month.

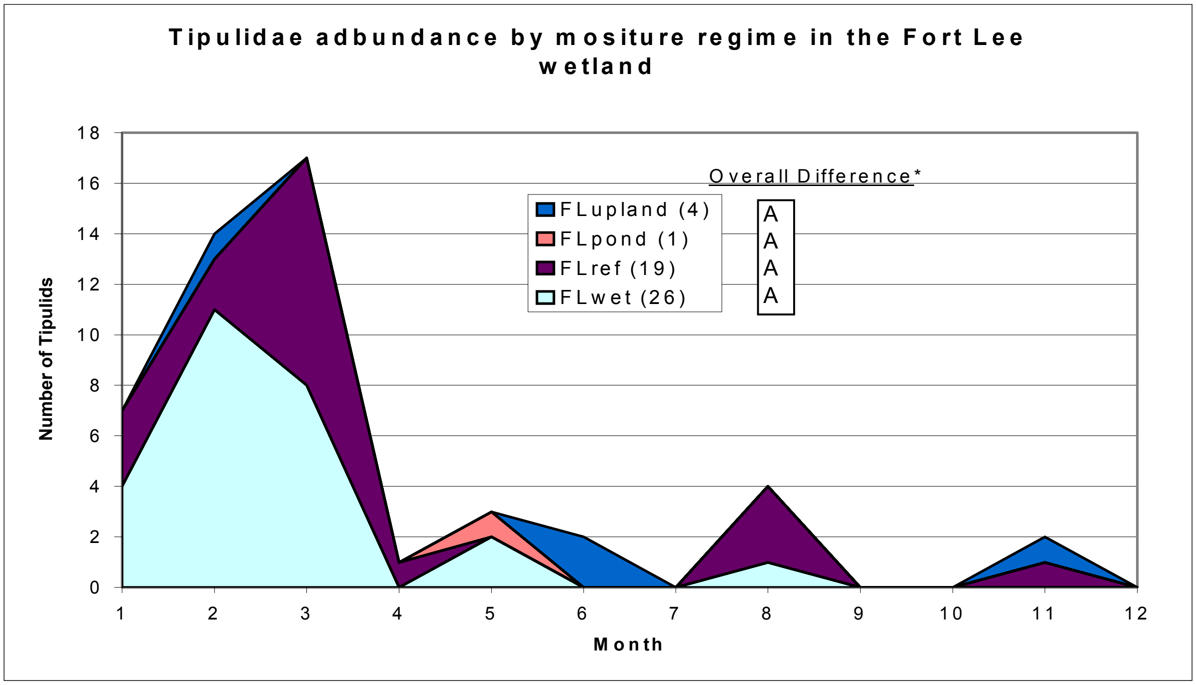

Figure 35c. *Tipulidae* abundance by moisture regime and month.
* Overall moisture regime treatment differences; regimes with the same letter are not significantly different (p=0.05).

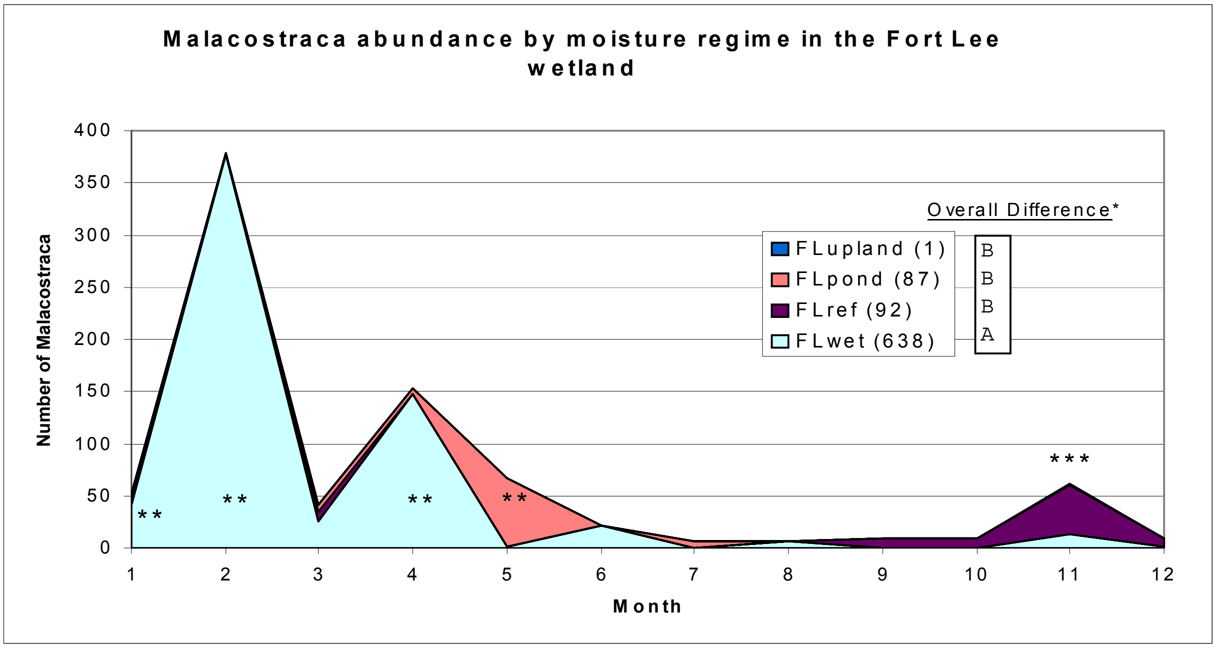

Figure 35d. *Malacostraca* abundance by moisture regime and month.
* Overall moisture regime treatment differences; regimes with the same letter are not significantly different (p=0.05).
** Moisture regime with ** is significantly greater than other regimes for a given month (p=0.05).
*** Reference *malacostraca* abundance is significantly greater than pond or upland (p=0.05).

Table 12. Total number of taxa and invertebrate abundance by moisture regime at Fort Lee.

	Fort Lee taxa and abundance totals											
phylum	**class**	**order**	**family**	**common name**	**wet**	**ref.**	**pond**	**upland**	**wet**	**ref.**	**pond**	**upland**
					# taxa	**# taxa**	**# taxa**	**# taxa**	**abund.**	**abund.**	**abund.**	**abund.**
Annelida	Hirudinea			leeches	0	0	1	0	0	0	1	0
	Oligochaeta			segmented worms	1	1	1	1	106	18	14	4
Arthropoda	Arachnida	Araneae/Acarina		spiders/mites	1	1	0	1	18	32	0	65
	Chilopoda			centipedes	0	1	0	1	0	2	0	9
	Diplopoda			millipedes	0	0	0	0	0	0	0	0
	Insecta	Coleoptera	Dytiscidae	predacious diving beetle	5	4	4	4	3	4	3	0
			Hydrophilidae	water scavenger beetle	0	0	0	0	1	2	6	1
			other	beetles	0	0	0	0	29	10	6	21
		Collembola		springtails	1	1	1	1	14	6	2	33
		Diptera	Chironomidae	midges	7	2	5	2	81	177	100	0
			Tipulidae	crane flies	0	0	0	0	26	19	1	4
			other	flies	0	0	0	0	7	0	5	1
		Hemiptera		true bugs	1	1	1	1	2	1	1	3
		Hymenoptera	Formicidae	ants	1	1	0	1	15	11	0	641 (43)*
		Lepidoptera		butterflies & moths	0	0	0	1	0	0	0	11
		Trichoptera		caddisflies	1	0	3	0	2	0	4	0
		other		insects	0	2	2	1	0	2	5	1
	Malacostraca	Amphipoda		scuds	3	2	3	1	46	13	75	1
		Decapoda	Cambaridae	crayfish	0	0	0	0	1	0	4	0
		Isopoda		sow bugs/woodlice	0	0	0	0	591	79	8	0
Mollusca	Bivalvia			clams & mussels	2	2	1	2	0	1	0	0
	Gastropoda	Stylommatophora		slugs	0	0	0	0	3	2	0	2
		other		snails	0	0	0	0	6	0	4	16
Nematoda				nematodes	1	1	1	0	3	3	2	0
overall					24	19	23	17	954	382	241	13 (215)*

* numbers in ( ) is the total abundance of *formicidae* without including 598 *formicidae* collected from a single litterbag in the 9th month

Table 13. Summary of common (> 5%) invertebrate taxa at each moisture regime.

Fort Lee				**Charles City**		
wet	**reference**	**pond**	**upland***	**wet**	**reference**	**pond**
Isopoda (62%)	Chironomidae (46%)	Chironomidae (41%)	Araneae (30%)	Araneae (30%)	Chironomidae (42%)	Chironomidae (63%)
Oligochaeta (11%)	Isopoda (21%)	Amphipoda (31%)	Formicidae (20%)	Chironomidae (18%)	Oligochaeta (25%)	Isopoda (10%)
Chironomidae (8.5%)	Araneae (8.4%)	Oligochaeta (5.8%)	Collemba (15%)	Coleoptera (17%)	Araneae (8.2%)	5 taxa (5%)
			Coleoptera (9.8%)	Tipulidae (16%)		
			Gastropoda (7.4%)	Collemba (11%)		
			Lepidoptera (5.1%)			

* calculations for Fort Lee upland do not include one litterbag in the 9th month which contained 598 *formicidae*.

significantly more *Malacostraca* and more than double the total invertebrate abundance than the reference wetland (Table 12). Dominant taxa from the reference wetland included *Chironomidae* and *Malacostraca*. The wet sites within the created wetland also exhibited these same dominant taxa with the addition of *oligochaeta* (Table 13).

Oligochaeta, Chironomidae, Tipulidae and *Malacostraca* were the most commonly observed detritivore taxa (Figure 35, Table 12 & 13). Detritivore numbers were highest during the winter/spring (*Tipulidae, Malacostraca*), fall/winter (*Chironomidae*) or both (*Oligochaeta*) (Figure 35 a-d). When the four taxa of detritivores were pooled for each month, the intermediate wet moisture regime exhibited greater abundance relative to the drier upland and wetter pond moisture regimes in the created wetland (Table 14). The detritivore abundance of the reference wetland was also lower than the corresponding wet regime in the created wetland. The patterns of detritivore abundance and decomposition rates by moisture regime are similar; the low 0.04 detritivores/replicate corresponded to slower rates of weight loss at the upland sites and the highest average of 2.25 detritivores/replicate for the wet moisture regime was associated with relatively rapid litter weight loss (see Chapter 2). While a direct causal relationship cannot be absolutely established, these results suggest that the invertebrate community, and detritivores in particular, play an important role in the rate of litter decomposition in wetlands, and may partially explain the more rapid decomposition in created wetlands relative to an adjacent natural wetland. The importance of detritivores at FL is also supported by the higher litter weight loss in the coarse mesh size litterbags when compared against the fine mesh.

Table 14. Average number of detritivores per replicate by moisture regime and wetland.

Average Number of Detritivores per replicate (*Oligochaeta, Chironomidae, Tipulidae, Malacostraca*)		
Site	**Moisture Regime**	**Average***
Fort Lee	wet	2.25A
	reference	0.80B
	pond	0.94B
	upland	0.04B
Charles City	wet	0.21B
	reference	0.57A
	pond	0.11B

* Overall moisture regime treatment differences, averages with the same letter at the same site are not significantly different (p=0.05)

Charles City

Invertebrate abundance in the CC wetlands varied seasonally, similar to FL, with reduced abundance during the summer months. The spikes in abundance of > 20 invertebrates per moisture regime per replicate at FL were not seen at CC (Figure 36). While invertebrate abundance in the wet moisture regime of the created wetland and natural reference wetland were similar (2.36 and 3.06 invertebrates/replicate respectively) abundance in the pond moisture regime (0.53 invertebrates/replicate) was much lower (Figure 36). This difference could be due to a combination of factors. Unlike the FL pond moisture regime, the pond areas of CC dried completely during the summer. Combined with this moisture effect, the litterbags became caked in clay when they dried, and there was no established vegetation in these areas, which would also have reduced invertebrate numbers. The age of the created wetland may also play a part; perhaps with more time, a more developed litter layer and/or more vegetation would improve the conditions for invertebrate colonization. The number of taxa for each moisture regime at CC followed the same pattern as overall abundance, with the pond areas of the created wetland less diverse than the reference natural wetland or the wet moisture regime (Figure 37).

Spiders (*Araneae*), beetles (*Coleoptera*), and midge larvae (*Chironomidae*) were the most common taxa in the wet moisture regime of the CC wetland (Table 15 & 16). Unlike the wet moisture regime for the FL created wetland, significant numbers of sow bugs or segmented worms were not observed at CC. *Chironomidae* and *Oligochaeta*, midge larvae and segmented worms respectively, were the dominant taxa in the natural wetland at CC (Table 15). With fewer than 20 invertebrates collected during the 12-month period, the pond moisture regime exhibited no significant differences among taxa.

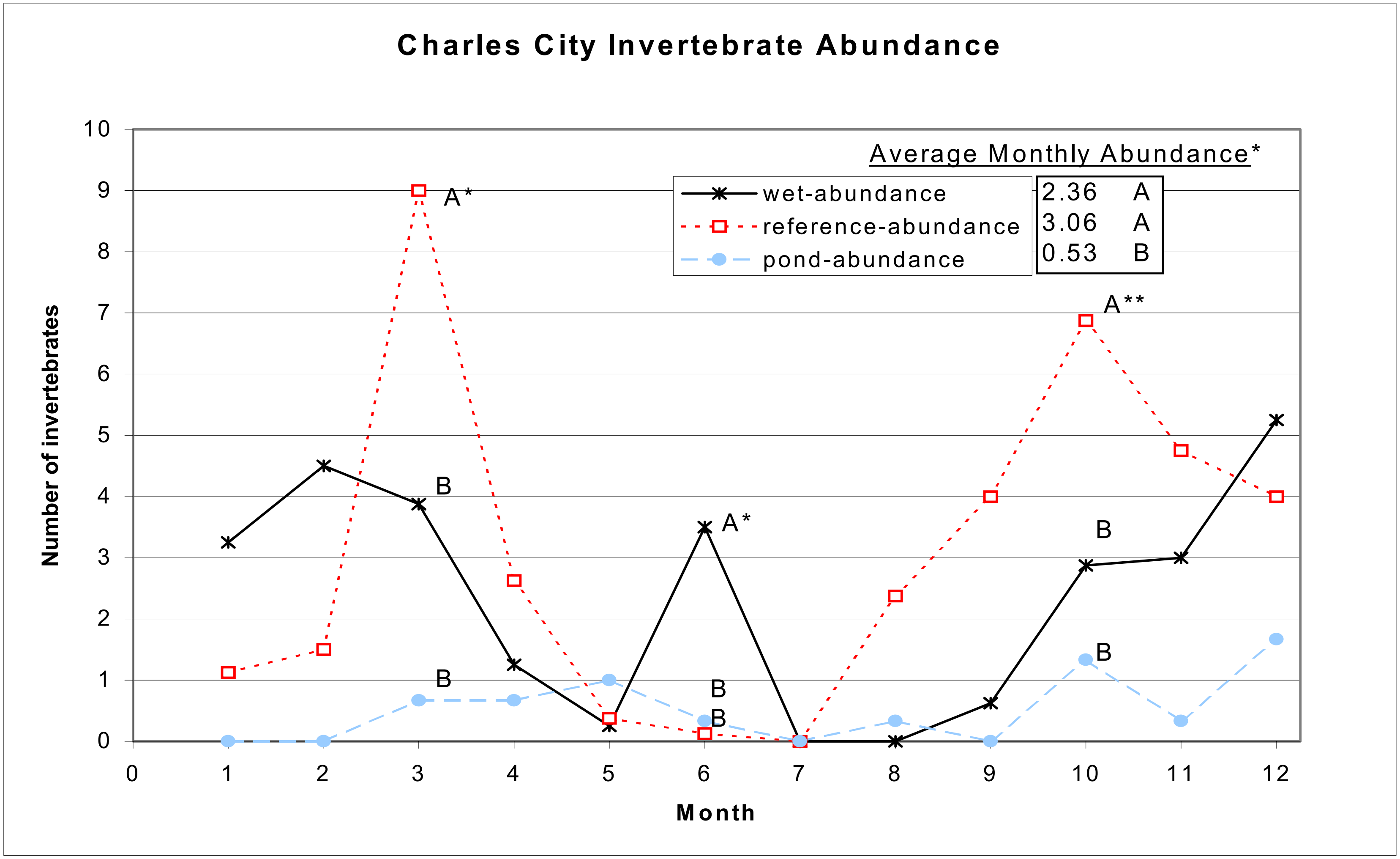

Figure 36. Invertebrate abundance by moisture regime in the Charles City wetlands.
* Monthly and overall moisture regime treatment differences; regimes with the same letter are not significantly different (p=0.05), ** (p=0.10).
Note: Differences indicated for even numbered months are based on forest litterbags only due to incomplete design.

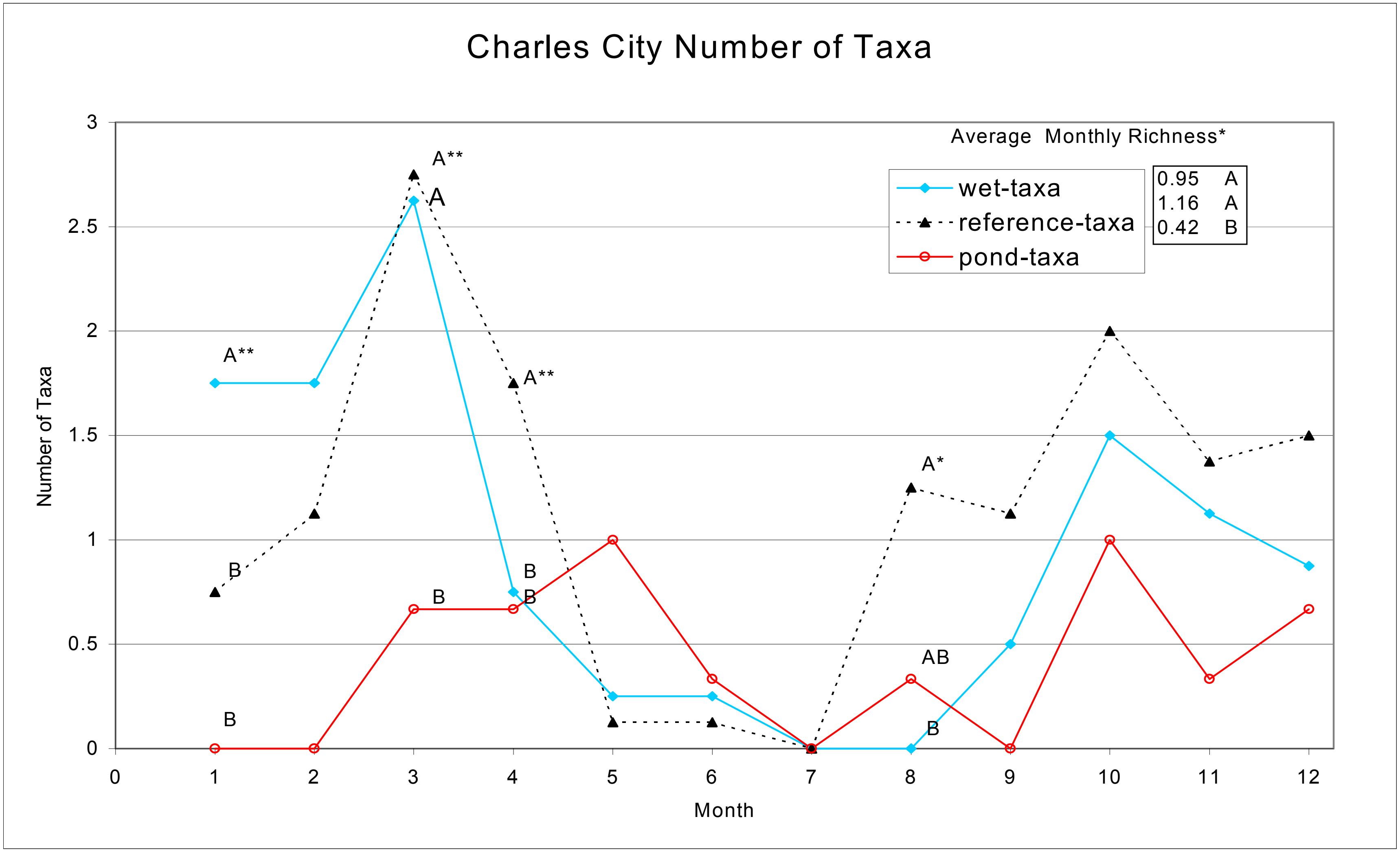

Figure 37. Number of invertebrate taxa by moisture regime and month in the Charles City wetlands.
* Monthly and overall moisture regime treatment differences; moisture regimes with the same letter are not significantly different (p=0.05), ** (p=0.10).
Note: Differences indicated for even numbered months are based on forest litterbags only due to the incomplete design.

Table 15. Abundance per replicate for *Oligochaeta, Arachnida, Coleoptera, Chironomidae, Tipulidae* and *Malacostraca* by moisture regime in the Charles City created and natural adjacent wetland.

Wetland	**Moisture Regime**	**taxa**	**month**												
			1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**average**
Charles City	**wet (created)**	Oligochaeta	0.00B**	0.00B*	0.00B**	0.00	0.00	0.00B*	0.00	0.00	0.00	0.25	0.00B*	0.25B*	0.04B**
		Arachnida	1.00AB	4.75A	2.75AB	0.50	0.25	6.75A	0.00	0.00	0.00	0.25	0.50B	0.00B	1.40A
		Coleoptera	3.00A	0.75B	3.00A	2.00	0.25	0.00B	0.00	0.00	0.00	0.50	0.50B	0.00B	0.83A
		Chironomidae	0.00B	0.00B	0.25B	0.00	0.00	0.00B	0.00	0.00	0.25	0.25	0.00B	9.25A	0.83A
		Tipulidae	0.50AB	0.00B	0.25B	0.00	0.00	0.00B	0.00	0.00	0.50	2.00	5.25A	1.00B	0.79AB
		Malacostraca	0.00B	0.00B	0.00B	0.00	0.00	0.00B	0.00	0.00	0.00	0.25	0.00B	0.00B	0.02B
	wet (forested)	Oligochaeta	0.00	0.00	4.50B*	0.25	0.00	0.00	0.00	2.75A**	4.75A*	1.00B*	3.00B**	2.25AB*	1.54B*
		Arachnida	1.75	1.75	1.00C	1.25	0.00	0.25	0.00	0.00B	0.00B	0.00B	0.00C	0.00B	0.50C
		Coleoptera	0.25	0.25	0.50C	1.25	0.00	0.00	0.00	0.25AB	0.00B	0.75B	0.25C	0.25B	0.31C
		Chironomidae	0.00	0.00	7.75A	0.25	0.00	0.00	0.00	0.00B	2.00AB	10.25A	5.75A	5.00A	2.58A
		Tipulidae	0.00	0.00	0.75C	0.00	0.00	0.00	0.00	0.50AB	0.00B	0.00B	0.00C	0.00B	0.10C
		Malacostraca	0.00	0.00	2.25BC	1.00	0.00	0.00	0.00	0.00B	0.25B	0.25B	0.00C	0.25B	0.33C
	pond	Oligochaeta	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.03
		Arachnida	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.03
		Coleoptera	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
		Chironomidae	0.00	0.00	0.33	0.00	0.33	0.00	0.00	0.33	0.00	1.00	0.33	1.67	0.33
		Tipulidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Malacostraca	0.00	0.00	0.33	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08

* monthly and overall (over 12 month period) differences by moisture regime, taxa with the same letter in the same column and moisture regime are not significantly different (p=0.05), ** (p=0.010).

Table 16. Invertebrate abundance and number of taxa by moisture regime at the Charles City wetland.

	Charles City taxa and abundance totals									
phylum	**class**	**order**	**family**	**common name**	**wet**	**ref.**	**pond**	**wet**	**ref.**	**pond**
					# taxa	**# taxa**	**# taxa**	**abund.**	**abund.**	**abund.**
Annelida	Hirudinea			leeches	0	0	0	0	0	0
	Oligochaeta			segmented worms	1	1	1	2	74	1
Arthropoda	Arachnida	Araneae/Acarina		spiders/mites	2	2	1	67	24	1
	Chilopoda			centipedes	0	1	0	0	9	0
	Diplopoda			millipedes	0	1	0	0	3	0
	Insecta	Coleoptera	Dytiscidae	predacious diving beetle	4	3	1	0	1	0
			Hydrophilidae	water scavenger beetle	0	0	0	2	1	0
			other	beetles	0	0	0	38	13	1
		Collembola		springtails	1	1	0	26	11	0
		Diptera	Chironomidae	midges	4	5	1	40	124	12
			Tipulidae	crane flies	0	0	0	37	5	0
			other	flies	0	0	0	3	4	0
		Hemiptera		true bugs	2	0	1	6	0	1
		Hymenoptera	Formicidae	ants	1	1	0	3	4	0
		Lepidoptera		butterflies & moths	1	1	0	1	2	0
		Trichoptera		caddisflies	0	0	0	0	0	0
		other		insects	1	1	0	1	1	0
	Malacostraca	Amphipoda		scuds	1	2	2	0	4	1
		Decapoda	Cambaridae	crayfish	0	0	0	0	0	0
		Isopoda		sow bugs/woodlice	0	0	0	1	12	2
Mollusca	Bivalvia			clams & mussels	0	0	0	0	0	0
	Gastropoda	Stylommatophora		slugs	0	0	0	0	0	0
		other		snails	0	0	0	0	0	0
Nematoda				nematodes	0	1	0	0	2	0
overall					**18**	**20**	**7**	**227**	**294**	**19**

There were differences between the abundance of different common detritivore taxa (*Oligochaeta, Chironomidae, Tipulidae* and *Malacostraca*) in the differing moisture regimes (Figure 38 a-d). *Oligochaeta* and *Chironomidae* abundance was higher in the adjacent natural reference wetland than in similar and wetter moisture regimes in the created CC wetland (Figure 38 a & b). The high number of segmented worms in the CC wetland was not seen in the FL natural wetland, which instead had a large number of *Malacostraca*. While the wet moisture regime contained more than 7-fold more T*ipulidae*, the difference was not statistically significant except during the 11th month (Figure 38 c). The reference natural wetland had more detritivores than the wet and pond moisture regimes of the created wetland at 0.57 versus 0.21 and 0.11 detritivores/replicate respectively (Table 14). It does not appear that macroinvertebrates had as much of an influence on decomposition in the CC mitigation wetland as the FL wetland. Despite higher abundances for two detritivore taxa and for pooled detritivore numbers, the reference natural wetland had slower weight and litter area decomposition rates than the similar moisture regime of the created wetland. The pond moisture regime in the created wetland also had similar litter decomposition rates to the reference, yet had very few invertebrates (Chapter 2 and 3). These results suggest physical or microbial factors play a more important role at CC than the macroinvertebrate community. It is unclear whether (1) this is a factor of the created wetland's young age and that a larger macrodetritivore community will develop over time, or (2) perhaps this is due to a difference between the drier wet flat created wetland at CC and the wetter riparian system at FL.

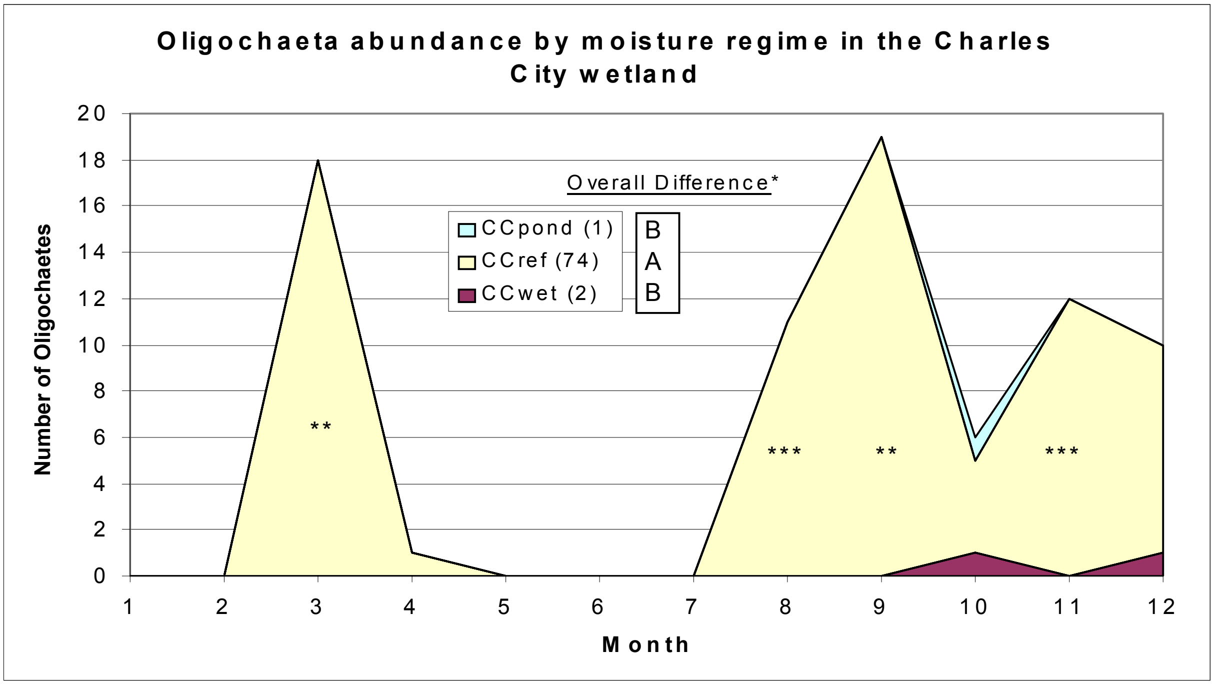

Figure 38a. *Oligochaeta* abundance by month and moisture regime at Charles City.
* Overall moisture regime treatment differences; regimes with the same letter are not significantly different (p=0.05).
** Moisture regime is significantly greater than other regimes for a given month (p=0.05), *** (p=0.10)

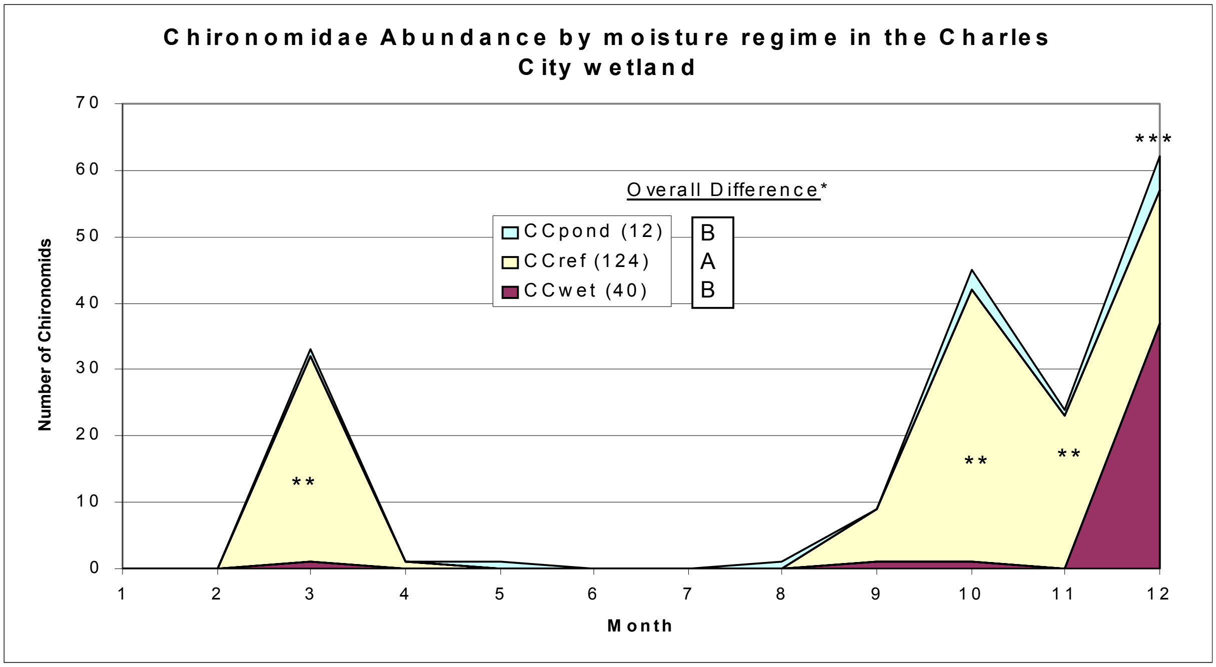

Figure 38b. *Chironomidae* abundance by month and moisture regime at Charles City.
* Overall moisture regime treatment differences; regimes with the same letter are not significantly different (p=0.05).
** Moisture regime is significantly greater than other regimes for a given month (p=0.05).
*** Wet > reference > pond for 12th month (p=0.10)

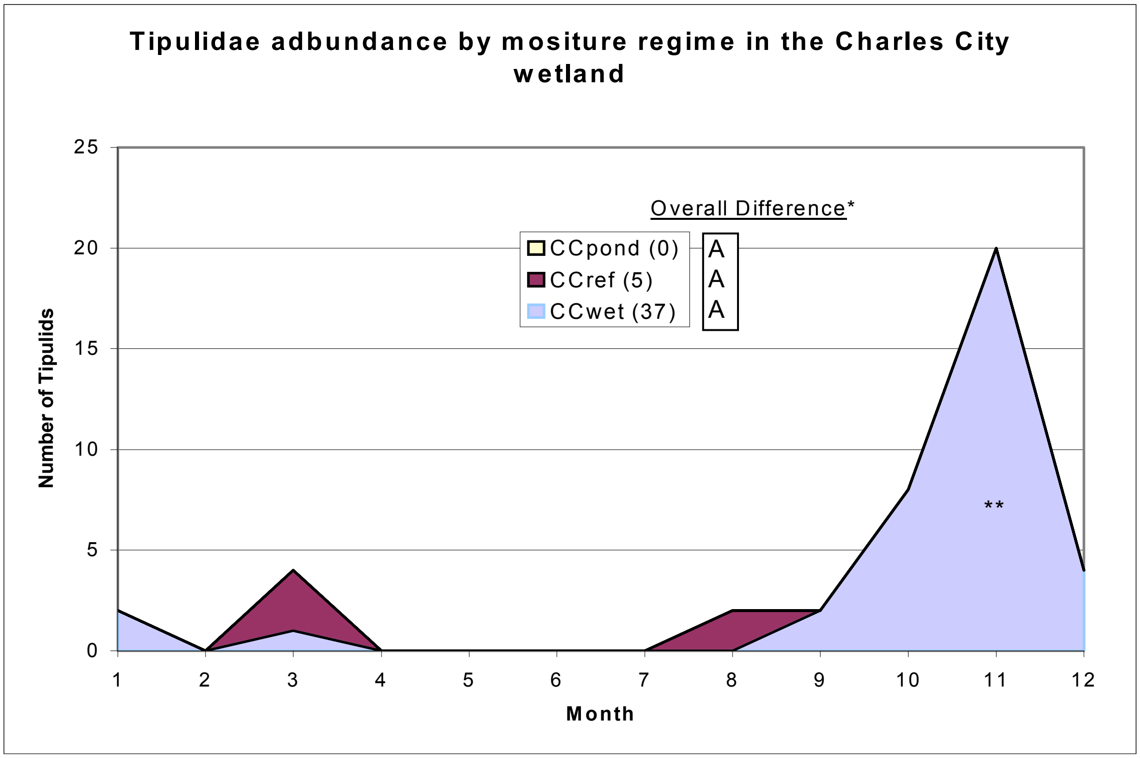

Figure 38c. *Tipulidae* abundance by month and moisture regime in Charles City.
* Overall moisture regime treatment differences; regimes with the same letter are not significantly different (p=0.05).
** Moisture regime is significantly greater than other regimes for a given month (p=0.05).

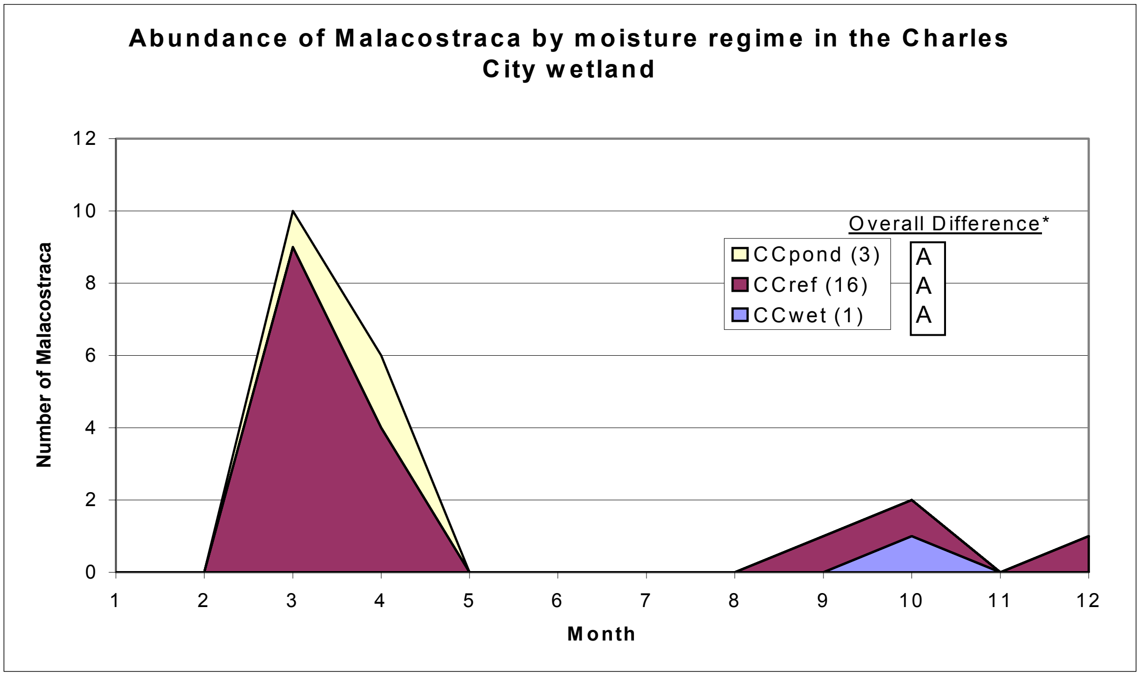

Figure 38d. *Malacostraca* abundance by month and moisture regime at Charles City.
* Overall moisture regime treatment differences; regimes with the same letter are not significantly different (p=0.05).

Conclusions

Macroinvertebrate populations sampled from litterbags at FL and CC showed differences (1) along a moisture gradient within the created wetlands and (2) between the created and adjacent natural wetlands with similar moisture regimes (wet vs. reference). When taxa which constitute more than 5% of the invertebrate abundance were examined (Table 13), midge larvae appeared to be the ubiquitous wetland taxa observed in all but the FL upland moisture regime. The two natural wetlands contained similar invertebrate populations dominated by midge larvae, although sow bugs and segmented worms were more important in the FL and CC natural wetlands respectively (Table 13). Despite similar moisture levels in the wet and reference regimes of the created and natural wetlands, the invertebrate communities were quite different. At FL, the created wetland contained higher numbers of *Malacostraca*, especially *Isopoda* (Table 13). At CC, the reverse was true; the natural wetland had more *Oligochaeta* and *Chironomidae* than created wetland areas with similar moisture regimes. This difference may be due to the young age of the CC created wetland relative to FL. Over time, similar invertebrate communities may develop. Age may not be the only factor involved, however, considering the drier conditions and compact clay soils at the created wet-flat wetland at CC relative to the riparian system at FL, which receives groundwater recharge.

Changes in invertebrate communities along a moisture gradient were most easily observed at the FL created wetland. As would be expected, the drier upland areas were dominated by terrestrial taxa such as spiders and ants and the permanently inundated pond areas by aquatic and semi-aquatic invertebrates such as midge larvae and scuds (Table 13). The intermediate wet areas that experienced alternating flooding and drying contained a mixture of species with some aquatic taxa such as midge larvae, along with semi-aquatic and terrestrial taxa such as sow bugs and segmented worms. It is not clear whether these differences in invertebrate communities along this moisture gradient were directly related to the water levels, or were a secondary result associated with the different vegetation types which varied from submerged plants to cattails to tall fescue and lespedeza from pond to upland conditions.

When taxa that typically contain detritivores were compared with litter decomposition rates at the FL wetland, the results followed the expected pattern of higher decomposition rates and detritivore populations in the wet and reference moisture regimes. Although the upland moisture regime had a similar number of total invertebrates, there were fewer detritivore taxa, 0.04 detritivores/replicate, which corresponded well with the slowest rate of decomposition. This correlation, along with faster rates of litter loss in coarse mesh litterbags relative to fine mesh at FL, suggests macrodetritivores play an important role in litter decomposition. Other factors such as temperature, moisture, vegetation, soil, physical forces, microbes, and micro-detritivores likely also play a part as indicated by the CC wetland results. Associated with relatively low detritivore abundance in the CC created wetland (0.21 and 0.11 detritivores/replicate for wet and pond), decomposition rates were similar or faster than in the adjacent natural wetland (Chapter 2 and 3). Despite the fact that the natural wetland had almost three-fold the number of detritivores than the wet moisture regime in the created wetland, weight loss was more rapid in the created wetland. Therefore, macrodetritivore abundance didn't seem to be as important as other physical and biological factors at CC. It is unclear whether the differences in macroinvertebrate communities and other aspects of decomposition between the CC created wetland and (1) the adjacent reference wetland and (2) the FL wetlands are a factor of wetland age, or due to soil, moisture or vegetation differences. It is possible that the young

CC created wetland detritivore community will increase in abundance and diversity as the site matures.

Chapter 5. Summary and Conclusions

Table 17 gives a summary of the results and statistical differences from the three results chapters of this thesis (i.e. Chapters 2-4). For a graphical representation of the detritivore abundance and weight/area loss results, see the conceptual diagrams in the Appendix for each wetland/moisture regime combination.

Objectives

The primary objective of this study was to compare litter decomposition between constructed wetlands and adjacent natural wetlands, which presumably represent the ecosystem that these two wetland systems were constructed to emulate. This comparison was tested by comparing the decomposition in adjacent forested wetlands with areas within the created wetland with a similar moisture regime (i.e. wet vs. reference; Table 17). For all litter weight and area loss comparisons, except for marsh litter at Fort Lee (FL), litter loss was more rapid in the created wetland than the adjacent forested wetland (Table 17). As a possible independent confirmation of this trend, soil organic matter levels did not increase over five years (1993-1998) in the FL constructed wetland (Cummings, 1999). This result is surprising considering the relatively intact litter layer and presumably active and diverse detritivore community of the natural forested wetland. The more rapid decomposition rates observed in the constructed wetlands may be due to higher soil temperatures, which have also been previously reported in constructed wetlands. With drastic differences in the vegetation, litter layer, and soil properties between constructed and forested wetlands, other factors beyond temperature may also be important. The rapid litter decomposition in the constructed wetlands could be considered as a positive for mitigation success; indicating the litter decomposition function recovers rapidly in these systems.

Table 17. Summary of litter weight loss, area loss, area:perimeter ratio, weight:area ratio. C:N ratio and macroinvertebrate results.

Site	**Litter type**	**Wetland type**	**Moisture regime**	**Litter weight loss**			**Litter area loss**			**Area: Perimeter ratio (average)**	**Weight: Area ratio (average)**	**Invert. abund.**	**Invert. diversity**	**Detrit-ivore abund.**	**C:N Ratio**
				Fine mesh single exp. k	Coarse Mesh single exp. k	Diff. (both mesh sizes)	Fine mesh single exp. k	Coarse Mesh single exp. k	Diff. (both mesh sizes)						
				yr^{-1}	yr^{-1}		yr^{-1}	yr^{-1}		cm^2:cm	g/m^2	# per replicate	# taxa per replicate	# per replicate	average
Fort Lee	**Forest**	**Created**	**pond**	0.99	1.21	B*	0.84	1.1	A*	0.247B*	82A*	5.03B*	1.64B*	0.94B*	37.4B*
			wet	1.13	1.46	A	0.91	1.13	A	0.208C	77.2B	10A	1.97A	2.25A	31.1C
			upland	0.73	0.91	C	0.58	0.73	C	0.261A	78.1B	4.33B	1.81AB	0.04B	38.8A
		Natural	**reference (wet)**	0.99	1.1	B	0.84	1.02	B	0.205C	81.8AB	3.99B	1.38B	0.8B	32.0C
	Marsh	**Created**	**pond**	0.621	0.767	B									48.9AB
			wet	0.731	0.913	A									43.2C
			upland	0.475	0.658	C									50.1A
		Natural	**reference (wet)**	0.731	0.804	A									45.6BC
Charles City	**Forest**	**Created**	**pond**	0.91	1.06	B	0.88	1.02	A	0.253A	77.8A	0.53B	0.42B	0.11B	37.7A
			wet	1.1	1.21	A	1.02	1.24	A	0.243A	77.9A	2.36A	0.95A	0.21B	36.0A
		Natural	**reference (wet)**	0.95	0.95	B	0.88	0.91	B	0.262A	73.6B	3.06A	1.16A	0.57A	34.4B
	Marsh	**Created**	**wet**	0.658	0.804	A									51.3A
		Natural	**reference (wet)**	0.511	0.548	B									46.8B

* Average values with the same letter in the same column and site/littertype combination are not significantly different ($p=0.05$).

Despite faster decomposition in the created wetland relative to the adjacent forested wetland for both FL and Charles City (CC), secondary comparisons of weight:area ratio, C:N ratio and detritivore taxa differ between FL and CC (Table 17). These differences, especially the high detritivore abundance in the FL created wetland, suggests that different factors are responsible for the faster rate of decomposition in the two wetlands. While the FL constructed wetland is 7 years older than the CC wetland, differences between the litter decomposition patterns may not be due to age. With a finer textured soil and no groundwater discharge at the CC constructed wetland, more than one factor may be involved. Although the high macroinvertebrate abundance in the FL created wetland may be associated with ecosystem age. A follow-up invertebrate study would be necessary at an older CC wetland to test this possibility without the confounding site difference between the two wetlands examined in this study.

This study also confirmed some well-established factors which influence litter decomposition in litterbags. The mixed marsh litter decomposed more slowly than the mixed forest leaf litter (Table 17). These differences in litter quality, which are often correlated to C:N ratios or other litter components, were supported by the initial C:N values for the marsh and forest litter. Similarly, coarse mesh litterbags produced more rapid litter decomposition (Table 17). While this difference is commonly attributed to the action of macroinvertebrates who have access to the litter in the coarse, but not the fine mesh, it could also be due to a bag effect as undecomposed fragments of litter fell through the coarse mesh. In reality, it is likely a combination of the action of detritivores and this bag effect.

Litter decomposition was also examined along a moisture gradient in the constructed wetlands, from permanently inundated to periodically flooded to upland areas without flooding. This gradient was best examined in the FL constructed wetland. Litter decomposition was slower for inundated pond and drier upland areas of the constructed wetland relative to the intermediate wet moisture regime (Table 17). This pattern suggests that moisture limited decomposition in the upland areas and anoxic conditions slowed decomposition in the permanently ponded areas.

A final objective was to assess the usefulness of the novel combination of litter decomposition methods used in this study, where weight and area loss, along with invertebrate numbers were followed over time. The combined technique has the advantage of being more than just the sum of its parts, new parameters such as the litter weight:area ratio were developed. As seen in the conceptual diagrams (Figures 39-46 in Appendix VI), instead of simply knowing litter lost weight over time, the relative importance of fragmentation and ingestion of whole leaf fragments could be compared to leaching and microbial action which reduces the mass without changing area or area:perimeter ratio. For example, by comparing the diagrams for FL wet and upland, it is apparent that litter became more quickly fragmented at the wet sites which contained correspondingly high number of detritivores relative to the upland area where leaching and microbial action dominated for the first 6 months of decomposition (Figure 40 & 43). In essence, the combined technique helps suggest answers to how litter decomposes and what factors are important instead of simply giving the traditional method's rate.

Considering the vast ecological differences between recently constructed wetlands and natural forested wetlands, I am left wondering whether we are comparing "apples and oranges." From my study of litter processing, I found myself many times discussing the uncertainty of whether the created wetland functions will change as the wetland changes from an emergent to a forested ecosystem. This "future uncertainty" concerning decomposition rates and associated factors in created forested wetlands, without literature to provide insight into the trajectory of site recovery, makes me question the validity of assessing wetland mitigation functional "success" (at least with regards to litter processing) before the system has even changed from an emergent to shrub/scrub or forested system. Based on this study, I have similar concerns regarding comparisons between relatively mature natural reference wetlands and early successional recently disturbed and created systems.

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Appendix I. Soil Water Levels at Fort Lee

Note: Blanks in "well level relative to surface" column indicate dry wells unless otherwise noted; positive well levels indicate ponding above the soil surface.

Fort Lee Wetland				
Date	Well	Treatment	Surface conditions in area of litterbag placement	well level relative to surface (cm)
10/3/1998	6 - wet	wet 4		
10/3/1998	5B	wet 1		-102
10/3/1998	5B2	wet 1		
10/3/1998	4LD	wet 2		-119
10/3/1998	7-4D	wet 3		-81
10/3/1998	7-4S	wet 3		
10/3/1998	front pond (1-line)	pond 3		
10/3/1998	deep pond (3-line)	pond 2		
10/3/1998	middle pond (7-line)	pond 1		
10/3/1998	5C	upland 1		
10/3/1998	6C	upland 2		
10/3/1998	7C	upland 3		
10/3/1998	ref 5	ref 4		
10/3/1998	2 F	ref 3		-103
10/3/1998		ref 2		
10/3/1998		ref 1		
10/31/1998	6 - wet	wet 4		
10/31/1998	5B	wet 1		-103
10/31/1998	5B2	wet 1		
10/31/1998	4LD	wet 2		-120
10/31/1998	7-4D	wet 3		-76
10/31/1998	7-4S	wet 3		
10/31/1998	front pond (1-line)	pond 3		
10/31/1998	deep pond (3-line)	pond 2		
10/31/1998	middle pond (7-line)	pond 1		
10/31/1998	5C	upland 1		-118
10/31/1998	6C	upland 2		-101
10/31/1998	7C	upland 3		
10/31/1998	ref 5	ref 4		
10/31/1998	2 F	ref 3		-106
10/31/1998		ref 2		
10/31/1998		ref 1		
12/4/1998	6 - wet	wet 4		
12/4/1998	5B	wet 1		-77
12/4/1998	5B2	wet 1		
12/4/1998	4LD	wet 2		-93
12/4/1998	7-4D	wet 3		-56
12/4/1998	7-4S	wet 3		-55
12/4/1998	front pond (1-line)	pond 3		

Date	Well	Treatment	Surface conditions in area of litterbag placement	well level relative to surface (cm)
12/4/1998	deep pond (3-line)	pond 2		
12/4/1998	middle pond (7-line)	pond 1		
12/4/1998	5C	upland 1		-89
12/4/1998	6C	upland 2		-74
12/4/1998	7C	upland 3		-64
12/4/1998	ref 5	ref 4		-75
12/4/1998	2 F	ref 3		-94
12/4/1998		ref 2		
12/4/1998		ref 1		
12/22/1998	6 - wet	wet 4	ponded 0-1.5"	no data
12/30/1998	5B	wet 1	ponded 1-2"	no data
12/30/1998	5B2	wet 1	ponded 1-2"	no data
12/31/1998	4LD	wet 2	ponded 0.5-1.5"	no data
12/22/1998	7-4D	wet 3	ponded 0.5-1"	no data
12/22/1998	7-4S	wet 3	ponded 0.5-1"	no data
12/22/1998	front pond (1-line)	pond 3	ponded 4-6"	no data
12/22/1998	deep pond (3-line)	pond 2	ponded 24 "	no data
12/30/1998	middle pond (7-line)	pond 1	ponded 4-6"	no data
12/30/1998	5C	upland 1	saturated soil	no data
12/30/1998	6C	upland 2	saturated soil	no data
12/22/1998	7C	upland 3	saturated soil	no data
12/31/1998	ref 5	ref 4	ponded 0-1"	no data
12/23/1998	2 F	ref 3	ponded 0-1"	no data
12/22/1998		ref 2	ponded 0-1"	no data
12/31/1998		ref 1	ponded 0-1"	no data
1/7/1999	6 - wet	wet 4		
1/7/1999	5B	wet 1		-1.8
1/7/1999	5B2	wet 1		7.9
1/7/1999	4LD	wet 2		-9.5
1/7/1999	7-4D	wet 3		-8.5
1/7/1999	7-4S	wet 3		-8.4
1/7/1999	front pond (1-line)	pond 3		
1/7/1999	deep pond (3-line)	pond 2		
1/7/1999	middle pond (7-line)	pond 1		
1/7/1999	5C	upland 1		-20
1/7/1999	6C	upland 2		-12
1/7/1999	7C	upland 3		-5.1
1/7/1999	ref 5	ref 4		6.9
1/7/1999	2 F	ref 3		-50
1/7/1999		ref 2		
1/7/1999		ref 1		
1/29/1999	6 - wet	wet 4	ponded 0-0.5"	
1/29/1999	5B	wet 1	ponded 0-1"	-3.9
1/29/1999	5B2	wet 1	ponded 0-1"	5.8
1/29/1999	4LD	wet 2	ponded 1"	-7.4

Date	Well	Treatment	Surface conditions in area of litterbag placement	well level relative to surface (cm)
1/29/1999	7-4D	wet 3	ponded 1"	-9.4
1/29/1999	7-4S	wet 3	ponded 1"	-8.4
1/29/1999	front pond (1-line)	pond 3	ponded 3"	
1/29/1999	deep pond (3-line)	pond 2	ponded 18"	
1/29/1999	middle pond (7-line)	pond 1	ponded 4-6"	
1/29/1999	5C	upland 1	saturated soil	-24
1/29/1999	6C	upland 2	saturated soil	-11
1/29/1999	7C	upland 3	saturated soil	-5.1
1/29/1999	ref 5	ref 4	saturated soil	6.3
1/29/1999	2 F	ref 3	ponded 0-0.5"	-25
1/29/1999		ref 2	ponded 0-0.5"	
1/29/1999		ref 1	ponded 0-0.5"	
3/1/1999	6 - wet	wet 4	ponded 1-2"	
3/1/1999	5B	wet 1	ponded 1-2"	-3.6
3/1/1999	5B2	wet 1	ponded 1-2"	7.0
3/1/1999	4LD	wet 2	ponded 1-2"	-5.3
3/1/1999	7-4D	wet 3	ponded 1-2"	-10
3/1/1999	7-4S	wet 3	ponded 1-2"	-8.4
3/1/1999	front pond (1-line)	pond 3	ponded 3-6"	
3/1/1999	deep pond (3-line)	pond 2	ponded 3-6"	
3/1/1999	middle pond (7-line)	pond 1	ponded 3-6"	
3/1/1999	5C	upland 1		-26
3/1/1999	6C	upland 2		-7.6
3/1/1999	7C	upland 3		-6.3
3/1/1999	ref 5	ref 4	saturated soil	2.3
3/1/1999	2 F	ref 3	saturated soil	-33
3/1/1999		ref 2	saturated soil	
3/1/1999		ref 1	saturated soil	
4/3/1999	6 - wet	wet 4	ponded 0.5-2"	
4/3/1999	5B	wet 1	ponded 0.5-2"	1.0
4/3/1999	5B2	wet 1	ponded 0.5-2"	10
4/3/1999	4LD	wet 2	ponded 0.5-2"	-1.9
4/3/1999	7-4D	wet 3	ponded 0.5-2"	-6.6
4/3/1999	7-4S	wet 3	ponded 0.5-2"	-6.0
4/3/1999	front pond (1-line)	pond 3		
4/3/1999	deep pond (3-line)	pond 2		
4/3/1999	middle pond (7-line)	pond 1	ponded 5-6"	
4/3/1999	5C	upland 1		-39
4/3/1999	6C	upland 2		-6.1
4/3/1999	7C	upland 3		-3.9
4/3/1999	ref 5	ref 4	ponded 0.5-2"	11
4/3/1999	2 F	ref 3	ponded 0.5-2"	-28
4/3/1999		ref 2	ponded 0.5-2"	
4/3/1999		ref 1	ponded 0.5-2"	
5/5/1999	6 - wet	wet 4	ponded 0.5-1"	

Date	Well	Treatment	Surface conditions in area of litterbag placement	well level relative to surface (cm)
5/5/1999	5B	wet 1	ponded 0.5-1"	-3.3
5/5/1999	5B2	wet 1	ponded 0.5-1"	8.2
5/5/1999	4LD	wet 2	ponded 0.5-1"	-11
5/5/1999	7-4D	wet 3	ponded 0.5-1"	-7.5
5/5/1999	7-4S	wet 3	ponded 0.5-1"	-7.8
5/5/1999	front pond (1-line)	pond 3	ponded 3"	
5/5/1999	deep pond (3-line)	pond 2	ponded 6"	
5/5/1999	middle pond (7-line)	pond 1	ponded 4"	
5/5/1999	5C	upland 1		-48
5/5/1999	6C	upland 2		-25
5/5/1999	7C	upland 3		-21
5/5/1999	ref 5	ref 4	saturated soil	-3.5
5/5/1999	2 F	ref 3	saturated soil	-36
5/5/1999		ref 2	saturated soil	
5/5/1999		ref 1	saturated soil	
5/31/1999	6 - wet	wet 4	saturated soil	
5/31/1999	5B	wet 1	saturated soil	-36
5/31/1999	5B2	wet 1	saturated soil	-7.0
5/31/1999	4LD	wet 2	saturated soil	-59
5/31/1999	7-4D	wet 3	saturated soil	-25
5/31/1999	7-4S	wet 3	saturated soil	-27
5/31/1999	front pond (1-line)	pond 3		
5/31/1999	deep pond (3-line)	pond 2		
5/31/1999	middle pond (7-line)	pond 1		
5/31/1999	5C	upland 1		-69
5/31/1999	6C	upland 2		-56
5/31/1999	7C	upland 3		-45
5/31/1999	ref 5	ref 4	saturated soil	-55
5/31/1999	2 F	ref 3	saturated soil	-72
5/31/1999		ref 2	saturated soil	
5/31/1999		ref 1	saturated soil	
7/8/1999	6 - wet	wet 4	ponded 1"	
7/8/1999	5B	wet 1	ponded 0.5-1.5"	
7/8/1999	5B2	wet 1	ponded 0.5-1.5"	-0.025
7/8/1999	4LD	wet 2	ponded 0-1"	-10
7/8/1999	7-4D	wet 3	ponded 1"	-7.2
7/8/1999	7-4S	wet 3	ponded 1"	-16
7/8/1999	front pond (1-line)	pond 3	ponded 3"	
7/8/1999	deep pond (3-line)	pond 2	ponded 16"	
7/8/1999	middle pond (7-line)	pond 1	ponded 4-5"	
7/8/1999	5C	upland 1	moist	-41
7/8/1999	6C	upland 2	moist	-20
7/8/1999	7C	upland 3	saturated soil	-8.5
7/8/1999	ref 5	ref 4	ponded 0.5-2"	14
7/8/1999	2 F	ref 3	ponded 0.5-2"	
7/8/1999		ref 2	ponded 0.5-2"	

Date	Well	Treatment	Surface conditions in area of litterbag placement	well level relative to surface (cm)
7/8/1999		ref 1	ponded 0.5-2"	
8/9/1999	6 - wet	wet 4	dry	
8/9/1999	5B	wet 1	dry	-84
8/9/1999	5B2	wet 1	dry	
8/9/1999	4LD	wet 2	dry	-100
8/9/1999	7-4D	wet 3	dry/moist	-64
8/9/1999	7-4S	wet 3	dry/moist	-65
8/9/1999	front pond (1-line)	pond 3	ponded 0.5"	
8/9/1999	deep pond (3-line)	pond 2	ponded 2"	
8/9/1999	middle pond (7-line)	pond 1	ponded 2-3"	
8/9/1999	5C	upland 1	dry	-106
8/9/1999	6C	upland 2	dry	-90
8/9/1999	7C	upland 3	dry	-79
8/9/1999	ref 5	ref 4	dry	-93
8/9/1999	2 F	ref 3	dry/damp	-103
8/9/1999		ref 2	dry/damp	
8/9/1999		ref 1	dry/damp	
9/14/1999	6 - wet	wet 4	ponded 0-1"	
9/14/1999	5B	wet 1	ponded 0-.5"	-11
9/14/1999	5B2	wet 1	ponded 0-.5"	4.9
9/14/1999	4LD	wet 2	ponded 0-.5"	-22
9/14/1999	7-4D	wet 3	ponded 0-1"	-16
9/14/1999	7-4S	wet 3	ponded 0-1"	-14
9/14/1999	front pond (1-line)	pond 3	ponded 3-4"	
9/14/1999	deep pond (3-line)	pond 2	ponded 8"	
9/14/1999	middle pond (7-line)	pond 1	ponded 5"	
9/14/1999	5C	upland 1	moist	-47
9/14/1999	6C	upland 2	damp/dry	-25
9/14/1999	7C	upland 3	damp/dry	-12
9/14/1999	ref 5	ref 4	saturated soil	6.6
9/14/1999	2 F	ref 3	saturated soil	-36
9/14/1999		ref 2	saturated soil	
9/14/1999		ref 1	saturated soil	
10/19/1999	6 - wet	wet 4	ponded 0.5-1"	2.9
10/19/1999	5B	wet 1	ponded 1"	-1.5
10/19/1999	5B2	wet 1	ponded 1"	10
10/19/1999	4LD	wet 2	ponded 1-2"	-5.6
10/19/1999	7-4D	wet 3	ponded 0.5-1.5"	-6.9
10/19/1999	7-4S	wet 3	ponded 0.5-1.5"	-6.9
10/19/1999	front pond (1-line)	pond 3	ponded 4"	15
10/19/1999	deep pond (3-line)	pond 2	ponded 24"	
10/19/1999	middle pond (7-line)	pond 1	ponded 8-12"	
10/19/1999	5C	upland 1	moist	-22
10/19/1999	6C	upland 2	damp/wet	-10

Date	Well	Treatment	Surface conditions in area of litterbag placement	well level relative to surface (cm)
10/19/1999	7C	upland 3	saturated soil	-3.6
10/19/1999	ref 5	ref 4	ponded 3-4" (flowing)	22
10/19/1999	2 F	ref 3	ponded 3-4" (flowing)	-6.2
10/19/1999		ref 2	ponded 3-4" (flowing)	
10/19/1999		ref 1	ponded 3-4" (flowing)	
11/24/1999	6 - wet	wet 4	ponded 0.5-1"	-1.3
11/24/1999	5B	wet 1	ponded 1-1.5"	-100
11/24/1999	5B2	wet 1	ponded 0.5-1.5"	-8.2
11/24/1999	4LD	wet 2	ponded 0.5-1.5"	98
11/24/1999	7-4D	wet 3	ponded 0.5"	-12
11/24/1999	7-4S	wet 3	ponded 0.5"	-9.7
11/24/1999	front pond (1-line)	pond 3	ponded 2-3"	9.6
11/24/1999	deep pond (3-line)	pond 2	ponded 6-8"	
11/24/1999	middle pond (7-line)	pond 1	ponded 4-5"	
11/24/1999	5C	upland 1	damp/saturated soil	-44
11/24/1999	6C	upland 2	damp	-20
11/24/1999	7C	upland 3	moist	-18
11/24/1999	ref 5	ref 4	ponded 1-2" (flowing)	14
11/24/1999	2 F	ref 3	ponded 1-2" (flowing)	-23
11/24/1999		ref 2	ponded 1-2" (flowing)	
11/24/1999		ref 1	ponded 1-2" (flowing)	
12/31/1999	6 - wet	wet 4	ponded 0.5-1.5"	0.48
12/31/1999	5B	wet 1	ponded 0.5-1"	-3.6
12/31/1999	5B2	wet 1	ponded 0.5-1"	7.9
12/31/1999	4LD	wet 2	ponded 1.5"	-8.3
12/31/1999	7-4D	wet 3	ponded 0.5-1"	-9.4
12/31/1999	7-4S	wet 3	ponded 0.5-1"	-8.4
12/31/1999	front pond (1-line)	pond 3	ponded 3"	11
12/31/1999	deep pond (3-line)	pond 2	ponded 14-16"	
12/31/1999	middle pond (7-line)	pond 1	ponded 4-6"	
12/31/1999	5C	upland 1	damp	-37
12/31/1999	6C	upland 2	damp	-16
12/31/1999	7C	upland 3	damp	-6.0
12/31/1999	ref 5	ref 4	ponded 0.5-2"	15
12/31/1999	2 F	ref 3	ponded 0.5-2"	-22
12/31/1999		ref 2	ponded 0.5-2"	
12/31/1999		ref 1	ponded 0.5-2"	
2/13/2000	6 - wet	wet 4		2.9
2/13/2000	5B	wet 1		1.6
2/13/2000	5B2	wet 1		11
2/13/2000	4LD	wet 2		-4.3
2/13/2000	7-4D	wet 3	ponded 2"	-6.9
2/13/2000	7-4S	wet 3	ponded 2"	-6.3
2/13/2000	front pond (1-line)	pond 3	ponded 3"	14
2/13/2000	deep pond (3-line)	pond 2	ponded 12-16"	

Date	Well	Treatment	Surface conditions in area of litterbag placement	well level relative to surface (cm)
2/13/2000	middle pond (7-line)	pond 1	ponded 4-5"	
2/13/2000	5C	upland 1		-24
2/13/2000	6C	upland 2		-6.4
2/13/2000	7C	upland 3		-4.2
2/13/2000	ref 5	ref 4	saturated to ponded 2"	11
2/13/2000	2 F	ref 3	saturated to ponded 2"	-21
2/13/2000		ref 2	saturated to ponded 2"	
2/13/2000		ref 1	saturated to ponded 2"	
3/19/2000	6 - wet	wet 4		4.4
3/19/2000	5B	wet 1		1.6
3/19/2000	5B2	wet 1		12
3/19/2000	4LD	wet 2		-3.7
3/19/2000	7-4D	wet 3		-4.8
3/19/2000	7-4S	wet 3		-4.5
3/19/2000	front pond (1-line)	pond 3		15
3/19/2000	deep pond (3-line)	pond 2		
3/19/2000	middle pond (7-line)	pond 1		
3/19/2000	5C	upland 1		-26
3/19/2000	6C	upland 2		-2.1
3/19/2000	7C	upland 3		-3.0
3/19/2000	ref 5	ref 4		11
3/19/2000	2 F	ref 3		-23
3/19/2000		ref 2		
3/19/2000		ref 1		
6/24/2000	6 - wet	wet 4	ponded 0-0.5"	-5.3
6/24/2000	5B	wet 1	ponded 0-0.5"	-15
6/24/2000	5B2	wet 1	ponded 0-0.5"	3.0
6/23/2000	4LD	wet 2	ponded 0.5-1"	-28
6/24/2000	7-4D	wet 3		-16
6/24/2000	7-4S	wet 3		-18
6/23/2000	front pond (1-line)	pond 3		11
6/23/2000	deep pond (3-line)	pond 2	ponded 8"	
6/24/2000	middle pond (7-line)	pond 1	ponded 10"	
6/23/2000	5C	upland 1	dry	-47
6/24/2000	6C	upland 2	moist	-40
6/24/2000	7C	upland 3	moist	-32
6/23/2000	ref 5	ref 4	saturated to ponded 2"	15
6/23/2000	2 F	ref 3	saturated to ponded 2"	-21
6/23/2000		ref 2	saturated to ponded 2"	
6/23/2000		ref 1	saturated to ponded 2"	
7/31/2000	6 - wet	wet 4	ponded 1"	-2.6
7/31/2000	5B	wet 1	ponded 1"	-7.3
7/31/2000	5B2	wet 1	ponded 1"	6.4
7/31/2000	4LD	wet 2		-13
7/31/2000	7-4D	wet 3		-12

Date	Well	Treatment	Surface conditions in area of litterbag placement	well level relative to surface (cm)
7/31/2000	7-4S	wet 3		-13
7/31/2000	front pond (1-line)	pond 3		11
7/31/2000	deep pond (3-line)	pond 2		
7/31/2000	middle pond (7-line)	pond 1	ponded 12-14"	
7/31/2000	5C	upland 1		-46
7/31/2000	6C	upland 2		-29
7/31/2000	7C	upland 3		-8.2
7/31/2000	ref 5	ref 4	ponded 1"	13
7/31/2000	2 F	ref 3	ponded 1"	-25
7/31/2000		ref 2	ponded 1"	
7/31/2000		ref 1	ponded 1"	
8/13/2000	6 - wet	wet 4	saturated soil	-13
8/13/2000	5B	wet 1	saturated soil	-28
8/13/2000	5B2	wet 1	saturated soil	-0.6
8/13/2000	4LD	wet 2	saturated soil	-47
8/13/2000	7-4D	wet 3	saturated soil	-21
8/13/2000	7-4S	wet 3	saturated soil	-25
8/13/2000	front pond (1-line)	pond 3	ponded 3"	9.6
8/13/2000	deep pond (3-line)	pond 2	ponded 12"	
8/13/2000	middle pond (7-line)	pond 1	ponded 8"	
8/13/2000	5C	upland 1	dry	-54
8/13/2000	6C	upland 2	dry	-45
8/13/2000	7C	upland 3	dry	-38
8/13/2000	ref 5	ref 4	saturated to ponded 2"	13
8/13/2000	2 F	ref 3	saturated to ponded 2"	-25
8/13/2000		ref 2	saturated to ponded 2"	
8/13/2000		ref 1	saturated to ponded 2"	
9/1/2000	6 - wet	wet 4	ponded 1-2"	-0.13
9/1/2000	5B	wet 1	ponded 1-2"	-2.1
9/1/2000	5B2	wet 1	ponded 1-2"	7.3
9/1/2000	4LD	wet 2	ponded 1-2"	-3.4
9/1/2000	7-4D	wet 3	ponded 1"	-9.1
9/1/2000	7-4S	wet 3	ponded 1"	-9.7
9/1/2000	front pond (1-line)	pond 3	ponded 6-8"	12
9/1/2000	deep pond (3-line)	pond 2		
9/1/2000	middle pond (7-line)	pond 1	ponded 8-10"	
9/1/2000	5C	upland 1		
9/1/2000	6C	upland 2	saturated soil	-9.8
9/1/2000	7C	upland 3	saturated soil to ponded 0.5"	-3.3
9/1/2000	ref 5	ref 4		20
9/1/2000	2 F	ref 3		
9/1/2000		ref 2		
9/1/2000		ref 1		
3/15/2001	6 - wet	wet 4	ponded 1-3"	0.79
3/15/2001	5B	wet 1	ponded 0.5-2"	-2.7

Date	Well	Treatment	Surface conditions in area of litterbag placement	well level relative to surface (cm)
3/15/2001	5B2	wet 1	ponded 0.5-2"	8.2
3/15/2001	4LD	wet 2	ponded 1-3"	-4.6
3/15/2001	7-4D	wet 3	ponded 0.5-2"	-9.7
3/15/2001	7-4S	wet 3	ponded 0.5-2"	-9.0
3/15/2001	front pond (1-line)	pond 3	ponded 4"	12
3/15/2001	deep pond (3-line)	pond 2	ponded 8-12"	
3/15/2001	middle pond (7-line)	pond 1	ponded 6-10"	
3/15/2001	5C	upland 1	damp	-20
3/15/2001	6C	upland 2	damp/saturated soil	-12
3/15/2001	7C	upland 3	saturated soil	-3.9
3/15/2001	ref 5	ref 4	ponded 0-2"	7.2
3/15/2001	2 F	ref 3	ponded 0-2"	-35
3/15/2001		ref 2	ponded 0-2"	
3/15/2001		ref 1	ponded 0-2"	

Appendix II. Soil Water Levels at Charles City

Note: Blanks in "well level relative to surface" column indicate dry wells unless otherwise noted; positive well levels indicate ponding above the soil surface.

Date	Well	Treatment	Surface moisture conditions in litterbag placement area	Well level relative to surface (cm)
12/26/1998	17A	WET 3	saturated to ponded 1"	no data
12/26/1998	17B	WET 3	saturated to ponded 1"	no data
12/26/1998	new 17	WET 3	saturated to ponded 1"	no data
12/26/1998	19A	WET 1	saturated to ponded 1"	no data
12/26/1998	19B	WET 1	saturated to ponded 1"	no data
12/26/1998	28A	WET 2	saturated to ponded 1"	no data
12/26/1998	28B	WET 2	saturated to ponded 1"	no data
12/26/1998	20A	POND 3	ponded 3"	no data
12/26/1998	20B	POND 3	ponded 3"	no data
12/26/1998	13A	POND 1	ponded 4"	no data
12/26/1998	13B	POND 1	ponded 4"	no data
12/26/1998	14	REF 1	saturated to ponded 1"	no data
12/26/1998	15	REF 2	saturated to ponded 1"	no data
12/26/1998	NEW REF	REF 4	saturated to ponded 1"	no data
12/26/1998	12A	WET 4	saturated to ponded 1"	no data
12/26/1998	12B	WET 4	saturated to ponded 1"	no data
12/26/1998	8A	POND 2	ponded 3"	no data
12/26/1998	8B	POND 2	ponded 3"	no data
12/26/1998	NEW 8	POND 2	ponded 3"	no data
1/28/1999	17A	WET 3	saturated soil to ponded 1"	no data
1/28/1999	17B	WET 3	saturated soil to ponded 1"	no data
1/28/1999	new 17	WET 3	saturated soil to ponded 1"	no data
1/28/1999	19A	WET 1	saturated soil to ponded 1"	no data
1/28/1999	19B	WET 1	saturated soil to ponded 1"	no data
1/28/1999	28A	WET 2	saturated soil to ponded 1"	no data
1/28/1999	28B	WET 2	saturated soil to ponded 1"	no data
1/28/1999	20A	POND 3	ponded 3-4"	no data
1/28/1999	20B	POND 3	ponded 3-4"	no data
1/28/1999	13A	POND 1	ponded 3-4"	no data
1/28/1999	13B	POND 1	ponded 3-4"	no data
1/28/1999	14	REF 1	saturated soil to ponded 1"	no data
1/28/1999	15	REF 2	saturated soil to ponded 1"	no data
1/28/1999	NEW REF	REF 4	saturated soil to ponded 1"	no data
1/28/1999	12A	WET 4	saturated soil to ponded 1"	no data
1/28/1999	12B	WET 4	saturated soil to ponded 1"	no data
1/28/1999	8A	POND 2	ponded 3-4"	no data
1/28/1999	8B	POND 2	ponded 3-4"	no data
1/28/1999	NEW 8	POND 2	ponded 3-4"	no data
4/3/1999	17A	WET 3	saturated to ponded 0.5"	no data
4/3/1999	17B	WET 3	saturated to ponded 0.5"	no data
4/3/1999	new 17	WET 3	saturated to ponded 0.5"	no data
4/3/1999	19A	WET 1	moist	no data

Date	Well	Treatment	Surface moisture conditions in litterbag placement area	Well level relative to surface (cm)
4/3/1999	19B	WET 1	moist	no data
4/3/1999	28A	WET 2	saturated to moist	no data
4/3/1999	28B	WET 2	saturated to moist	no data
4/3/1999	20A	POND 3	ponded 2-3"	no data
4/3/1999	20B	POND 3	ponded 2-3"	no data
4/3/1999	13A	POND 1	ponded 2-3"	no data
4/3/1999	13B	POND 1	ponded 2-3"	no data
4/3/1999	14	REF 1	saturated to ponded 1"	no data
4/3/1999	15	REF 2	saturated to ponded 1"	no data
4/3/1999	NEW REF	REF 4	saturated to ponded 1"	no data
4/3/1999	12A	WET 4	saturated to ponded 0.5"	no data
4/3/1999	12B	WET 4	saturated to ponded 0.5"	no data
4/3/1999	8A	POND 2	ponded 2-3"	no data
4/3/1999	8B	POND 2	ponded 2-3"	no data
4/3/1999	NEW 8	POND 2	ponded 2-3"	no data
5/6/1999	17A	WET 3	moist to saturated	-33.5
5/6/1999	17B	WET 3	moist to saturated	-26.8
5/6/1999	new 17	WET 3	moist to saturated	
5/6/1999	19A	WET 1	moist	-25.6
5/6/1999	19B	WET 1	moist	-29.7
5/6/1999	28A	WET 2	moist	-22.6
5/6/1999	28B	WET 2	moist	-19.5
5/6/1999	20A	POND 3	ponded 2-3"	-21.6
5/6/1999	20B	POND 3	ponded 2-3"	-11.7
5/6/1999	13A	POND 1	ponded 2-3"	-4.4
5/6/1999	13B	POND 1	ponded 2-3"	-11.7
5/6/1999	14	REF 1	saturated soil	-2.8
5/6/1999	15	REF 2	saturated soil	-4.9
5/6/1999	NEW REF	REF 4	saturated soil	
5/6/1999	12A	WET 4	saturated soil	-6.4
5/6/1999	12B	WET 4	saturated soil	-16.9
5/6/1999	8A	POND 2	ponded 2-3"	-6.7
5/6/1999	8B	POND 2	ponded 2-3"	-5.0
5/6/1999	NEW 8	POND 2	ponded 2-3"	
5/31/1999	17A	WET 3	dry	
5/31/1999	17B	WET 3	dry	
5/31/1999	new 17	WET 3	dry	
5/31/1999	19A	WET 1	dry	
5/31/1999	19B	WET 1	dry	
5/31/1999	28A	WET 2	dry	
5/31/1999	28B	WET 2	dry	
5/31/1999	20A	POND 3	dry and cracked	
5/31/1999	20B	POND 3	dry and cracked	
5/31/1999	13A	POND 1	moist and cracked	
5/31/1999	13B	POND 1	moist and cracked	
5/31/1999	14	REF 1	dry	
5/31/1999	15	REF 2	dry	

Date	Well	Treatment	Surface moisture conditions in litterbag placement area	Well level relative to surface (cm)
5/31/1999	NEW REF	REF 4	dry	
5/31/1999	12A	WET 4	dry and cracked	
5/31/1999	12B	WET 4	dry and cracked	
5/31/1999	8A	POND 2	ponded 1-2"	
5/31/1999	8B	POND 2	ponded 1-2"	
5/31/1999	NEW 8	POND 2	ponded 1-2"	
7/7/1999	17A	WET 3	dry	
7/7/1999	17B	WET 3	dry	
7/7/1999	new 17	WET 3	dry	
7/7/1999	19A	WET 1	dry	
7/7/1999	19B	WET 1	dry	
7/7/1999	28A	WET 2	dry	
7/7/1999	28B	WET 2	dry	
7/7/1999	20A	POND 3	dry	
7/7/1999	20B	POND 3	dry	
7/7/1999	13A	POND 1	dry	
7/7/1999	13B	POND 1	dry	
7/7/1999	14	REF 1	dry	
7/7/1999	15	REF 2	dry	
7/7/1999	NEW REF	REF 4	dry	
7/7/1999	12A	WET 4	dry	
7/7/1999	12B	WET 4	dry	
7/7/1999	8A	POND 2	dry	
7/7/1999	8B	POND 2	dry	
7/7/1999	NEW 8	POND 2	dry	
8/9/1999	17A	WET 3	dry and cracked	
8/9/1999	17B	WET 3	dry and cracked	
8/9/1999	new 17	WET 3	dry and cracked	
8/9/1999	19A	WET 1	dry and cracked	
8/9/1999	19B	WET 1	dry and cracked	
8/9/1999	28A	WET 2	dry	
8/9/1999	28B	WET 2	dry	
8/9/1999	20A	POND 3	dry and cracked	
8/9/1999	20B	POND 3	dry and cracked	
8/9/1999	13A	POND 1	dry and cracked	
8/9/1999	13B	POND 1	dry and cracked	
8/9/1999	14	REF 1	dry	
8/9/1999	15	REF 2	dry	
8/9/1999	NEW REF	REF 4	dry	
8/9/1999	12A	WET 4	dry	
8/9/1999	12B	WET 4	dry	
8/9/1999	8A	POND 2	damp	
8/9/1999	8B	POND 2	damp	
8/9/1999	NEW 8	POND 2	damp	
9/18/1999	17A	WET 3	1-3" STANDING WATER	-17.1
9/18/1999	17B	WET 3	1-3" STANDING WATER	5.2

Date	Well	Treatment	Surface moisture conditions in litterbag placement area	Well level relative to surface (cm)
9/18/1999	new 17	WET 3		
9/18/1999	19A	WET 1	1-3" STANDING WATER	-9.4
9/18/1999	19B	WET 1	1-3" STANDING WATER	14.5
9/18/1999	28A	WET 2	2-3" STANDING WATER	11.8
9/18/1999	28B	WET 2	2-3" STANDING WATER	
9/18/1999	20A	POND 3	8" WATER	-13.9
9/18/1999	20B	POND 3	8" WATER	-12.3
9/18/1999	13A	POND 1	8" WATER	-32.4
9/18/1999	13B	POND 1	8" WATER	15.1
9/18/1999	14	REF 1	2", 1-2", 2" WATER	5.1
9/18/1999	15	REF 2	2", 1-2", 2" WATER	1.8
9/18/1999	NEW REF	REF 4		
9/18/1999	12A	WET 4	1" WATER	
9/18/1999	12B	WET 4	1" WATER	14.5
9/18/1999	8A	POND 2	8-10" WATER	-3.0
9/18/1999	8B	POND 2	8-10" WATER	13.0
9/18/1999	NEW 8	POND 2		
10/19/1999	17A	WET 3	0-.5"	-24.7
10/19/1999	17B	WET 3	0-.5"	-7.3
10/19/1999	NEW 17	WET 3		
10/19/1999	19A	WET 1	sat - 0.5"	-23.7
10/19/1999	19B	WET 1	sat - 0.5"	0.2
10/19/1999	28A	WET 2	sat - 0.5"	-0.1
10/19/1999	28B	WET 2	sat - 0.5"	2.4
10/19/1999	20A	POND 3	3"	-18.8
10/19/1999	20B	POND 3	3"	-14.8
10/19/1999	13A	POND 1	3-4"	-0.1
10/19/1999	13B	POND 1	3-4"	2.0
10/19/1999	14	REF 1	sat-0.25"	-1.0
10/19/1999	15	REF 2	sat-0.25"	-5.5
10/19/1999	NEW REF	REF 4		
10/19/1999	12A	WET 4	2 " standing	
10/19/1999	12B	WET 4	2 " standing	-18.4
10/19/1999	8A	POND 2	4-5"	-14.9
10/19/1999	8B	POND 2	4-5"	-16.2
10/19/1999	NEW 8	POND 2		
11/23/1999	17A	WET 3	MOIST-SAT	-26.5
11/23/1999	17B	WET 3	MOIST-SAT	-34.8
11/23/1999	new 17	WET 3	MOIST-SAT	-71.2
11/23/1999	19A	WET 1	MOIST	-27.1
11/23/1999	19B	WET 1	MOIST	-22.4
11/23/1999	28A	WET 2	MOIST	-8.6
11/23/1999	28B	WET 2	MOIST	-4.9
11/23/1999	20A	POND 3	3-4"	-22.5
11/23/1999	20B	POND 3	3-4"	-16.3
11/23/1999	13A	POND 1	4"	-19.3
11/23/1999	13B	POND 1	4"	-2.9

Date	Well	Treatment	Surface moisture conditions in litterbag placement area	Well level relative to surface (cm)
11/23/1999	14	REF 1	MOIST/SAT	-5.6
11/23/1999	15	REF 2	MOIST/SAT	-8.2
11/23/1999	NEW REF	REF 4	MOIST	-6.1
11/23/1999	12A	WET 4	SAT	
11/23/1999	12B	WET 4	SAT	-8.0
11/23/1999	8A	POND 2	4-5"	-8.8
11/23/1999	8B	POND 2	4-5"	-12.9
11/23/1999	NEW 8	POND 2	4-5"	-135.9
12/30/1999	17A	WET 3	WET-0.25"	-5.8
12/30/1999	17B	WET 3	WET-0.25"	-28.1
12/30/1999	new 17	WET 3	WET-0.25"	-40.1
12/30/1999	19A	WET 1	SAT	-19.8
12/30/1999	19B	WET 1	SAT	-0.2
12/30/1999	28A	WET 2	SAT-0.25"	-1.3
12/30/1999	28B	WET 2	SAT-0.25"	1.2
12/30/1999	20A	POND 3	2-3"	-6.0
12/30/1999	20B	POND 3	2-3"	-8.1
12/30/1999	13A	POND 1	2-3"	-10.8
12/30/1999	13B	POND 1	2-3"	-0.1
12/30/1999	14	REF 1	WET-1"	0.8
12/30/1999	15	REF 2	WET-1"	-1.8
12/30/1999	NEW REF	REF 4	0-0.5"	2.4
12/30/1999	12A	WET 4	SAT	-3.7
12/30/1999	12B	WET 4	SAT	-26.9
12/30/1999	8A	POND 2	3"	-7.0
12/30/1999	8B	POND 2	3"	-8.9
12/30/1999	NEW 8	POND 2	3"	-163.0
2/11/2000	17A	WET 3	0.5-1"	-5.8
2/11/2000	17B	WET 3	0.5-1"	-9.2
2/11/2000	new 17	WET 3	0.5-1"	-8.1
2/11/2000	19A	WET 1	0.5"	-8.8
2/11/2000	19B	WET 1	0.5"	0.5
2/11/2000	28A	WET 2	0.25"	0.5
2/11/2000	28B	WET 2	0.25"	3.0
2/11/2000	20A	POND 3	3"	-3.3
2/11/2000	20B	POND 3	3"	-2.3
2/11/2000	13A	POND 1	3-4"	7.8
2/11/2000	13B	POND 1	3-4"	2.6
2/11/2000	14	REF 1	1-2"	5.1
2/11/2000	15	REF 2	1-2"	2.1
2/11/2000	NEW REF	REF 4	1-2"	7.0
2/11/2000	12A	WET 4	0.5-1"	-14.0
2/11/2000	12B	WET 4	0.5-1"	-3.5
2/11/2000	8A	POND 2	3"	-2.7
2/11/2000	8B	POND 2	3"	-0.7
2/11/2000	NEW 8	POND 2	3"	-173.7

Date	Well	Treatment	Surface moisture conditions in litterbag placement area	Well level relative to surface (cm)
3/19/2000	17A	WET 3	H20 0.67' HIGHER OUTSIDE	-21.9
3/19/2000	17B	WET 3	H20 0.70' HIGHER OUTSIDE	-25.3
3/19/2000	new 17	WET 3	H20 1.64 FT HIGHER OUTSIDE	-39.8
3/19/2000	19A	WET 1	SAT	-25.9
3/19/2000	19B	WET 1	SAT	-2.9
3/19/2000	28A	WET 2	SAT	-1.3
3/19/2000	28B	WET 2	SAT	1.8
3/19/2000	20A	POND 3		-28.9
3/19/2000	20B	POND 3		-30.9
3/19/2000	13A	POND 1	PONDED	-5.6
3/19/2000	13B	POND 1	PONDED	-1.4
3/19/2000	14	REF 1	PONDED	3.6
3/19/2000	15	REF 2	PONDED	0.9
3/19/2000	NEW REF	REF 4	PONDED	5.8
3/19/2000	12A	WET 4	H20 0.47' HIGHER OUTSIDE	-14.3
3/19/2000	12B	WET 4	H20 0.22' HIGHER OUTSIDE	-6.2
3/19/2000	8A	POND 2		-7.9
3/19/2000	8B	POND 2		-2.5
3/19/2000	NEW 8	POND 2	PONDED AT 2.80'	
5/1/2000	17A	WET 3	1"	-5.5
5/1/2000	17B	WET 3	1"	-33.5
5/1/2000	new 17	WET 3	1"	-31.8
5/1/2000	19A	WET 1	DAMP-DRY	-13.4
5/1/2000	19B	WET 1	DAMP-DRY	-15.7
5/1/2000	28A	WET 2	DAMP-DRY	-12.3
5/1/2000	28B	WET 2	DAMP-DRY	-4.6
5/1/2000	20A	POND 3	DAMP-DRY	-8.4
5/1/2000	20B	POND 3	DAMP-DRY	-11.1
5/1/2000	13A	POND 1	0.5 "	-6.8
5/1/2000	13B	POND 1	0.5 "	-1.4
5/1/2000	14	REF 1	WET	2.1
5/1/2000	15	REF 2	WET	-0.3
5/1/2000	NEW REF	REF 4	0.5"	3.9
5/1/2000	12A	WET 4	0.5-1"	-17.4
5/1/2000	12B	WET 4	0.5-1"	-7.4
5/1/2000	8A	POND 2	H20 0.18' HIGHER OUTSIDE	-4.9
5/1/2000	8B	POND 2	H20 0.18' HIGHER OUTSIDE	-4.4
5/1/2000	NEW 8	POND 2	H20 AT 2.65' OUTSIDE	
6/27/2000	17A	WET 3	GRD DRY HARD, CRACKED	
6/27/2000	17B	WET 3	GRD DRY HARD, CRACKED	
6/27/2000	new 17	WET 3	GRD DRY HARD, CRACKED	-96.1
6/27/2000	19A	WET 1	GRD DRY HARD, CRACKED	
6/27/2000	19B	WET 1	GRD DRY HARD, CRACKED	
6/27/2000	28A	WET 2	GRD HARD, DRY	
6/27/2000	28B	WET 2	GRD HARD, DRY	
6/27/2000	20A	POND 3	GRD DRY HARD, CRACKED	
6/27/2000	20B	POND 3	GRD DRY HARD, CRACKED	

Date	Well	Treatment	Surface moisture conditions in litterbag placement area	Well level relative to surface (cm)
6/27/2000	13A	POND 1	GRD DRY	
6/27/2000	13B	POND 1	GRD DRY	
6/27/2000	14	REF 1	GRD DRY	
6/27/2000	15	REF 2	GRD DRY	
6/27/2000	NEW REF	REF 4	GRD DRY	-146.0
6/27/2000	12A	WET 4	GRD DRY HARD, CRACKED	
6/27/2000	12B	WET 4	GRD DRY HARD, CRACKED	
6/27/2000	8A	POND 2	0.5" AT BAGS	
6/27/2000	8B	POND 2	0.5" AT BAGS	
6/27/2000	NEW 8	POND 2	0.5" AT BAGS	-169.1
7/30/2000	17A	WET 3	0.5-1"	-17.7
7/30/2000	17B	WET 3	0.5-1"	-3.1
7/30/2000	new 17	WET 3	0.5-1"	-30.3
7/30/2000	19A	WET 1	SAT-0.5"	-2.1
7/30/2000	19B	WET 1	SAT-0.5"	-5.0
7/30/2000	28A	WET 2		-1.0
7/30/2000	28B	WET 2		1.2
7/30/2000	20A	POND 3		0.1
7/30/2000	20B	POND 3		-9.6
7/30/2000	13A	POND 1		-19.6
7/30/2000	13B	POND 1		-1.4
7/30/2000	14	REF 1	MOIST	-34.5
7/30/2000	15	REF 2	MOIST	
7/30/2000	NEW REF	REF 4		-82.3
7/30/2000	12A	WET 4		-21.0
7/30/2000	12B	WET 4		-5.6
7/30/2000	8A	POND 2	1"	
7/30/2000	8B	POND 2	1"	1.4
7/30/2000	NEW 8	POND 2	1"	-147.1
8/13/2000	17A	WET 3	SAT-0.5"	-18.9
8/13/2000	17B	WET 3	SAT-0.5"	-4.0
8/13/2000	new 17	WET 3	SAT-0.5"	-32.1
8/13/2000	19A	WET 1	SAT-0.5"	-8.2
8/13/2000	19B	WET 1	SAT-0.5"	5.3
8/13/2000	28A	WET 2	SAT-0.5"	-0.4
8/13/2000	28B	WET 2	SAT-0.5"	0.3
8/13/2000	20A	POND 3	4"	-1.7
8/13/2000	20B	POND 3	4"	-5.6
8/13/2000	13A	POND 1	H20 AT WELLS 0.5", 3" AT STRIPS	
8/13/2000	13B	POND 1	H20 AT WELLS 0.5", 3" AT STRIPS	-0.4
8/13/2000	14	REF 1	DAMP	
8/13/2000	15	REF 2	DAMP	
8/13/2000	NEW REF	REF 4	DAMP	-97.9
8/13/2000	12A	WET 4	SAT-0.5"	
8/13/2000	12B	WET 4	SAT-0.5"	-2.9
8/13/2000	8A	POND 2	3"	

Date	Well	Treatment	Surface moisture conditions in litterbag placement area	Well level relative to surface (cm)
8/13/2000	8B	POND 2	3"	1.1
8/13/2000	NEW 8	POND 2	3"	-152.9
9/4/2000	17A	WET 3	3-4"	-13.1
9/4/2000	17B	WET 3	3-4"	6.1
9/4/2000	new 17	WET 3	3-4"	-8.1
9/4/2000	19A	WET 1	2-3"	7.7
9/4/2000	19B	WET 1	2-3"	2.3
9/4/2000	28A	WET 2	2-3"	4.5
9/4/2000	28B	WET 2	2-3"	8.2
9/4/2000	20A	POND 3	2"	8.6
9/4/2000	20B	POND 3	2"	-4.1
9/4/2000	13A	POND 1	2" WELL, 8-10" STRIPS	
9/4/2000	13B	POND 1	2" WELL, 8-10" STRIPS	9.3
9/4/2000	14	REF 1	2-3"	10.3
9/4/2000	15	REF 2	2-3"	6.7
9/4/2000	NEW REF	REF 4	2"	4.9
9/4/2000	12A	WET 4	1"	-6.4
9/4/2000	12B	WET 4	1"	0.5
9/4/2000	8A	POND 2	1" AT WELL, 10" AT STRIP	-34.4
9/4/2000	8B	POND 2	1" AT WELL, 10" AT STRIP	9.4
9/4/2000	NEW 8	POND 2	1" AT WELL, 10" AT STRIP	-160.9
3/14/2001	17A	WET 3	2-4"	-1.5
3/14/2001	17B	WET 3	2-4"	4.6
3/14/2001	new 17	WET 3	2-4"	2.6
3/14/2001	19A	WET 1	SAT-1"	6.5
3/14/2001	19B	WET 1	SAT-1"	0.8
3/14/2001	28A	WET 2	SAT-1"	-0.7
3/14/2001	28B	WET 2	SAT-1"	2.1
3/14/2001	20A	POND 3	3-6"	-4.2
3/14/2001	20B	POND 3	3-6"	-1.4
3/14/2001	13A	POND 1	3-4"	1.7
3/14/2001	13B	POND 1	3-4"	0.5
3/14/2001	14	REF 1	SAT-3"	3.0
3/14/2001	15	REF 2	SAT-3"	-0.6
3/14/2001	NEW REF	REF 4	SAT-2"	4.2
3/14/2001	12A	WET 4	SAT	4.0
3/14/2001	12B	WET 4	SAT	2.3
3/14/2001	8A	POND 2	6-8"	0.3
3/14/2001	8B	POND 2	6-8"	3.6
3/14/2001	NEW 8	POND 2	6-8"	

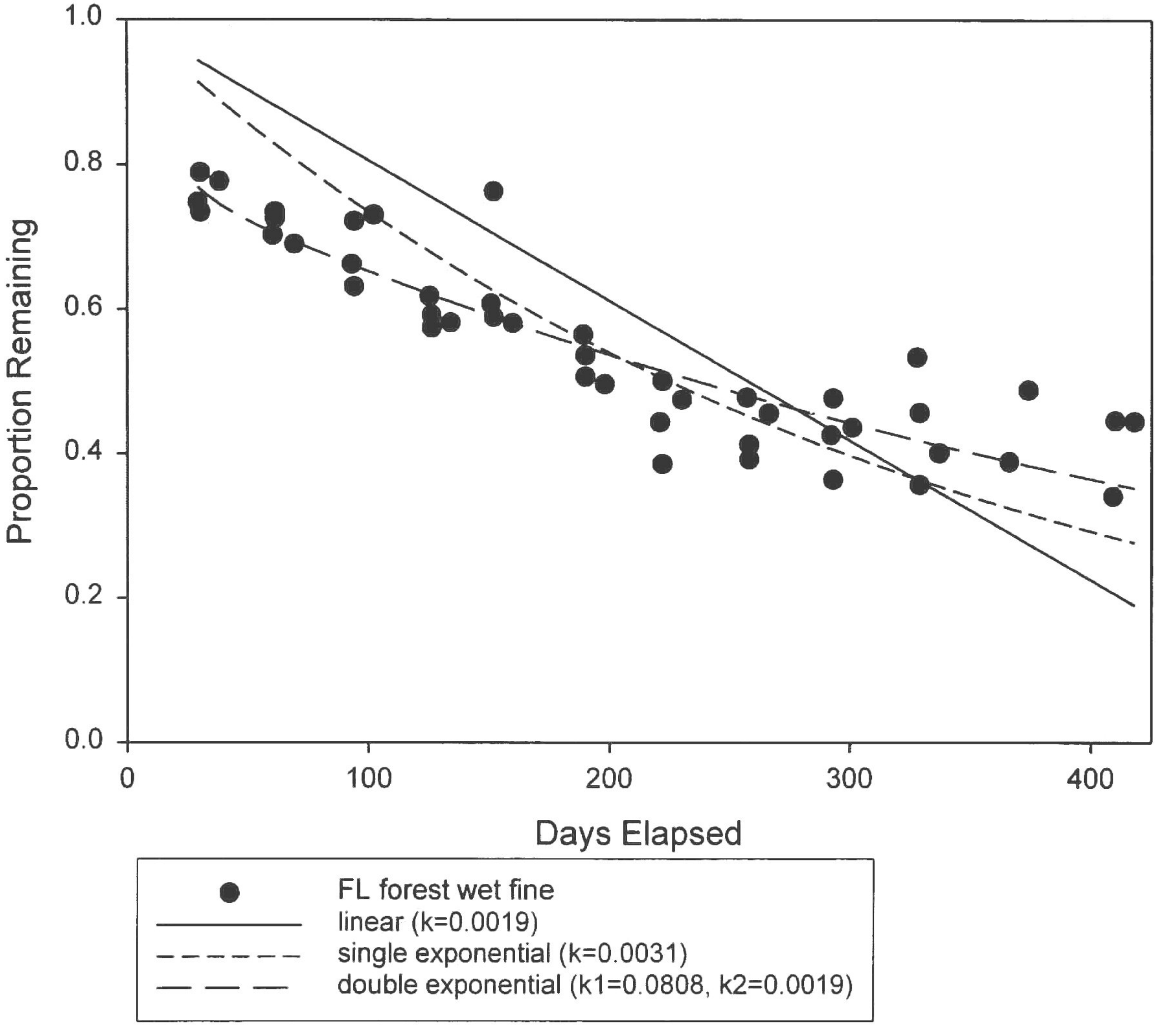
Appendix III. Fort Lee Soil Chemical Properties (from Cummings, 1999)

Wetland	depth	n	pH	% N	% C
Reference – 1993	5-15 cm	15	4.76	0.18	2.89
	40-50 cm	15	4.86	0.08	0.92
	90-100 cm	15	5.31	0.05	0.14
Mitigation – 1993	5-15 cm	15	5.31	0.07	0.82
	40-50 cm	15	5.31	0.04	0.14
	90-100 cm	15	5.41	0.04	0.06
Mitigation - 1998	5-15 cm	6	5.63	0.03	0.76
	40-50 cm	6	5.10	0.01	0.26
	90-100 cm	6	5.22	0.00	0.03

Appendix IV. Charles City Soil Chemical Properties

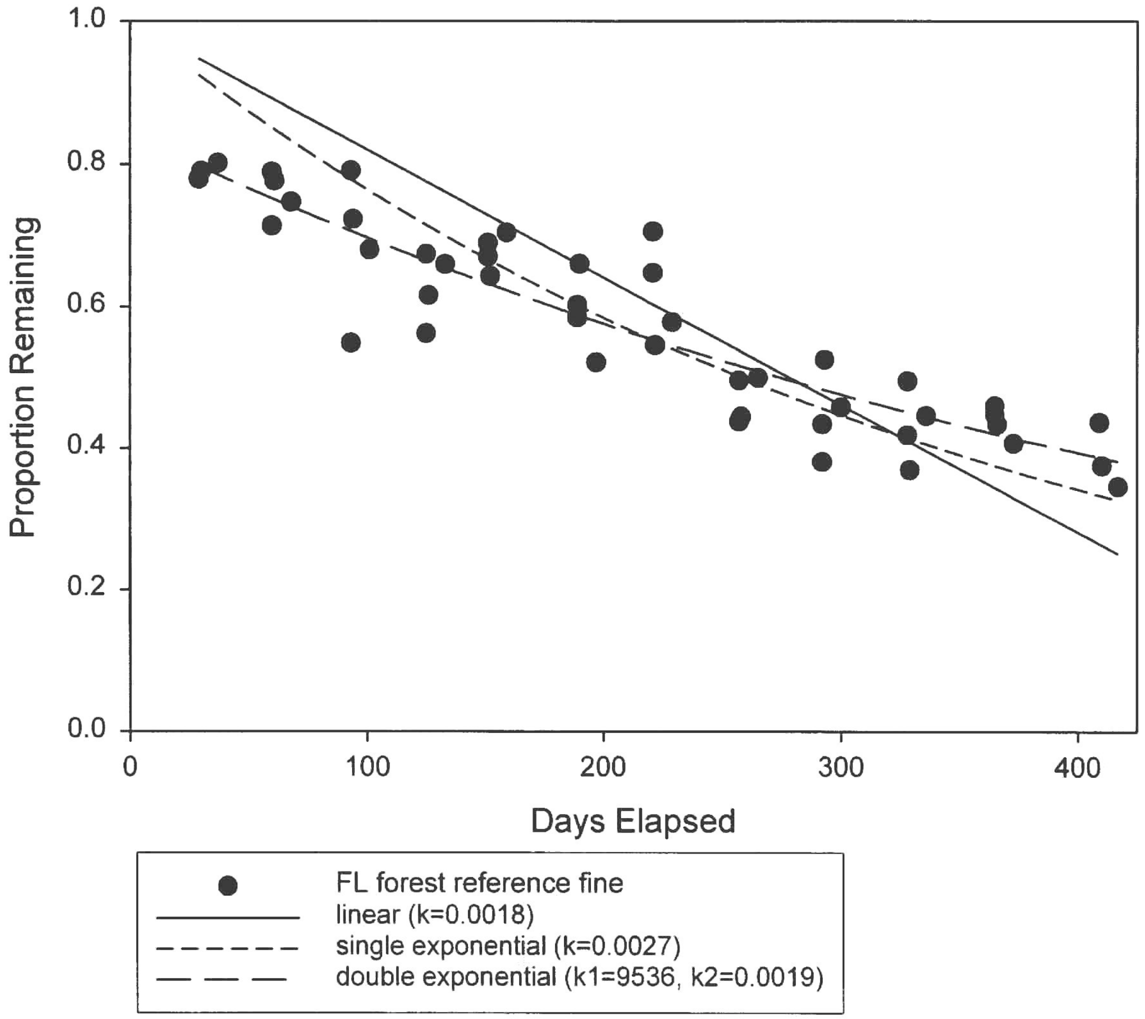
Site	Horizon	Depth (range) (cm)	n	% C	% N	pH	P (ppm)	K (ppm)	Ca (ppm)	Mg (ppm)	Zn (ppm)	Mn (ppm)	Cu (ppm)	Fe (ppm)	B (ppm)
wet	surface	0-2	4	1.76	0.116										
	A	0-20	4	1.08	0.085	5.75	1.5	29	573	120	1.8	16.1	0.65	47	0.13
	Btg1	8-61	4	0.23	0.055	4.53	1.0	30	78	117	1.8	9.8	1.1	23	0.08
	Cg1	64-147	4	0.143	0.046										
pond	surface	0-2	3	1.41	0.134										
	A	0-15	3	1.40	0.100	5.70	1.0	34	488	113	1.7	16	1.0	89	0.17
	Btg1	8-71	3	0.32	0.050	4.57	1.0	33	116	120	1.8	9.9	1.2	48	0.03
	Cg1	71-142	3	0.154	0.035										
reference	O	3-0	4	30.57	1.556										
	A	0-15	4	2.14	0.157	4.18	3.3	37	75	34	2.6	3.3	0.3	43	0.05
	Btg1	13-99	4	0.62	0.089	4.45	1.0	20	96	67	1.6	1.5	0.7	61	0.0
	Cg1	99-163	4	0.199	0.042										

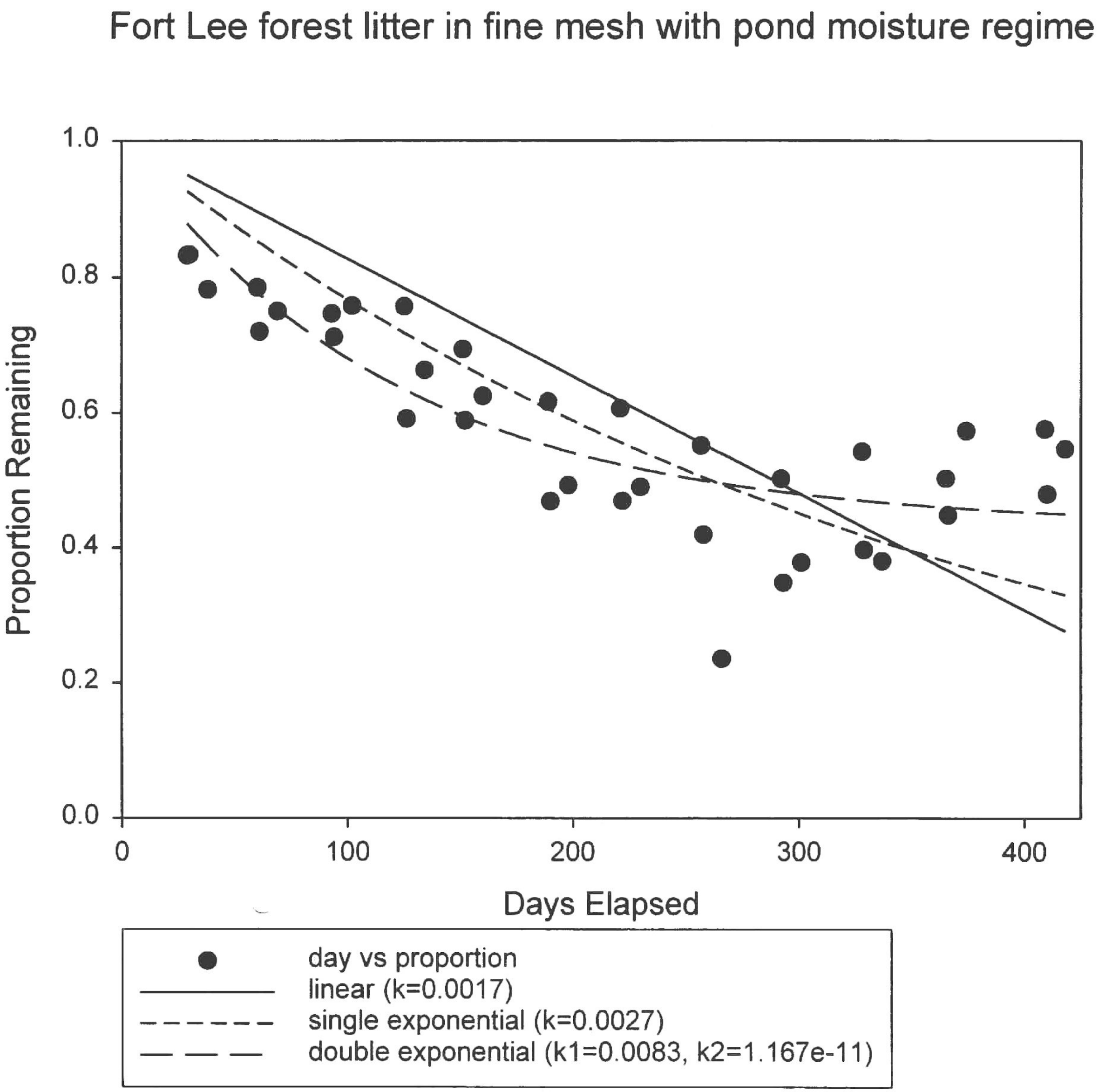
Appendix V: Fine mesh litterbag weight loss models



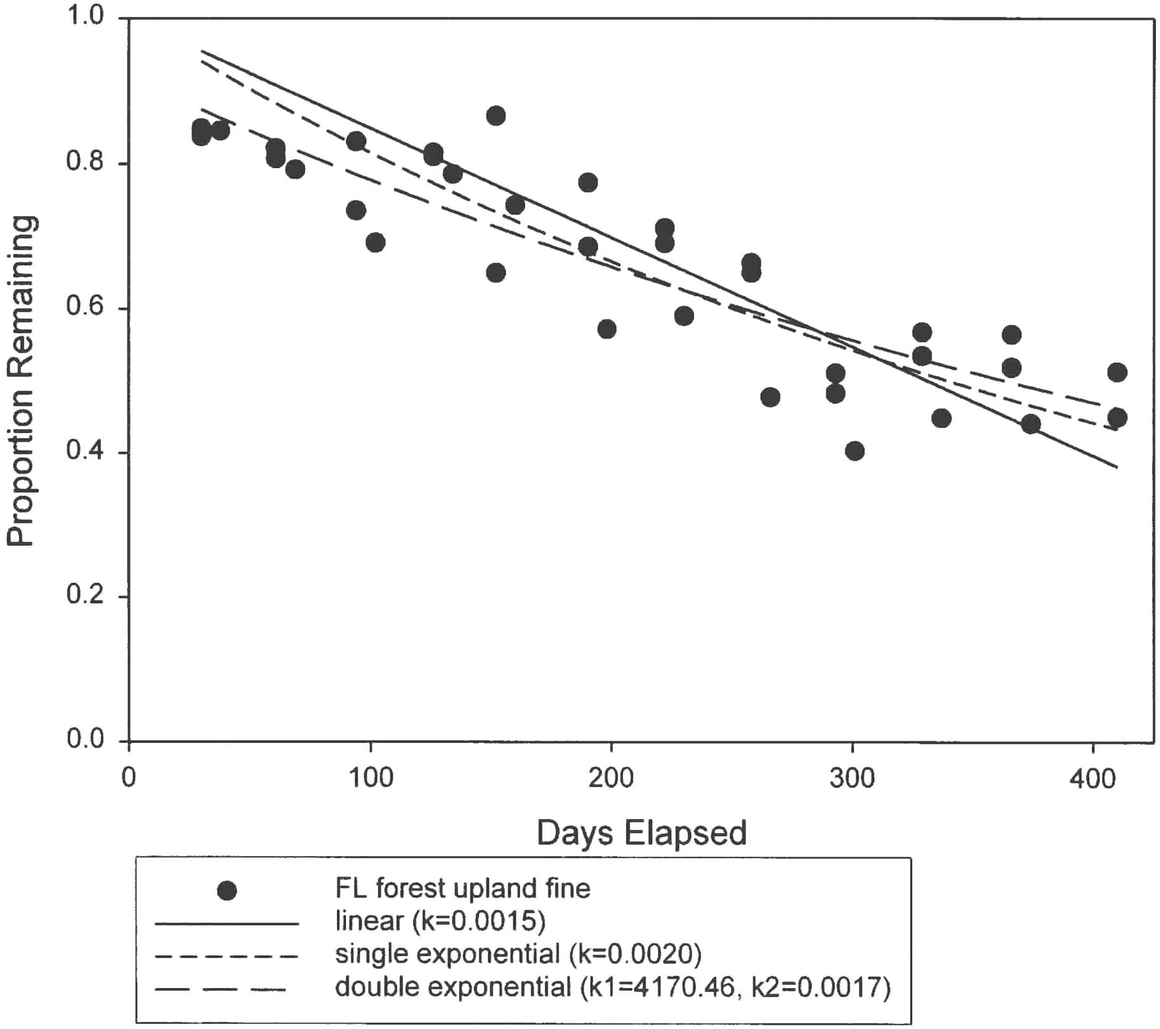
Fort Lee forest litter in fine mesh with wet moisture regime

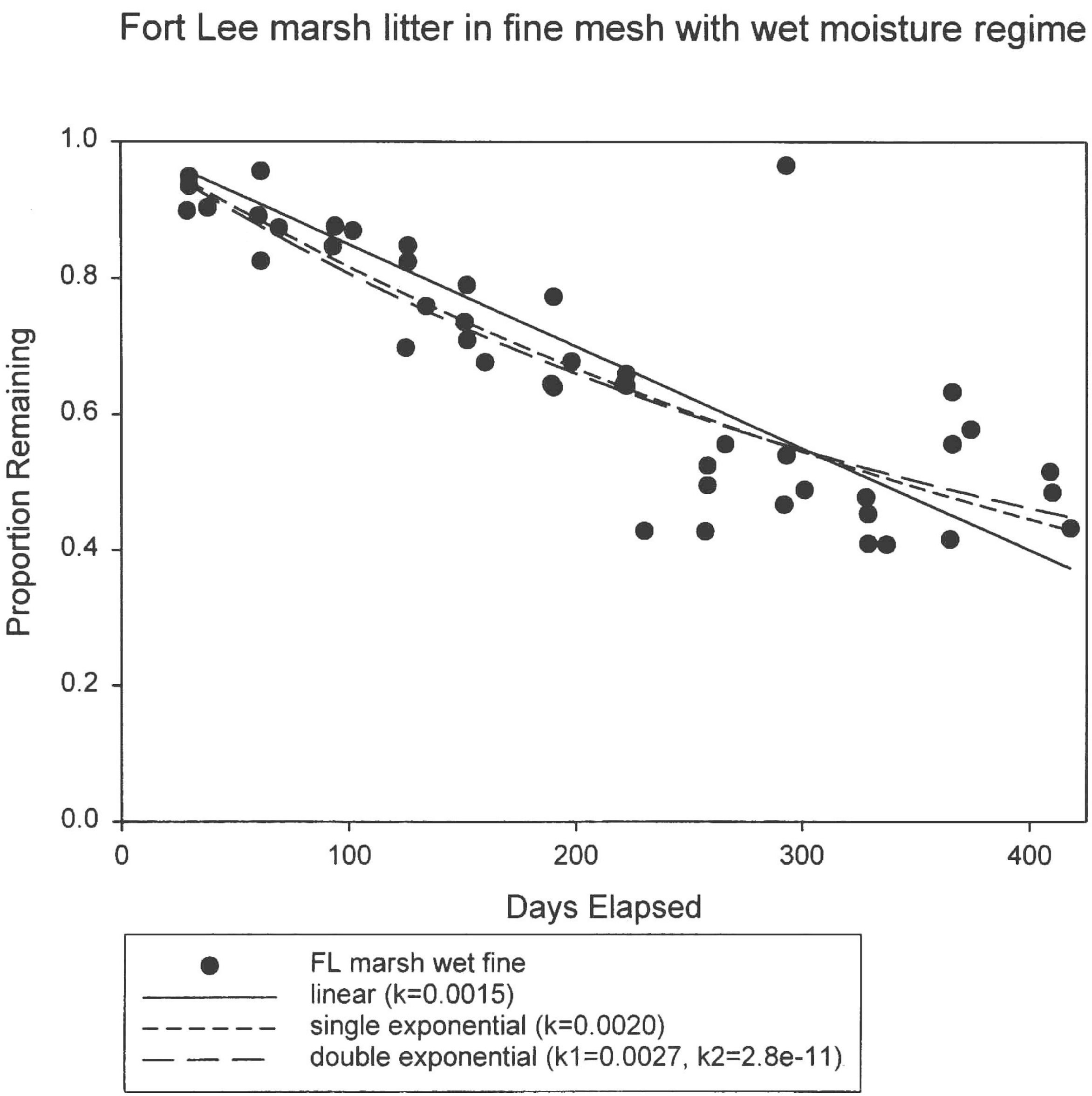
Fort Lee forest litter in fine mesh with reference moisture regime



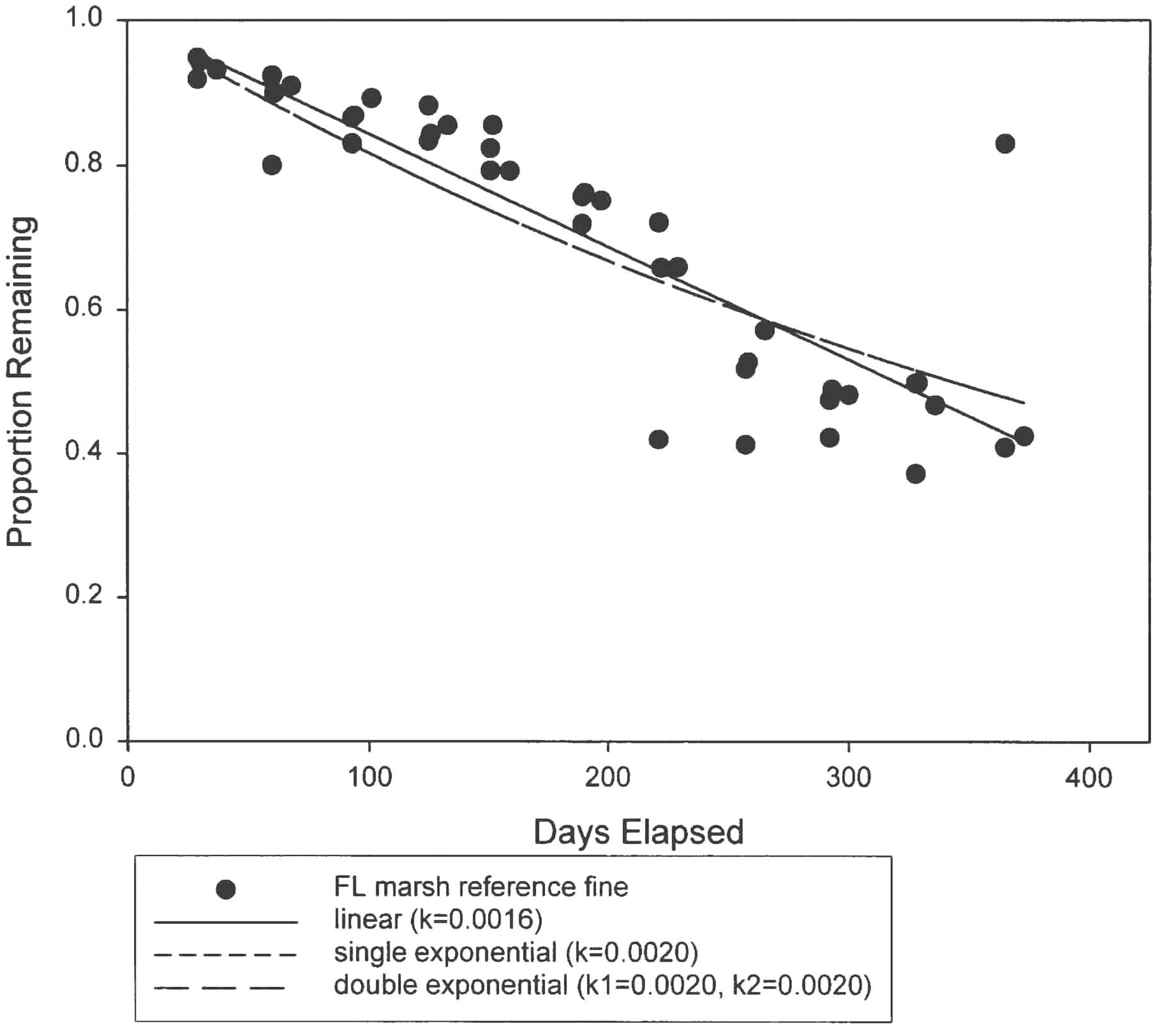

Fort Lee forest litter in fine mesh with pond moisture regime
Proportion Remaining
1.0
0.8
0.6
0.4
0.2
0.0
0
100
200
300
400
Days Elapsed
● day vs proportion
linear (k=0.0017)
single exponential (k=0.0027)
double exponential (k1=0.0083, k2=1.167e-11)

Fort Lee forest litter in fine mesh with upland moisture regime

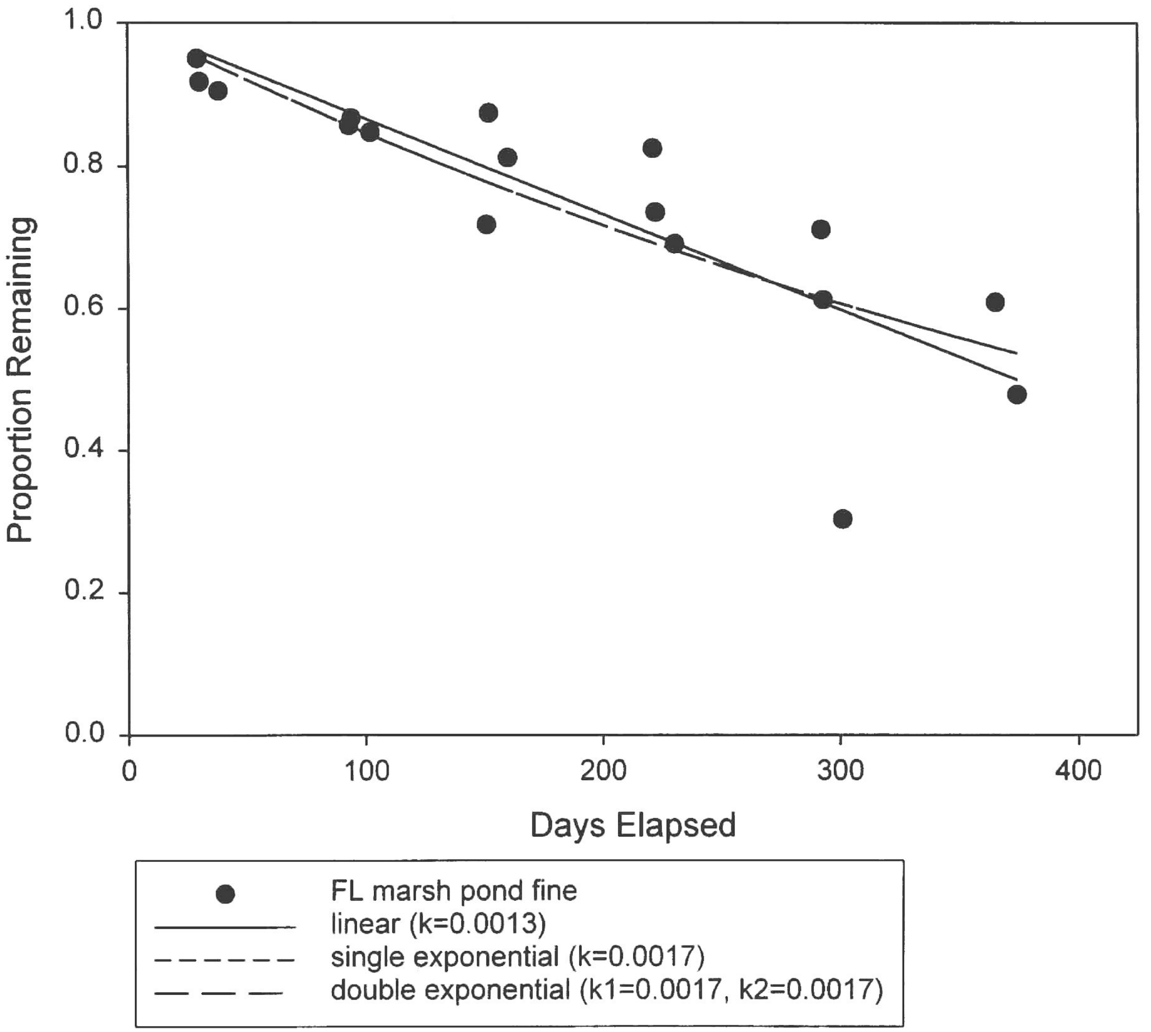


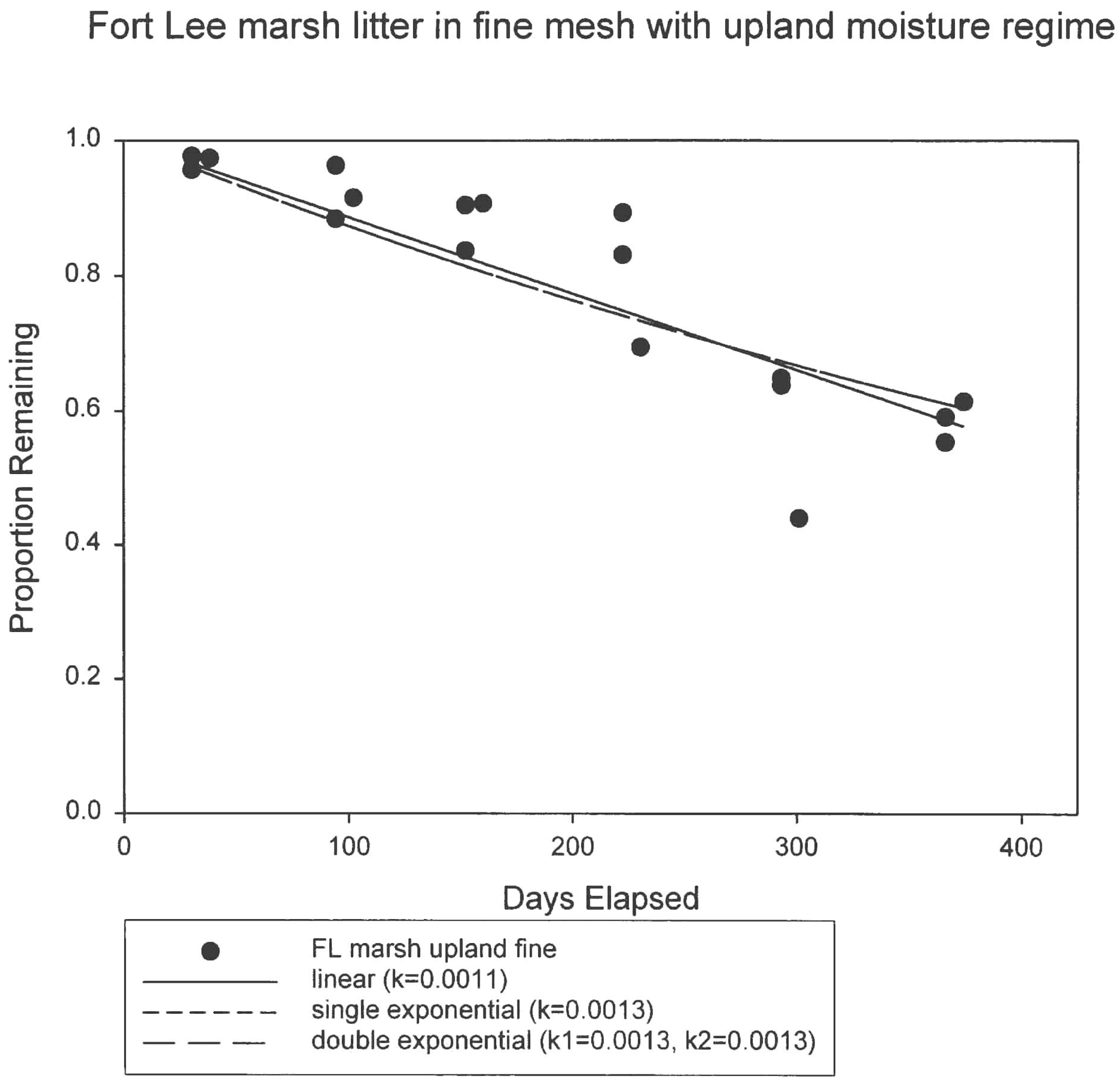

Fort Lee marsh litter in fine mesh with wet moisture regime
Proportion Remaining
1.0
0.8
0.6
0.4
0.2
0.0
0
100
200
300
400
Days Elapsed
● FL marsh wet fine
linear (k=0.0015)
single exponential (k=0.0020)
double exponential (k1=0.0027, k2=2.8e-11)

Fort Lee marsh litter in fine mesh with reference moisture regime

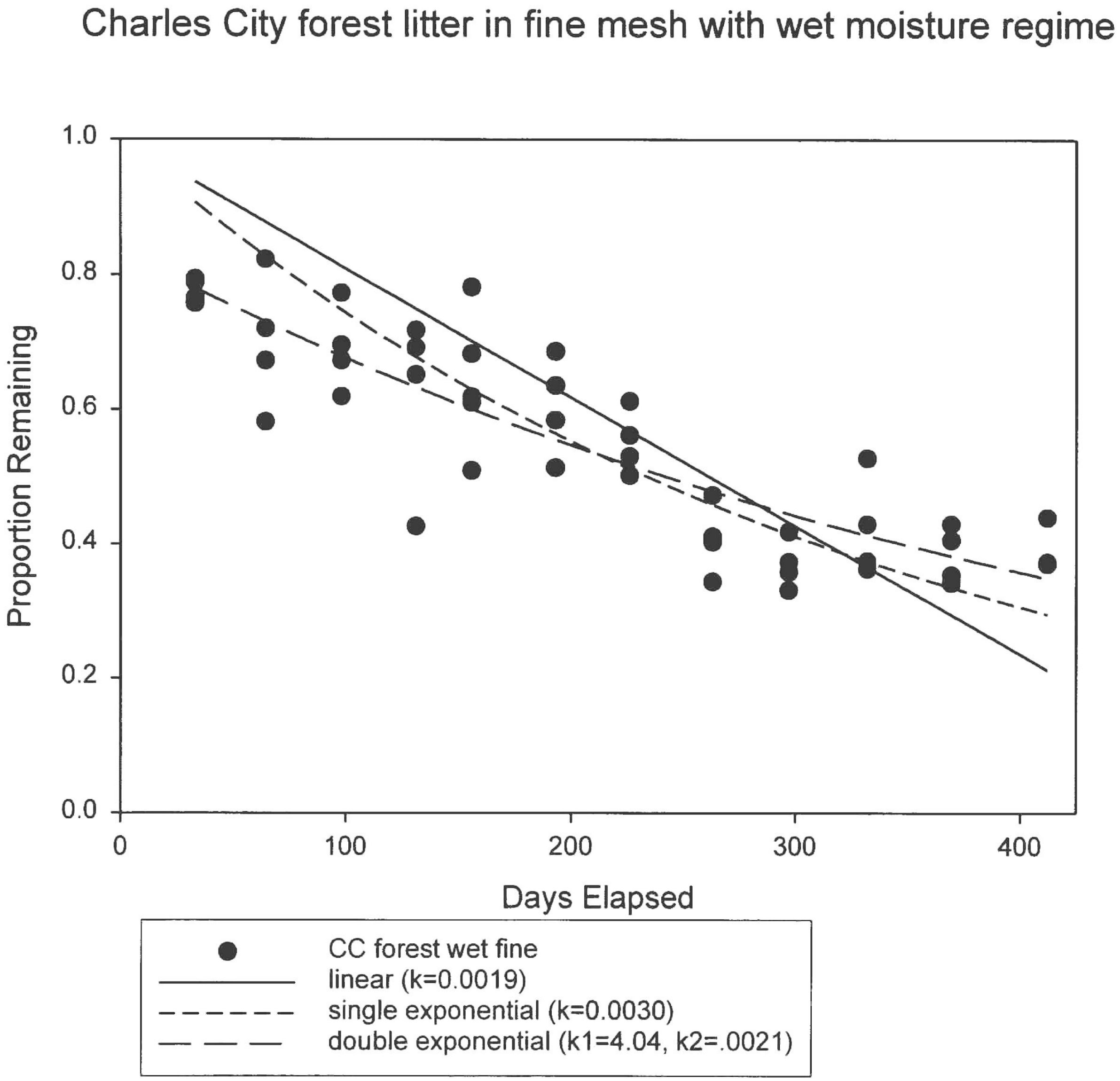


Fort Lee marsh litter in fine mesh with pond moisture regime

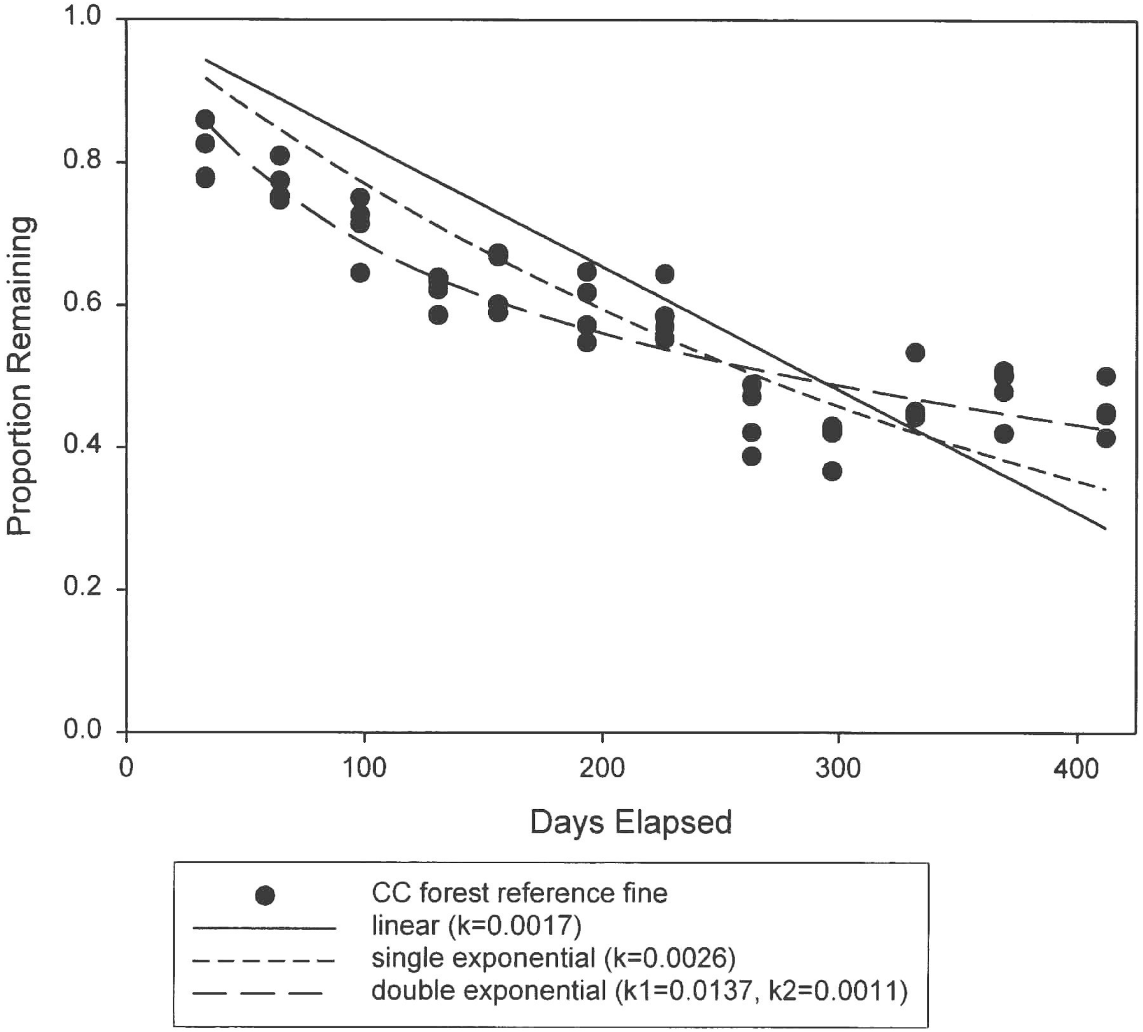


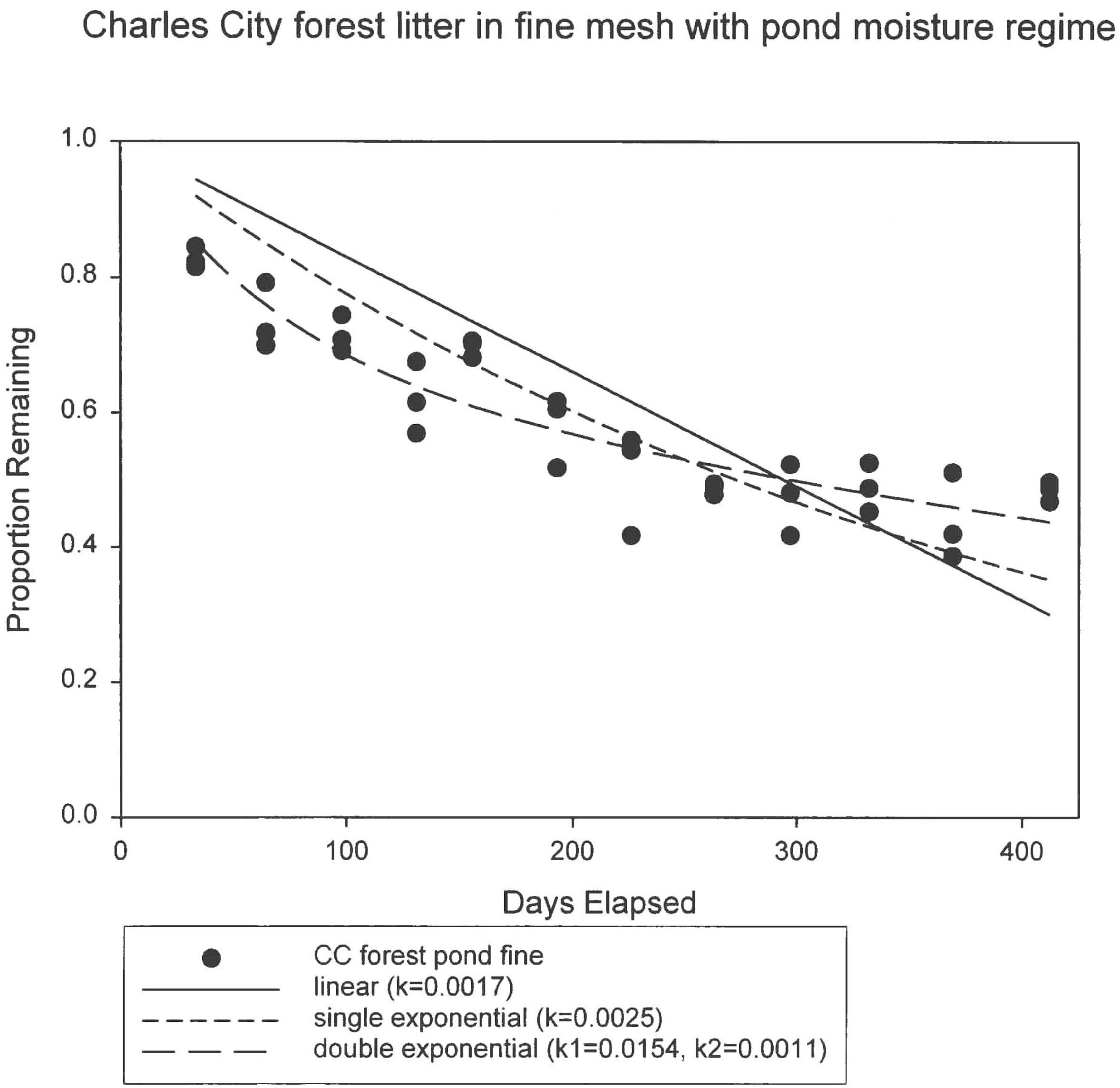


Fort Lee marsh litter in fine mesh with upland moisture regime

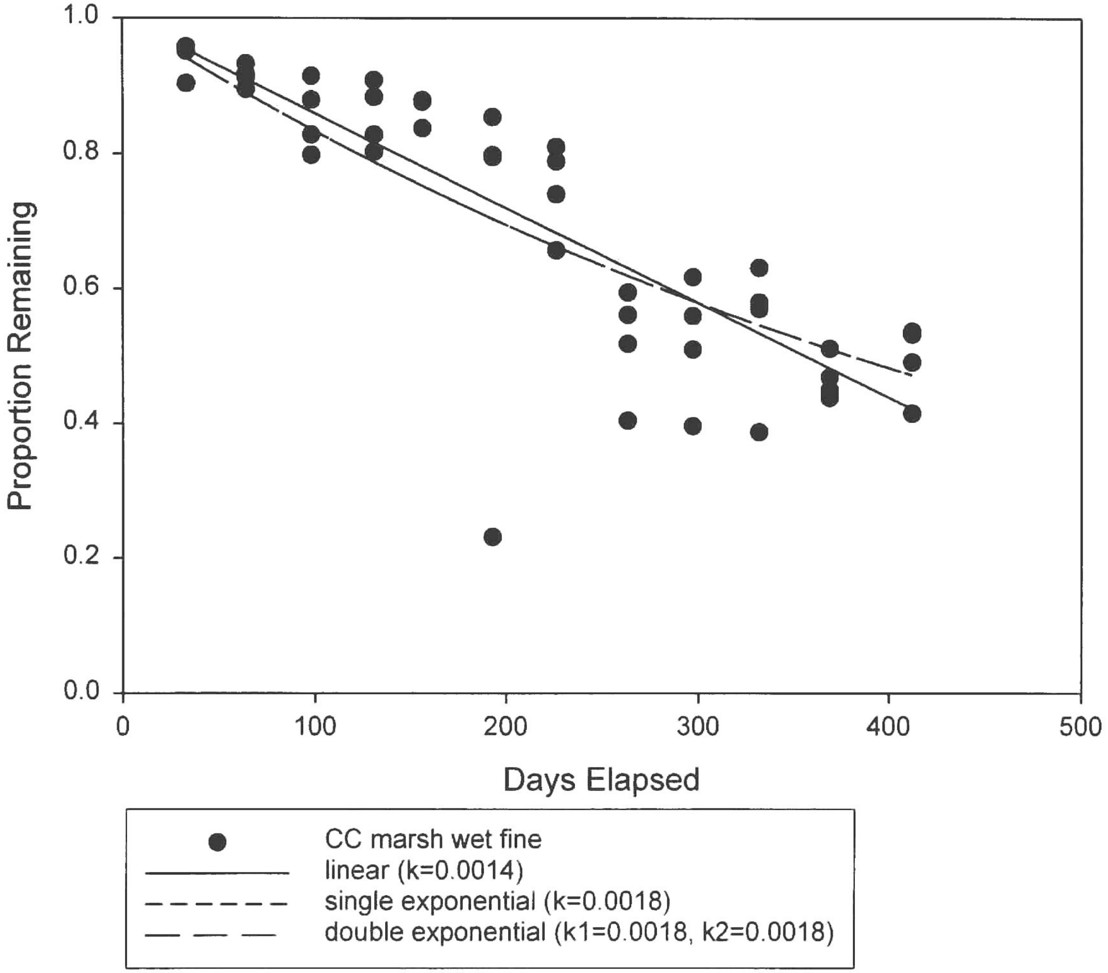

Charles City forest litter in fine mesh with wet moisture regime
1.0
0.8
0.6
0.4
0.2
0.0
Proportion Remaining
0
100
200
300
400
Days Elapsed
CC forest wet fine
linear (k=0.0019)
single exponential (k=0.0030)
double exponential (k1=4.04, k2=.0021)

Charles City forest litter in fine mesh with reference moisture regime

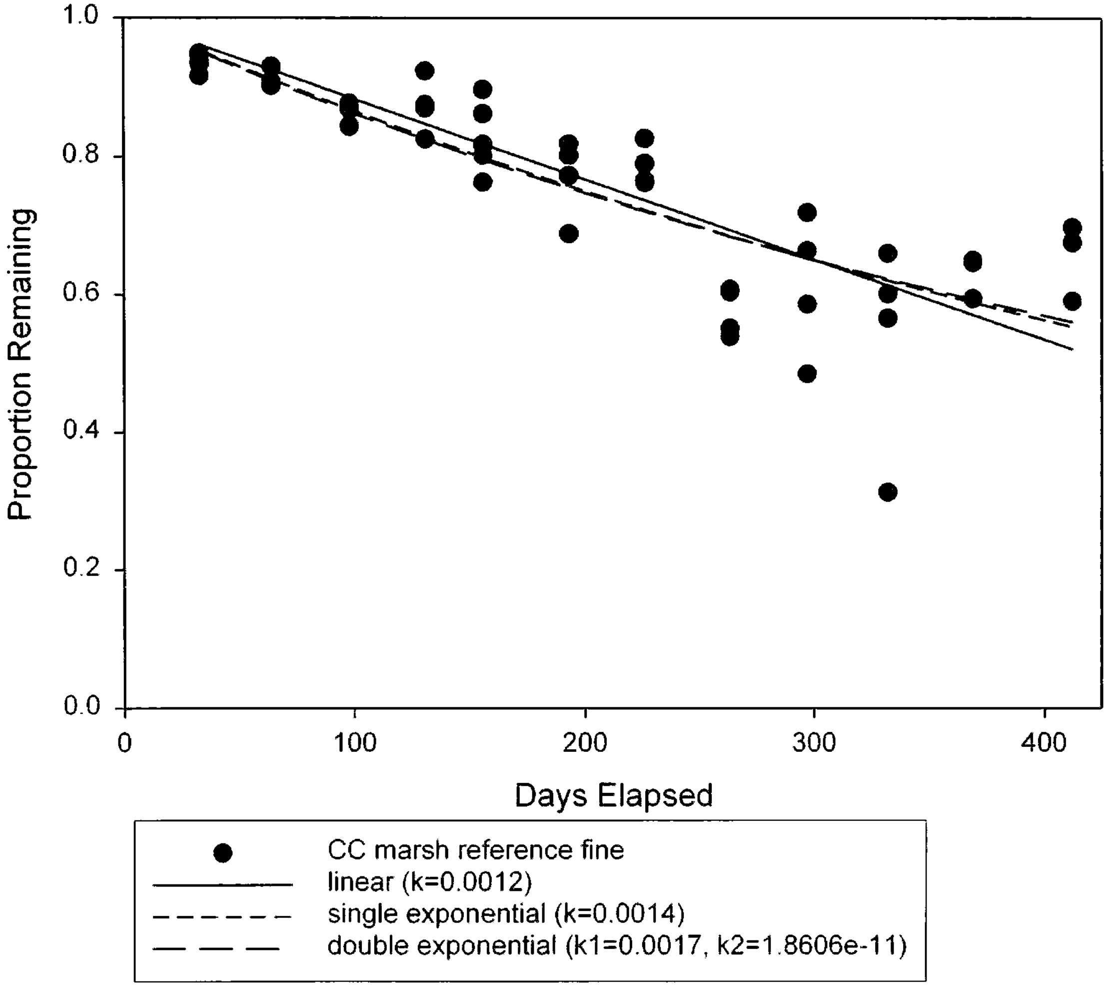



Charles City forest litter in fine mesh with pond moisture regime
Proportion Remaining
1.0
0.8
0.6
0.4
0.2
0.0
0
100
200
300
400
Days Elapsed
● CC forest pond fine
linear (k=0.0017)
single exponential (k=0.0025)
double exponential (k1=0.0154, k2=0.0011)

Charles City marsh litter in fine mesh with wet moisture regime



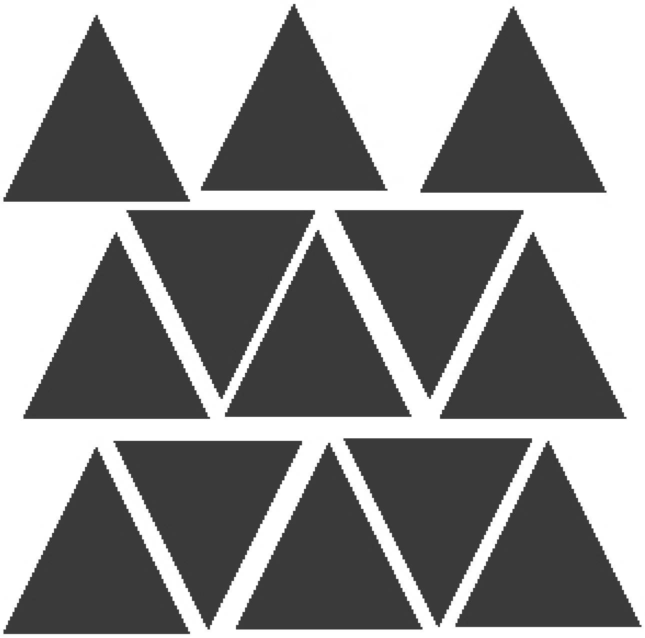
Charles City marsh litter in fine mesh with reference moisture regime



Appendix VI: Conceptual Diagrams of Decomposition

Figure Explanation

To assist with collectively analyzing litter weight loss, area loss, area:perimeter ratio and invertebrates collected from the litterbags, conceptual diagrams were created combining these different factors (Figure 39). Based on the measured litter area along with area:perimeter ratio, the size and number of equilateral triangles were calculated by treatment for the forest litter. Any geometric shape could have been used, but triangles were selected because of the typically angular, although irregular, nature of the litter. In order to display these triangles on paper, each triangle represents the area of 10 triangles as calculated (e.g. for the initial litter represented in Figure 39, 130 triangles of the same size would be needed to equal the measured 532 cm^2 area with a perimeter of 1118 cm). The shade of the triangles was based on the density (ratio weight to area of litter), with darker colors indicating a higher weight for the same area. For each wetland/moisture regime combination, these figures were produced for litter from coarse mesh size litterbags collected after 1, 3, 6 and 12 months of exposure. For the common detritivore taxa, (*Oligochaeta, Chironomidae, Tipulidae*, and *Isopoda*) cumulative abundance was also shown by graphics of the invertebrates between the litter triangles (Figure 40 & 41). Similar to the concept that each triangle represents 10 calculated triangles, some invertebrate images represent more than one invertebrate as indicated in Figure 39. Due to the relatively low number of litterbags used to create each diagram, some variability in values between months may not be due to treatment differences. For numerical averages and overall values with LSD mean separations, see Table 17.



area is 10 x 10 cm

each triangle = 10 actual triangles

Initial Litter Values

ash free weight: 4.68
area: 532 cm2
area:perimeter: 0.476
weight:area: 88.5 g/m2

Weight : Area ratio (g/m2)

▲ 60 g /m2
▲ 70 g/m2
▲ 80 g/m2
▲ 90 g/m2
▲ 100+ g/m2

Cumulative Detritivores
each invertebrate represents the amount in the ( )

Oligochaeta (5)
Chironomidae (5)
Tipulidae (1)
Isopoda (10)

Figure 39. Control conceptual diagram for litter decomposition and legend

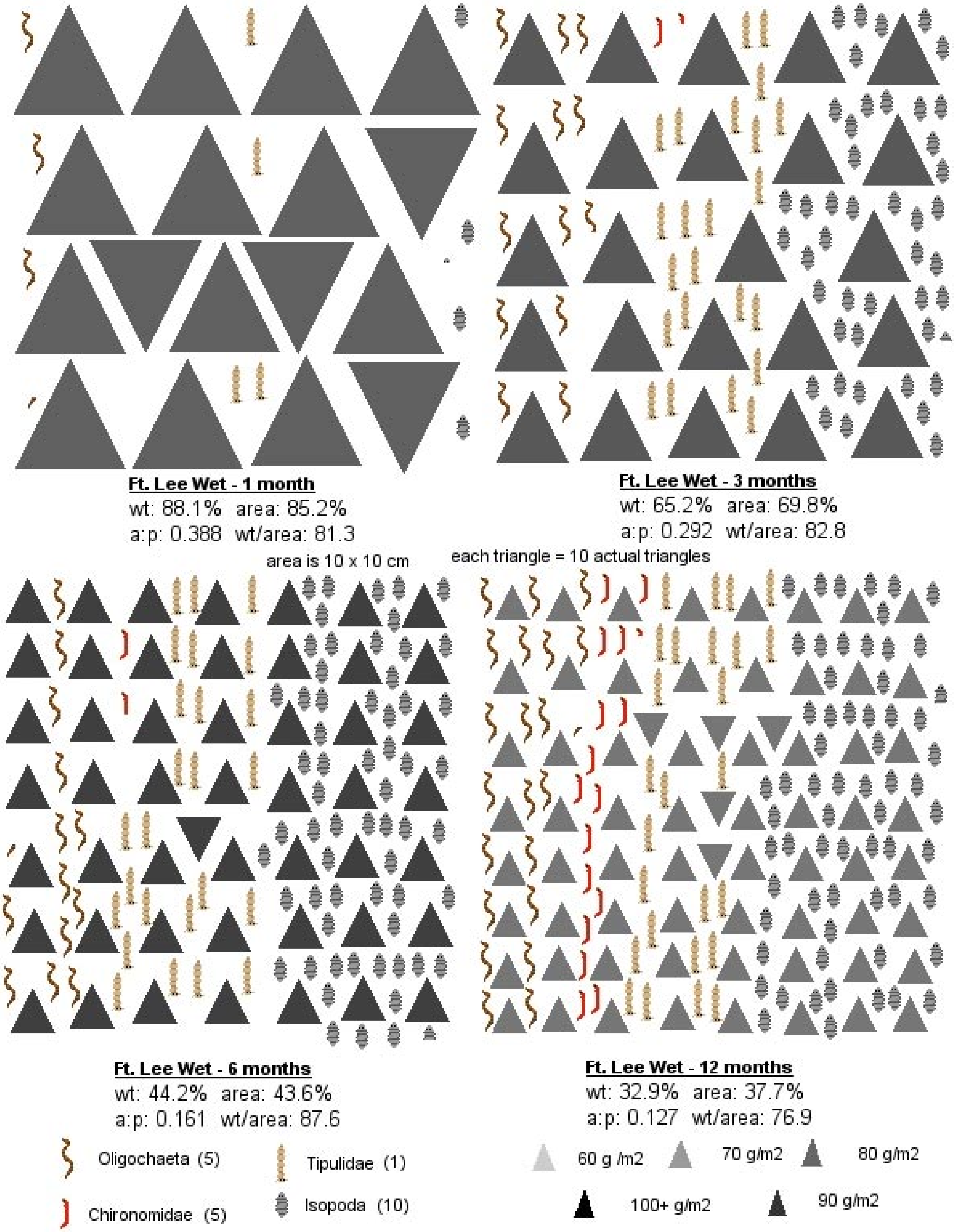
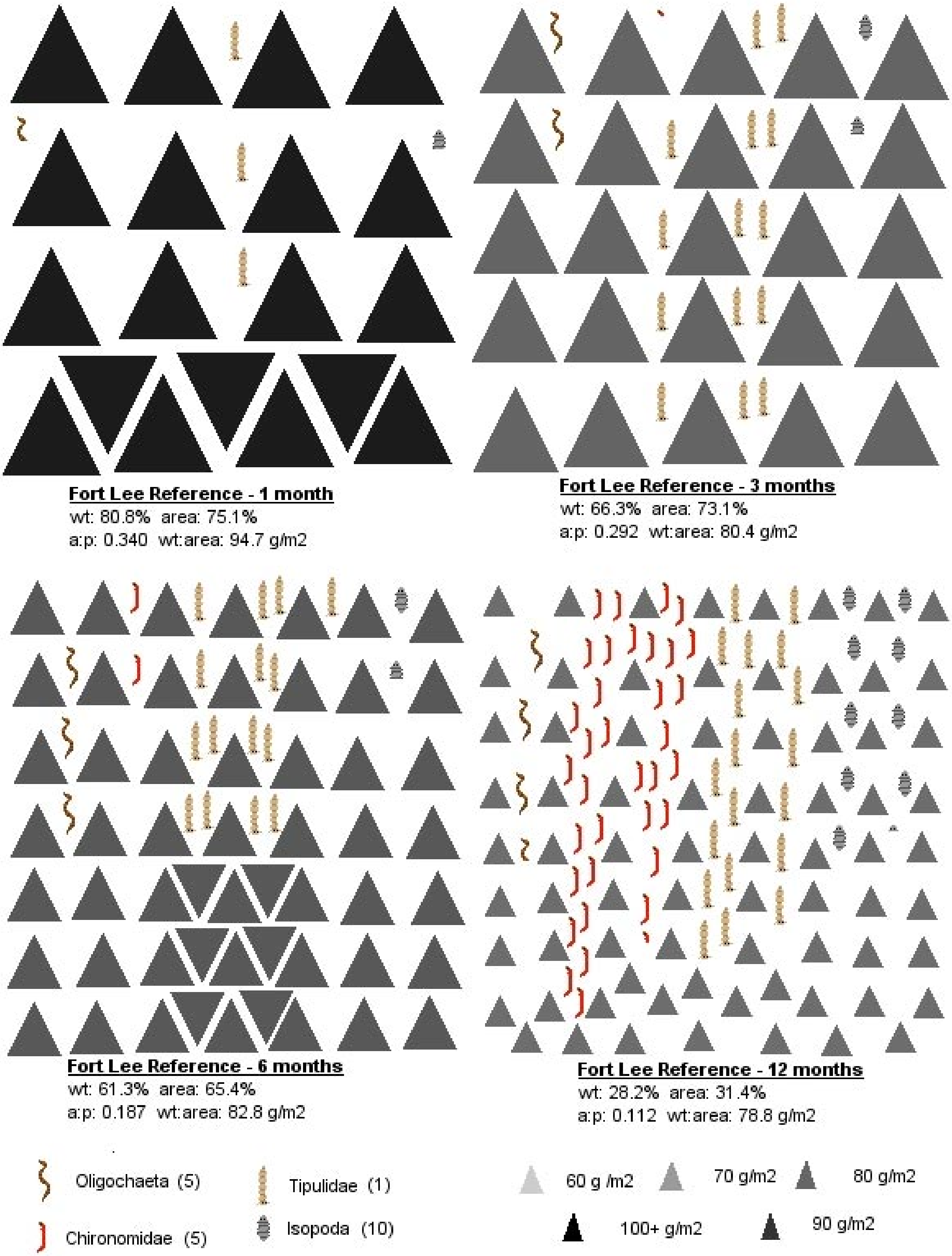


Figure 40. Fort Lee wet moisture regime conceptual diagram for litter decomposition



Fort Lee Reference - 1 month
wt: 80.8% area: 75.1%
a:p: 0.340 wt:area: 94.7 g/m2

Fort Lee Reference - 3 months
wt: 66.3% area: 73.1%
a:p: 0.292 wt:area: 80.4 g/m2

Fort Lee Reference - 6 months
wt: 61.3% area: 65.4%
a:p: 0.187 wt:area: 82.8 g/m2

Fort Lee Reference - 12 months
wt: 28.2% area: 31.4%
a:p: 0.112 wt:area: 78.8 g/m2

Figure 41. Fort Lee reference moisture regime conceptual diagram for litter decomposition

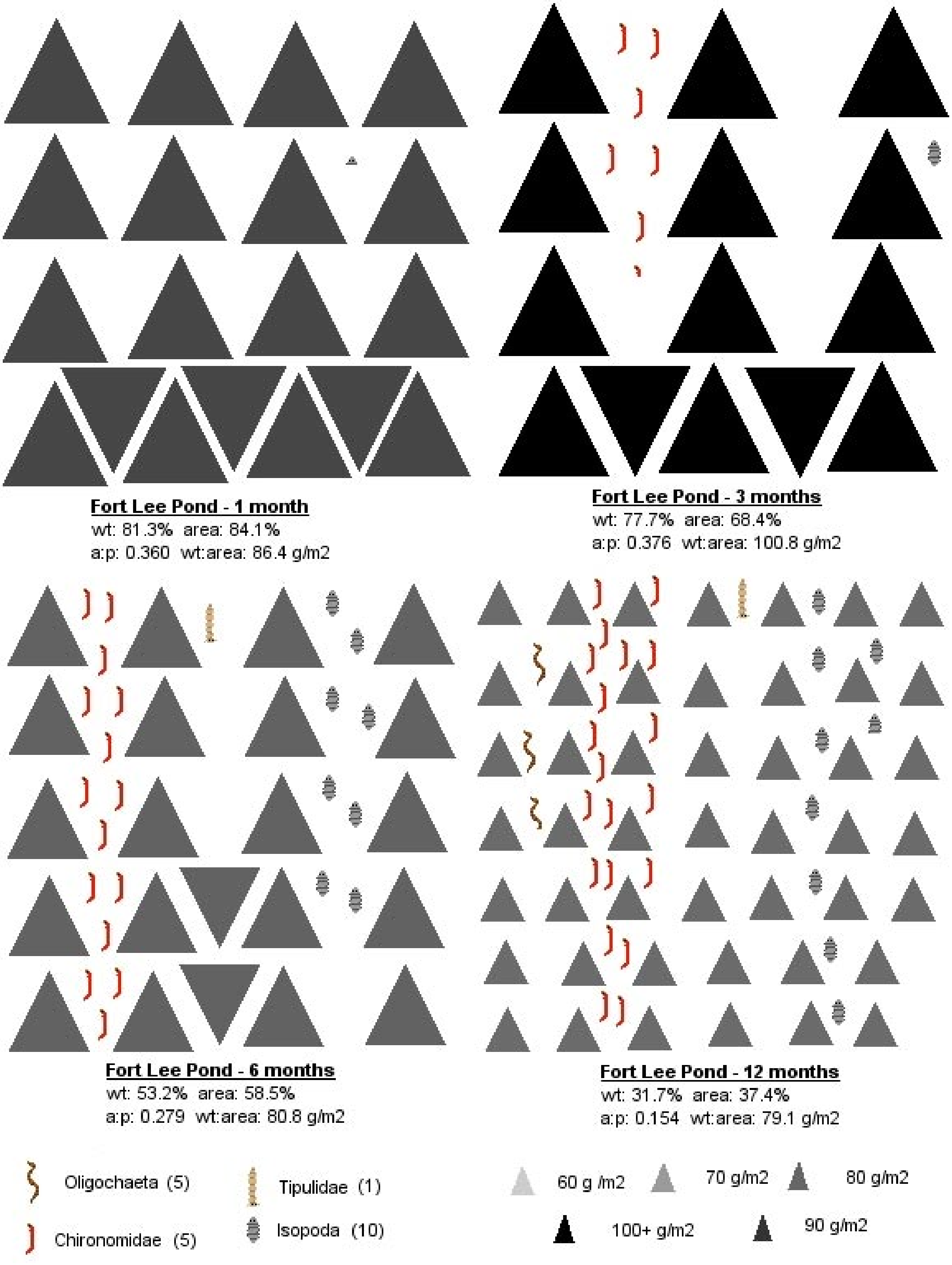


Figure 42. Fort Lee pond moisture regime conceptual diagram for litter decomposition

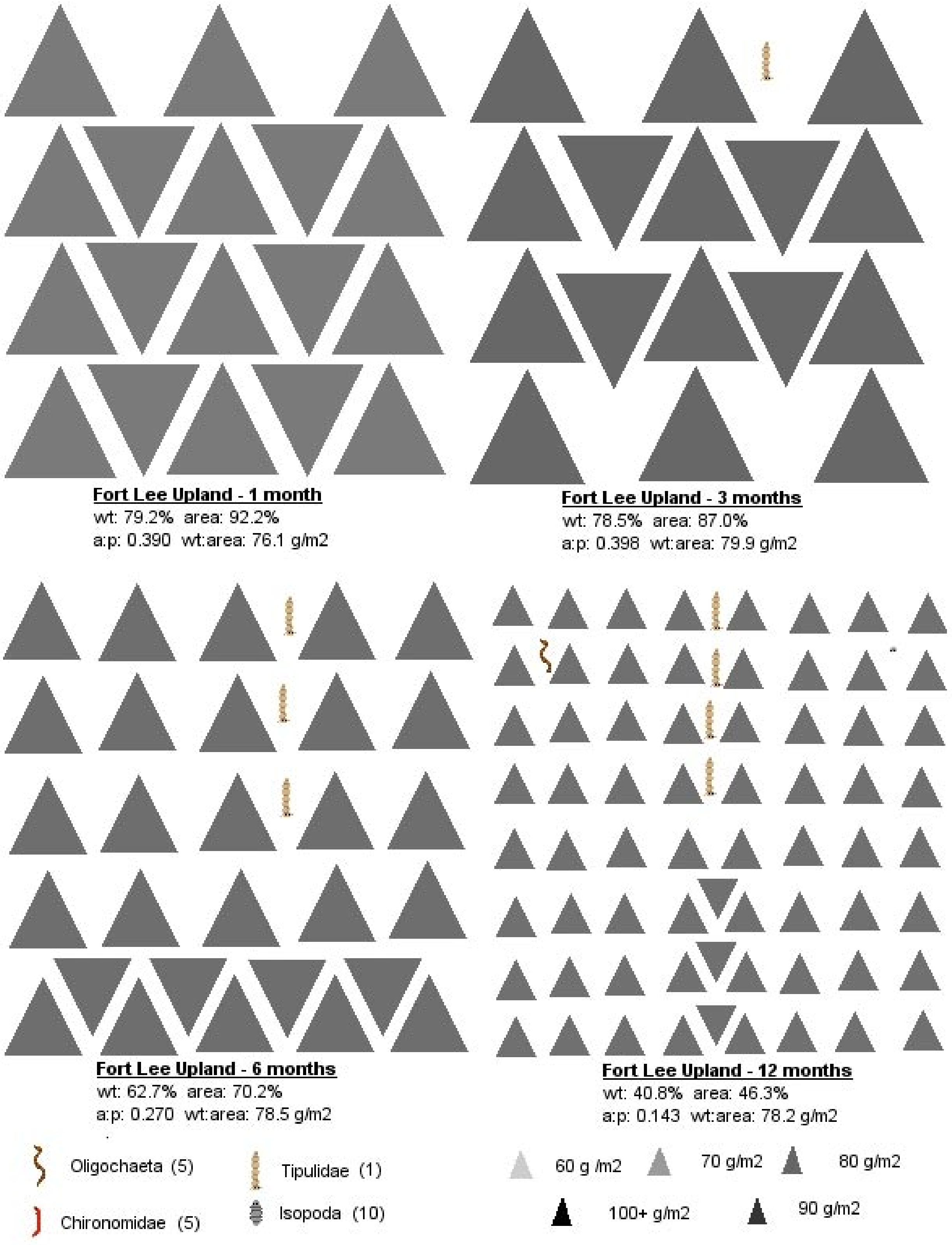
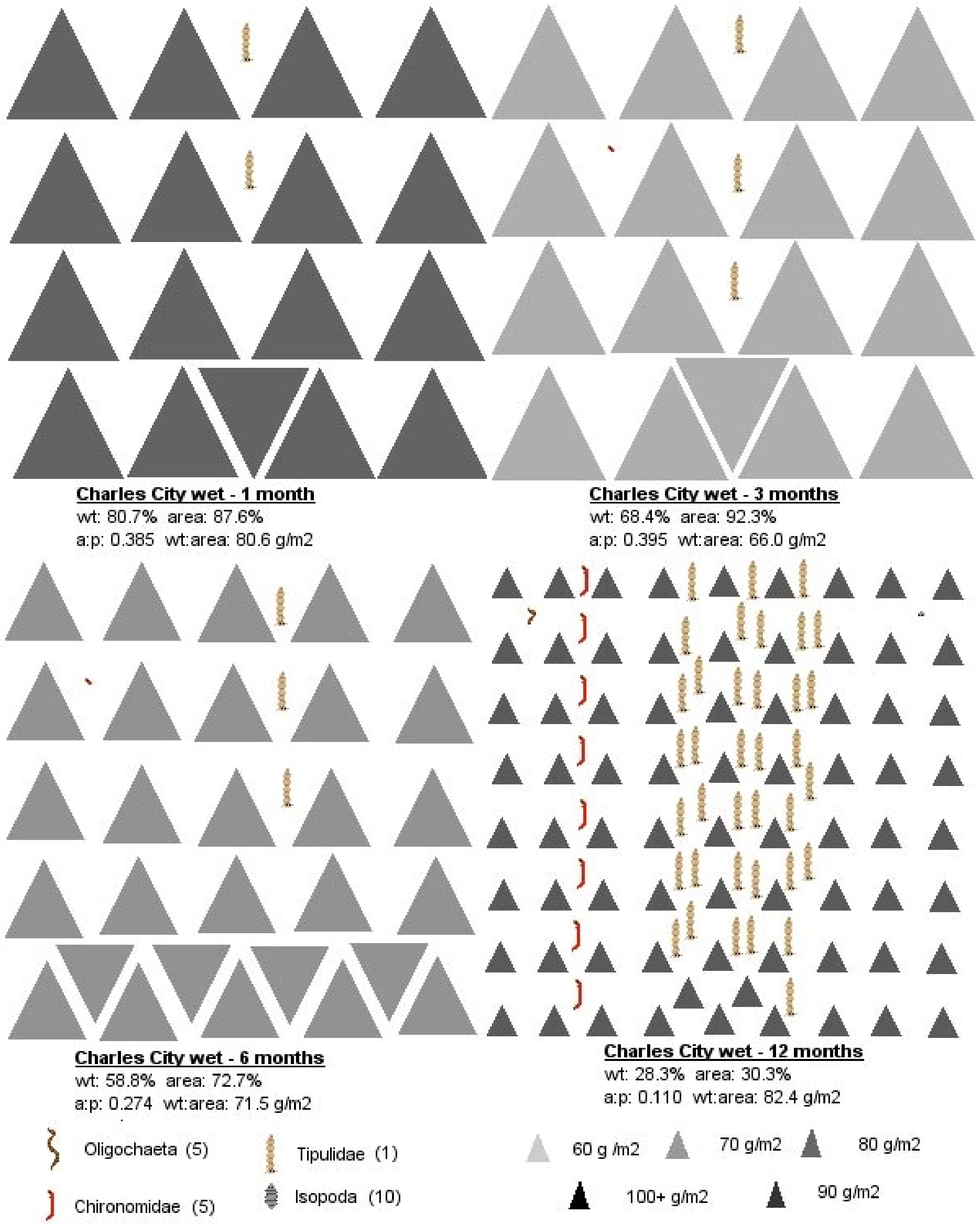


Figure 43. Fort Lee upland moisture regime conceptual diagram for litter decomposition



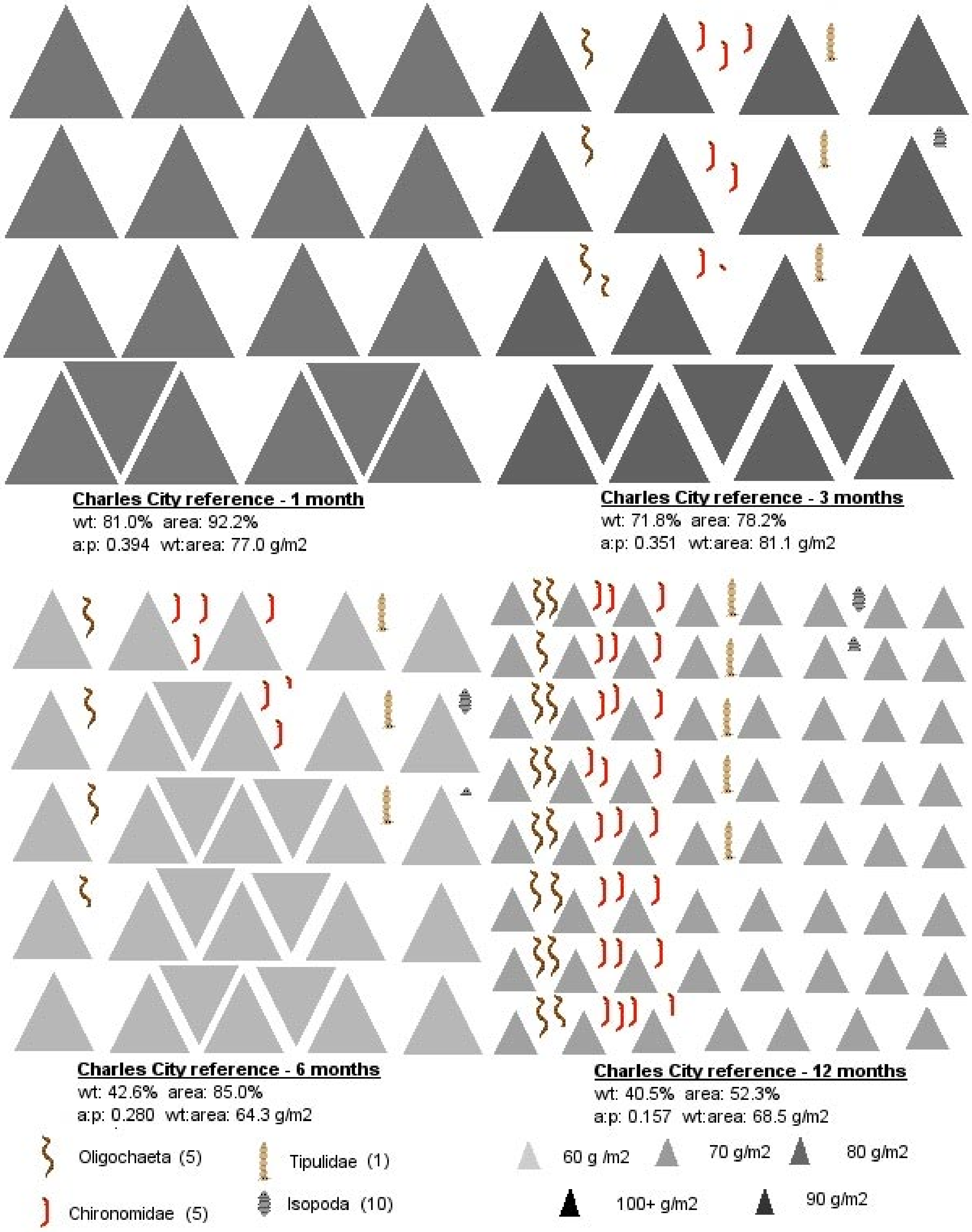
Charles City wet - 1 month
wt: 80.7% area: 87.6%
a:p: 0.385 wt:area: 80.6 g/m2

Charles City wet - 3 months
wt: 68.4% area: 92.3%
a:p: 0.395 wt:area: 66.0 g/m2

Charles City wet - 6 months
wt: 58.8% area: 72.7%
a:p: 0.274 wt:area: 71.5 g/m2

Charles City wet - 12 months
wt: 28.3% area: 30.3%
a:p: 0.110 wt:area: 82.4 g/m2

Figure 44. Charles City wet moisture regime conceptual diagram for litter decomposition



Charles City reference - 1 month
wt: 81.0% area: 92.2%
a:p: 0.394 wt:area: 77.0 g/m2

Charles City reference - 3 months
wt: 71.8% area: 78.2%
a:p: 0.351 wt:area: 81.1 g/m2

Charles City reference - 6 months
wt: 42.6% area: 85.0%
a:p: 0.280 wt:area: 64.3 g/m2

Charles City reference - 12 months
wt: 40.5% area: 52.3%
a:p: 0.157 wt:area: 68.5 g/m2

Figure 45. Charles City reference moisture regime conceptual diagram for litter decomposition

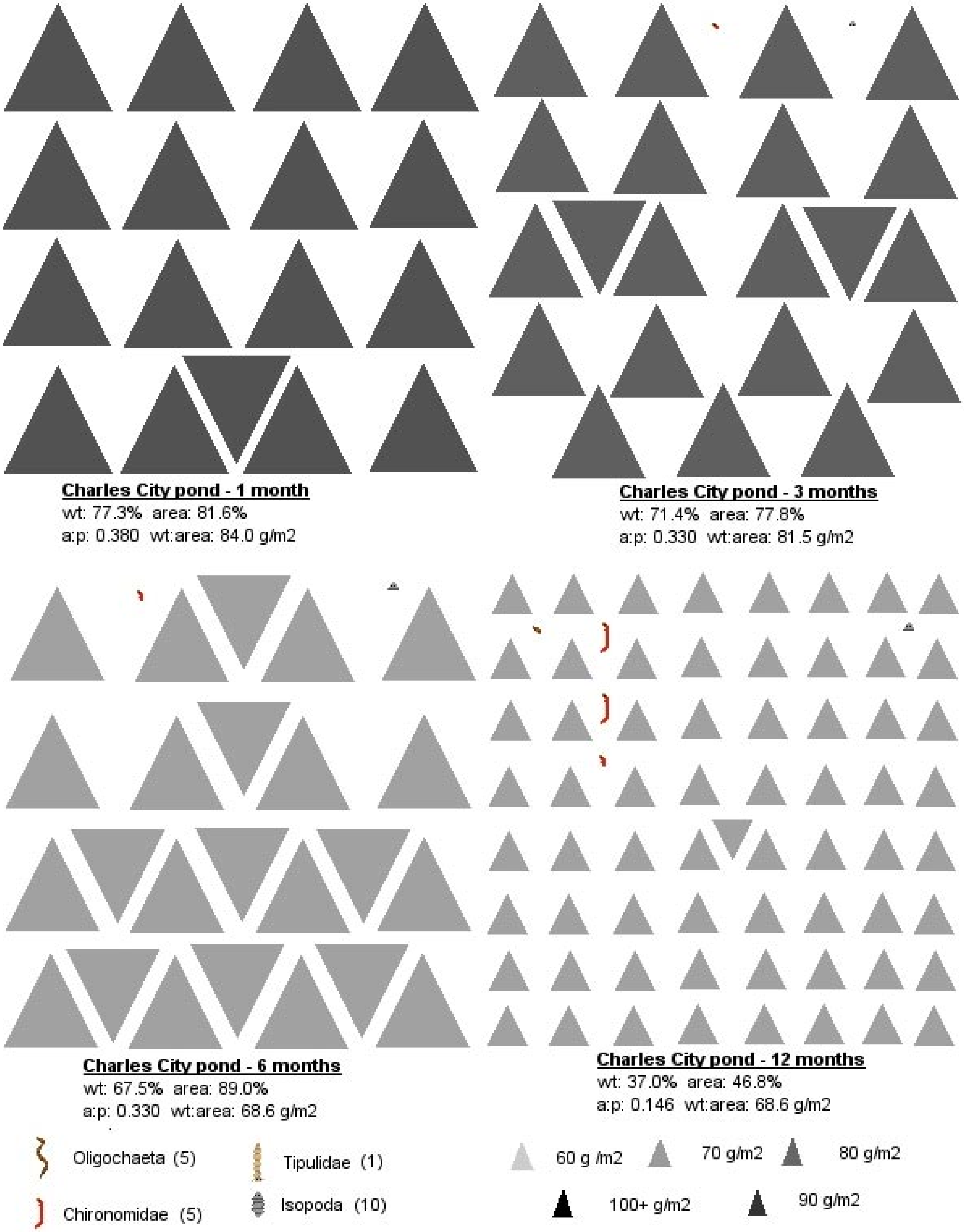


Figure 46. Charles City pond moisture regime conceptual diagram for litter decomposition

Vita

John Michael "Mike" Schmidt was born March 7, 1976 in St. Paul Minnesota. Mike moved from Minnesota with his parents (James R. and Jean) and brothers (James E. and Joseph) to Herndon, Virginia in 1981. Mike attended Thomas Jefferson High School for Science and Technology in Alexandria, Virginia from 1990 until 1994. During his senior year of high school, he began a mentorship project with Dr. W. Lee Daniels at Virginia Tech to determine the optimal ratio of sawdust and sewage biosolids to prevent nitrate contamination while supporting plant growth. Mike continued this research as an undergraduate for his Honors Baccalaureate dual degree major in Biology and Environmental Science at Virginia Tech. Along with scientific pursuits, he became involved and helped lead several environmental (Environmental Science Student Organization; Environmental Coalition) and honor societies (University Honors Associates; Golden Key National Honor Society). Having taken advantage of the wonderful opportunities available at Virginia Tech, he was recognized with several college, university and national (Barry Goldwater Scholar, 1996; Morris K. Udall Scholar, 1996; All-USA Academic First Team, USA TODAY, 1997) awards and scholarships. Secondary interests in art, archeology and history of science led to a summer spent studying formally and informally in Italy and Great Britain. After graduating Summa Cum Laude in 1998, Mike enrolled as a Master's student in Crop and Soil Environmental Sciences. In 1999, he we awarded an EPA Science to Achieve Results (STAR) Fellowship. On July 31, 1999, he married his high school girlfriend and veterinary student, Elizabeth Embree, in the War Memorial Chapel. Not surprising considering the union of an environmentalist and a veterinarian, Mike and Elizabeth have a wide variety, menagerie even, of pets (esp. for a two-bedroom apartment). While a graduate student, Mike continued his extracurricular involvement as Vice President for Membership and subsequently President of Omicron Delta Kappa Leadership Honor Society and through the Blacksburg Sustainability Project; involvement which was recognized in 1999 with the USLA Graduate Student Leader of the Year Award. After finishing his Master's degree, Mike will enroll in the University College London for a MSc in Public Understanding of Environmental Change sponsored by a Fulbright Student Grant.