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Leaf litter processing by macrodetritivores in natural and restored Neotropical mangrove forests

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LEAF LITTER PROCESSING
BY MACRODETRITIVORES IN
NATURAL AND RESTORED
NEOTROPICAL MANGROVE FORESTS

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Oceanography and Coastal Sciences

by

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TABLE OF CONTENTS

ACKNOWLEDGEMENTS	ii
LIST OF TABLES	vi
LIST OF FIGURES	viii
ABSTRACT.....	xii
CHAPTER ONE: INTRODUCTION	1
Factors Controlling Degradation of Plant Material.....	1
Abiotic Factors	3
Temperature	3
Moisture	4
Nutrients	5
pH.....	7
Oxygen	7
Biotic Factors	8
Plant Species, Tissue Type, and Chemical Composition	8
Decomposer Organisms	12
Mangrove Leaf Litter Degradation	12
Wetland Restoration.....	15
Research Goals.....	18
Project Significance	19
CHAPTER TWO: METHODS AND MATERIALS	20
Study Sites.....	20
Rookery Bay	20
Windstar	21
Ft. Pierce	22
Experimental Design.....	23
Methods.....	24
Forest Structure	24
Environmental Factors	24
Litter Dynamics.....	25
Macrodetritivore Dynamics	25
Feeding Trials	28
Statistical Analysis.....	29
CHAPTER THREE: FOREST STRUCTURE, ENVIRONMENTAL CONDITIONS, AND LITTER DYNAMICS.....	31
Forest Structure	31
Environmental Factors	32
Porewater Salinity	32
Light	36
Temperature	37

Litter Dynamics.....	38
Litter Fall.....	38
Litter Standing Stocks	41
Leaf Turnover Rates.....	46
CHAPTER FOUR: MACRODETRITIVORE DYNAMICS	54
Macrodetritivore Densities.....	54
<i>Melampus coffeus</i> Densities.....	54
Crab Burrow Densities.....	57
Leaf Consumption by Macrodetritivores	58
Leaf Degradation Rates.....	65
Leaf Nutrients.....	68
Macrodetritivore Feeding Trials	70
CHAPTER 5: SUMMARY AND DISCUSSION	75
Introduction.....	75
Methods and Materials.....	78
Study Sites.....	78
Experimental Design.....	80
Forest Structure	80
Environmental Factors	81
Litter Dynamics.....	81
Macrodetritivore Dynamics	82
Feeding Trials	83
Statistical Analysis.....	84
Results.....	84
Forest Structure	84
Abiotic Factors.....	85
Litter Dynamics.....	88
Macrodetritivore Densities.....	89
Macrodetritivore Leaf Consumption.....	90
Leaf Degradation Rates.....	93
Leaf Consumption Rates	94
Leaf Nutrients.....	96
Macrodetritivore Feeding Trials	98
Discussion	98
Macrodetritivore Community Variation	98
Variation in Leaf Litter Consumption Rates.....	102
Comparison of Restored and Natural Mangrove Forests.....	123
Conclusions	125
LITERATURE CITED	127
VITA	142

LIST OF TABLES

Table 1. Retrieval schedule for tethered leaves during detritivore study. Numbers indicate number of days after placement that leaves were retrieved. An “N” indicates leaves used in nutrient analysis were retrieved.	29
Table 2. Mangrove forest structure from Rookery Bay, Windstar, and Ft. Pierce sites.	31
Table 3. Comparison of differences in porewater salinity (ppt) among nine mangrove forest sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.....	34
Table 4. Comparisons of differences in porewater salinity between different areas and forest types in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.	35
Table 5. Light levels corrected for ambient light for nine sites in Southwest Florida, measured during summer 1999. Each value is based on nine plots, with 4 nearly simultaneous readings taken at each plot and referenced to readings taken in full light. Values are percentage of full light.	38
Table 6. Components of litter fall from nine mangrove forest sites in Naples (Rookery Bay and Windstar) and Ft. Pierce, Florida. For Ft. Pierce sites sample period = 378 days (17 April 1999 through 30 April 2000), for Naples sites sample period = 368 days (31 March 1999 through 3 April 2000). <i>Rhizophora</i> mangle reproductive tissues include flowers, propagules,. <i>A. germinans</i> reproductive tissues include flowers and propagules. <i>L. racemosa</i> reproductive tissues include flowers and seeds. Miscellaneous includes unidentifiable leaf fragments, frass, and <i>R. mangle</i> stipules. N = 9 for all sites. Values are g dry weight m ⁻² day ⁻¹ ± 1 SE.	42
Table 7. Comparisons of litter fall between different areas and forest types in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.....	45
Table 8. Components of standing litter fall from nine mangrove forest sites in Naples (Rookery Bay and Windstar) and Ft. Pierce, Florida. <i>Rhizophora</i> mangle reproductive tissues include flowers, propagules,. <i>A. germinans</i> reproductive tissues include flowers and propagules. <i>L. racemosa</i> reproductive tissues include flowers and seeds. Miscellaneous includes unidentifiable leaf fragments, frass, and <i>R. mangle</i> stipules. N = 36 for all sites. Values are g dry weight m ⁻² ± 1 SE.	47
Table 9. Comparison of differences in standing litter for main effects and interaction between sites and seasons in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida from spring 1999 through winter 2000.....	51
Table 10. Comparisons of differences in standing litter between different areas and forest types in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.	52
Table 11. <i>Melampus coffeus</i> densities (Number of <i>M. coffeus</i> m ⁻²) comparison for sites and seasons in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.	55

Table 12. <i>Melampus coffeus</i> densities compared among different locations and forest types in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.....	56
Table 13. Crustacean burrow density comparison for sites and seasons in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.	58
Table 14. Comparison of percentage of leaves “attacked” (defined by visible evidence of consumption) by macrodetritivores between sites, seasons, and species in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida during seasonal sampling from spring 1999 to winter 2000.	60
Table 15. Differences in percentage of leaves “attacked” (defined by visible evidence of consumption) by macrodetritivores in different areas and forest types in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.	64
Table 16. Comparison of degradation rates (percent mass loss day ⁻¹) for main effects and interaction between sites, seasons, and species in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.....	69
Table 17. Comparisons of degradation rates between different areas and forest types in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.....	71
Table 18. Comparison of the initial percent nitrogen, percent carbon and carbon:nitrogen ratio of leaves among sites, seasons, and species in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.....	72
Table 19. Mangrove forest structure from Rookery Bay, Windstar, and Ft. Pierce sites.	85
Table 20. Environmental variables from nine mangrove forest sites in Naples and Ft. Pierce, Florida.	86
Table 21. Comparison of leaf consumption by macrodetritivores between sites, seasons, and species in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida during seasonal sampling from spring 1999 to winter 2000.	95
Table 22. Comparison of the initial percent nitrogen, percent carbon and carbon:nitrogen ratio of leaves among sites, seasons, and species in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.....	97
Table 23. Litter cycling data from nine mangrove forest sites in Naples and Ft. Pierce, Florida.	104
Table 24. A summary of mangrove macrodetritivore studies in different geographic regions.....	114

LIST OF FIGURES

Figure 1. Map showing research locations: a. Windstar (Naples, Florida); b. Rookery Bay (Naples, Florida); c. Ft. Pierce, Florida.....	21
Figure 2. Regression of <i>A. germinans</i> leaf area on mass.....	27
Figure 3. Regression of <i>L. racemosa</i> leaf area on mass.....	27
Figure 4. Regression of <i>R. mangle</i> leaf area on mass.	28
Figure 5. Porewater salinity values (ppt) for each site from Summer 1998 through Winter 2000 measured in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.	37
Figure 6. Mean maximum temperatures measured in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida, from Summer 1998 through Winter 2000. Values are 0C. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.	39
Figure 7. Regression of light and maximum temperature in nine mangrove forests in Naples and Fort Pierce, Florida.....	39
Figure 8. Regression of maximum temperature and salinity at nine sites in Naples and Fort Pierce, Florida.	40
Figure 9. Average minimum temperatures measured in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida. Values are 0C. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.....	40
Figure 10. Regression of soil salinity and leaf litter fall at nine mangrove forest sites in Naples and Ft. Pierce, Florida.	45
Figure 11. Regression of litter fall and standing litter at nine mangrove forest sites in Naples and Fort Pierce, Florida.....	50
Figure 12. Mangrove leaf turnover rates for nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida. Values are number of times leaves turn over in 1 year. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.	53

Figure 13. Regression of porewater salinity and turnover rate at nine mangrove forest sites in Naples and Fort Pierce, Florida.....	53
Figure 14. <i>Melampus coffeus</i> densities (# of <i>M. coffeus</i> m ⁻²) at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.....	54
Figure 15. Crab burrows (Mean \pm 1 SE) at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.	57
Figure 16. Example of partially consumed a) <i>A. germinans</i> and b) <i>R. mangle</i> leaves. (a) is typical of <i>M. coffeus</i> consumption, while (b) is typical of crustacean feeding activity.	59
Figure 17. Attack of leaves by site and season at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida. Values are mean percentage \pm 1 SE of tethered leaves that were visibly damaged by macrodetritivores. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.....	61
Figure 18. Attack of leaves by species and site at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida. Values are mean percentage \pm 1 SE of tethered leaves that were visibly damaged by macrodetritivores. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.....	63
Figure 19. Attack of leaves by species and season at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration. Values are mean percentage \pm 1 SE of tethered leaves that were visibly damaged by macrodetritivores.	66
Figure 20. Regression of percent of leaves attacked to annual consumption rates of mangrove leaves at eight sites in at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida (excludes Ft. Pierce fringe, where crustaceans were the primary consumers of leaf litter).....	67

Figure 21. Degradation of leaves by site and season at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida. Values are % mass loss day ⁻¹ ± 1 SE. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.....	68
Figure 22. Carbon:nitrogen ratio for seven mangrove sites in at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida during Fall 1998. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.....	72
Figure 23. Carbon:nitrogen ratio for nine mangrove sites in at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida during Spring 1999. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.....	73
Figure 24. Changes in the carbon:nitrogen ratio of three mangrove species at nine sites in at nine sites in Naples and Fort Pierce, Florida during Fall 1998.....	73
Figure 25. Changes in the carbon:nitrogen ratio of three mangrove species at nine sites in at nine sites in Naples and Fort Pierce, Florida during Spring 1999.	74
Figure 26. Mass loss of mangrove leaf species during laboratory feeding trials with <i>M. coffeus</i>	74
Figure 27. Example of partially consumed a) <i>A. germinans</i> , b) <i>L. racemosa</i> , and c) <i>R. mangle</i> leaves.....	91
Figure 28. Attack of leaves by site and season at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida. Values are mean percentage ± 1 SE of tethered leaves that were visibly damaged by macrodetritivores. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.....	93
Figure 29. Attack of leaves by species and site at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida. Values are mean percentage ± 1 SE of tethered leaves that were visibly damaged by macrodetritivores. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.....	94

Figure 30. Carbon:nitrogen ratio for nine mangrove sites in at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida during Spring 1999. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.....	97
Figure 31. Mass loss of mangrove leaf species during laboratory feeding trials with <i>M. coffeus</i>	98
Figure 32. Cycling of matter within nine mangrove forests in Naples and Ft. Pierce, Florida. Pie charts represent relative amounts of standing litter and numbers within pie charts are percentages of standing leaf litter.	105

ABSTRACT

Knowledge of mangrove litter dynamics is crucial to an understanding of the energetic links between mangrove ecosystems and nearby estuaries and coastal waters. Previous research into the role played by macrodetritivores in Neotropical mangrove litter processing has been contradictory. This study used leaf tethering to examine the effects of macrodetritivores on initial rates of mangrove litter degradation in South Florida, USA. Leaf litter dynamics experiments were run in both natural and restored mangrove forests to assess functionality of the restoration projects. Although less important than in some other parts of the world (*e.g.*, the Indo-Pacific), macrodetritivores played a significant role in increasing *in situ* leaf degradation within mangrove forests on both east and west coasts of Florida. In contrast to Indo-Pacific forests, gastropods were the primary macrodetritivores usually observed feeding on abscised mangrove leaves in South Florida. During leaf tethering trials, macrodetritivores (the gastropod *Melampus coffeus* and grapsid crabs) attacked between 1.7 and 29.6% of deployed leaves at different sites and accounted for 24.0% more leaf mass loss compared to non-attacked leaves. Macrodetritivores increased leaf litter degradation in several different mangrove forest types and under different environmental conditions within this study. In addition, macrodetritivore degradation rates varied among site histories (natural versus restored) and macrodetritivore characteristics. Although macrodetritivore community populations were greater in restored forests, litter cycling processes were similar to nearby reference forests. Litter and environmental characteristics were also examined to help understand macrodetritivore impacts on litter cycling. Litter fall rates varied from 0.4 ± 0.1 to 3.2 ± 0.3 g m⁻² d⁻¹ at the several sites. Standing stocks of litter on the forest floor varied widely within and among sites and ranged from 29 g m⁻² to 559 g m⁻² with an overall mean of 269 g m⁻². Differences in litter fall and

litter standing crop across sites and seasons were partly attributable to environmental variables (*i.e.*, temperature, porewater salinity, forest structure, and light). The restored mangrove forests observed during this study appear to have gained some natural functionality of leaf litter dynamics as compared to nearby reference forests.

CHAPTER ONE: INTRODUCTION

Mangrove forest ecosystems are important as sources of energy and nursery areas for fisheries and wildlife (Odum and Heald 1972, Rodelli *et al.* 1984, John and Lawson 1990), timber production (Noakes 1955, Clough and Scott 1989), and storm protection (Teas 1977, Christensen 1978). Detrital export from mangrove forests is a source of nutrients and energy to nearby ecosystems such as Biscayne Bay, Florida (Fleming *et al.* 1990), the Great Barrier Reef of Australia (Alongi 1990), Gazi Bay, Kenya (Hemminga *et al.* 1994) and the Guayas River Estuary Ecosystem of Ecuador (Cifuentes *et al.* 1996). Particulate carbon export from mangrove forests to nearby waters has been estimated to vary from $160 \text{ kg C m}^{-2} \text{ yr}^{-1}$ (Twilley 1985) to $3322 \text{ kg C m}^{-2} \text{ yr}^{-1}$ (Robertson 1986). Coastal-oriented development, mangrove timber harvesting, and shrimp pond mariculture will continue to put pressure on these mangrove forests (Boto *et al.* 1984, Rodelli *et al.* 1984). Thus, the restoration of mangrove ecosystems has become an important concern on a global scale. Our understanding of how these systems function in their natural state must be enhanced to improve attempts at restoration in disturbed sites or the creation of new mangrove forests in legal mitigation processes.

Knowledge of mangrove litter dynamics is crucial in understanding the energetic links between mangrove forests and adjacent aquatic systems (Twilley *et al.* 1997, Wafar *et al.* 1997, Gong and Ong 1990). This introductory section will discuss the carbon cycle, decomposition, the role of macrodetritivores in the initial degradation of plant litter and present a brief overview of wetland and mangrove restoration.

Factors Controlling Degradation of Plant Material

The process of decomposition, *i.e.*, the breakdown of organic matter into simpler organic and inorganic components, occupies a key position in carbon cycling on both global

and local scales. Litter decay is important in carbon cycling processes in both terrestrial (Melillo *et al.* 1982, Attiwill and Adams 1993) and wetland (Brinson *et al.* 1981, Wilson *et al.* 1986, Jordan *et al.* 1989) ecosystems.

Transfer of matter and energy between three basic ecosystem components (the plant, herbivore, and decomposition subsystems) maintains the integrity of the carbon cycling system (Swift *et al.* 1979). Primary producers, *e.g.* plants, fix carbon from CO₂ into plant material through photosynthesis. Estimates of productivity vary widely for different ecosystems (Whittaker 1975). If leaves or other plant materials are consumed directly, they enter the herbivore subsystem; if the materials senesce and fall before consumption, they become part of the decomposer subsystem (storage and export are also possibilities). Carbon can go through several levels of consumers (*e.g.*, detritivores, primary and secondary carnivores) before complete conversion of organic carbon into CO₂ (*i.e.*, CO₂ respiration) occurs. Regardless of the number of steps in the herbivore subsystem (*e.g.*, secondary and tertiary predators), the non-respired carbon will eventually enter the decomposer subsystem through sloppy feeding (*e.g.*, leaf shredding by crustaceans), excretion, and organism demise.

The decomposition process results in the mineralization of organic matter into its component elements and the formation of soils (Swift *et al.* 1979). Understanding decomposition processes is generally held critical to evaluation of food webs (*e.g.*, Brinson *et al.* 1981, Webster and Benfield 1986, Proffitt *et al.* 1993). Three discrete phases occur during decomposition: leaching, decomposer, and refractory (Benner and Hodson 1985, Valiela *et al.* 1985). During the initial fast phase of leaching, water action removes soluble substances from litter. The decomposer phase is slower, and various detritivores and microbial decomposers control organic matter losses. In the final phase, decomposition

occurs at a slower rate than the other two because the remaining components are much more refractory.

Decomposition rates vary greatly both among and within ecosystems (Swift *et al.* 1979, Brinson *et al.* 1981, Valiela *et al.* 1985). Wetlands, including mangrove forests, share many properties of decomposition with upland ecosystems. The interaction of many factors, both biotic and abiotic, influences the rate of decomposition within a given ecosystem (Brinson *et al.* 1981, Anderson and Swift 1983). The composition of the litter, abiotic factors, and decomposer communities play different roles in decomposition. These different factors can act as “feed-back mechanisms” with one another, increasing or decreasing the decomposition rate (Swift *et al.* 1979).

One of the most important distinctions between wetlands and terrestrial ecosystems is the absence of oxygen in wetlands. In decompositional processes, this means that the soil organisms must be at least partially adapted to anaerobic conditions. A high percentage of respiration in salt marshes has been attributed to sulfate reduction (Howarth and Teal 1979, Sørensen *et al.* 1979, Howes *et al.* 1984) and other anaerobic decomposition processes, such as reduction of carbon dioxide to methane (Lipschultz 1981, Howes *et al.* 1985). However, many of the decompositional processes and controls occurring in upland systems are also seen in wetlands. Therefore, information gleaned from terrestrial ecosystem decomposition studies can be applicable to wetlands.

Abiotic Factors

Temperature

A direct correlation between temperature and decomposition rate has been demonstrated, attributed primarily to effects on activity of decomposer organisms (Valiela *et al.* 1985). However, it is somewhat difficult to separate effects of temperature and those of

the climate as a whole when comparing decomposition rates from different ecosystems (Madge 1965). Anderson (1973) showed that soil respiration rates (as a measure of decomposition) were highly correlated with increasing temperatures in a *Castanea* woodland. Soil is a less efficient conductor of heat than water, and therefore its moisture content can significantly affect the temperature regime in soil (Swift *et al.* 1979). The organisms that decompose wood generally prefer temperatures between 25 and 30 °C, but some fungi exhibit growth well above and below this range (Käärik 1974).

Temperature is a controlling factor of decomposition in both wetland and terrestrial ecosystems. White and Trepani (1982) related an increase in water temperature to higher decomposition rates in *Spartina alterniflora*. In a study of the Great Sippewissett Marsh, an increase in decay rate occurred under higher temperatures during the decomposer phase (Valiela *et al.* 1985). Mackey and Smail (1996) compared *Avicennia marina* leaf degradation rates at eight different locations (from their study and previously published studies) and found a latitudinal trend they related to a difference in average temperature at the different sites. Also, in their study, both leaves and twigs of *Avicennia marina* decomposed significantly slower in winter than in summer.

Moisture

Up to a point, the presence of water increases the decomposition rate of most plants, but in the anaerobic environment that develops when soil is waterlogged, decomposition is usually inhibited unless organisms are present that are adapted to those conditions (Williams and Gray 1974). Moisture content affects leaching rates of litter components differently, depending on the solubility of those components. With increased moisture content, leaching losses by water-soluble components such as simple phenolics and flavanoids will exceed that of less soluble components such as lignin (Horner *et al.* 1988). Decomposition of wood

is inhibited with a moisture content less than 35% due to the decrease in growth and mortality of wood decay fungi (Lopez-Real and Swift 1975). Miller and Johnson (1964) found that soil CO₂ evolution was maximized in a range from -0.5 to -0.15 bar and minimized below -50 bar.

Regularly flooded wetlands that provide a moist and aerobic environment, such as tidal marshes and mangroves, produce optimum conditions for decomposition. McKee and Seneca (1982) found that decay of *Spartina alterniflora* and *Juncus roemarianus* was slowed when litter was constantly submerged compared to litter that was exposed to tidal flushing and resulting aerobic conditions. In a study of upper and lower intertidal zones in a Belizean mangrove forest, Middleton and McKee (2001) found mangrove leaves in the lower intertidal zone decomposed faster than those placed in the upper intertidal zone; no zonation effect was observed for roots. Decomposition of *Avicennia marina* leaves and twigs was significantly faster in a down-shore position compared to an area that received less tidal input (Mackey and Smail 1996). Flores-Verdugo *et al.* (1990) found that water increased *Laguncularia racemosa* decomposition rates, whether due to rainfall or leaf submergence. A mixed leaf microcosm study of deciduous trees demonstrated that pulsed flooding can increase decomposition rates (Lockaby *et al.* 1996).

Nutrients

One of the most important factors affecting degradation of organic matter is nutrient content. During decomposition, both relative and actual nutrient concentrations can change due to the addition of nutrients by fungi (Fell *et al.* 1984) and bacteria, and the loss of more soluble compounds (Suberkropp *et al.* 1976, Swift *et al.* 1979). For example, during decomposition of mangrove litter, nitrogen concentration and mass increased in different trials (Fell *et al.* 1980, Rice 1982, Day *et al.* 1982, Twilley *et al.* 1986), possibly due to

feeding and growth of microbial organisms and carbon leaching (Fell *et al.* 1975). Qualls (1984) associated faster decomposition rates in blackwater stream swamps with nutrient enrichment. Day *et al.* (1982) attributed relatively high rates of decomposition to high nitrate and phosphate concentrations in seasonal flood waters.

Nitrogen is often thought to be limiting in decomposition processes (Webster and Benfield 1986). In microcosm experiments, Coûteaux *et al.* (1991) demonstrated that increasing the C/N ratio in leaf litter can decrease decomposition rates, although the response is species dependent (Cotrufo *et al.* 1994). Supplements of nitrogen have increased decomposition in several experiments with upland (Findlay 1934, Allison and Cover 1960, Berg *et al.* 1982) and wetland (Haines and Hanson 1979, Marinucci *et al.* 1983, Valiela *et al.* 1985) plants. Carbon:nitrogen ratios in *Rhizophora mangle* leaf litter decreased from 120 to 43 over a fifteen week experiment (Newell *et al.* 1984), and higher nitrogen levels may increase palatability of mangrove leaf litter to detritivores (Robertson *et al.* 1992). In a recent survey, however, Rybczyk *et al.* (1996) reported varying effects upon decomposition rates among 24 published nutrient enrichment experiments.

Carbon loss in *Typha domingensis* and *Cladium jamaicense* was positively correlated with phosphate concentrations (Qualls and Richardson 2000). Increasing phosphate (PO_4) concentrations in a woodland stream resulted in higher decomposition rates (Elwood *et al.* 1981). Suberkropp and Chauvet (1995) correlated decomposition rates with nitrate (NO_3^-) concentrations in hard-water streams. However, some studies show no change (Triska and Sedell 1976, Newbold *et al.* 1983) or a decrease (Lockaby *et al.* 1996) in decomposition rates after addition of nutrients.

pH

The pH of a soil can have complex effects on both litter and the decomposers that consume it. The lowest pH values (and therefore the greatest acidities) are usually seen in horizons containing products of primary decomposition, usually the upper layers (Frankland *et al.* 1963). Organic soils tend to be acidic, but anaerobic respiration (*e.g.*, $\text{SO}_4^{=}$ reduction), as seen in wetland ecosystems, causes an increase in pH by the consumption of hydrogen ions, resulting in stabilization of pH near 7 (Patrick and Delaune 1977). Soil pH can vary across the intertidal zone in mangrove forests (Giglioli and Thornton 1965). Reported mean pH values for mangrove soils in Belize were 6.33 in a *Rhizophora mangle*-dominated zone and 6.14 in an *Avicennia germinans*-dominated zone (McKee 1995) and ranged from 5.2 to 7.0 in mangrove forests in southwest Florida (Coultas 1977, McKee 1993).

Of the decomposer organisms, microorganisms living in water films in the soil are the most susceptible to variations in pH, although many of them have adaptations designed to cope with shifts in pH (Swift *et al.* 1979). Williams and Gray (1974) stated that at low pH values (<5.0), many decomposer organisms become inactive or decrease activity. In an English Lake District hardwood forest, Bocock and Gilbert (1957) noted that litter feeding invertebrates were more prevalent in locations with near neutral (pH = 6.2-6.3) sites compared to acidic sites (pH = 3.2-3.65). Breakdown of *Nuphar lutea* leaves was slower in an acid moorland pool when compared to eutrophic and alkaline lakes (Brock *et al.* 1985). *Acer rubrum* leaf material experienced slower decomposition rates at pH 4 compared to pH 5 and 7 (Qualls and Haines 1990).

Oxygen

Wetland soils are often anaerobic due to water filling the pore space between soil particles and aggregates (Gambrell and Patrick 1978). Lack of oxygen may be a controlling

factor in decomposition within the soil (Brinson *et al.* 1981, Alongi *et al.* 1998). For example, buried *Avicennia marina* roots decomposed slower than roots exposed at the soil surface (Albright 1976). When exposed on an intermittently flooded soil surface (*i.e.*, an intertidal zone), leaf litter will not experience a complete oxygen deficiency.

Biotic Factors

Plant Species, Tissue Type, and Chemical Composition

The type of litter (*e.g.*, leaves or woody material) has a profound effect on the decomposition rate. Different fractions of litter tissue (*e.g.*, soluble sugars, cellulose, and lignin) differ in decomposition rates with soluble sugars exhibiting the highest rate and lignin the lowest rate (Minderman 1968). Morphology (short, medium or tall growth form) of *Spartina alterniflora* altered decomposition rates due to variation in amount of stem material (McKee and Seneca 1982). In forested systems, woody material and roots generally decompose slower (Platt *et al.* 1965, Waid 1974), and reproductive organs decompose faster (Swift *et al.* 1979) than leaves as a consequence of variations in lignin content and nutrient concentrations.

Differences in decomposition among litter types are seen in wetlands. Decomposition rates for roots and rhizomes of four macrophytes from a northern prairie fresh marsh were either comparable to (*Typha glauca*, *Scolochloa festucacea* and *Scirpus lacustris*) or greater than (*Phragmites australis*) published rates for shoot litter (Wrubleski *et al.* 1997). Brock *et al.* (1985) found that belowground structures of *Nuphar lutea* decomposed slower than aboveground parts. In salt marshes, decomposition of belowground root material is usually slower than decomposition of aboveground shoot material (Hackney and de la Cruz 1980, Van der Valk and Attiwill 1983). Possible explanations for differences between salt and fresh marsh decomposition rates include

different nutrient concentrations (Van der Valk *et al.* 1991, Melillo *et al.* 1984) and variation in structural materials (Puriveth 1980). Brinson (1977) found that *Nyssa aquatica* twigs in a North Carolina swamp decomposed at a much slower rate than leaves of the same species. Stems of two tree species from a Michigan peatland decomposed slower than leaves of those species (Chamie and Richardson 1978). Leaf laminae of the freshwater macrophyte *Nelumbo lutea*, with a relatively low amount of support tissue, had a much faster decomposition rate than leaf petioles of the same species (Hill 1985).

Mangrove litter types exhibit differences in decay rates similar to those of other forested wetlands. *Rhizophora mangle* plant parts containing higher lignin concentrations (*e.g.*, wood) decomposed more slowly than *R. mangle* leaves (Benner and Hodson 1985). Mangrove leaves on a Belizean forest floor decomposed much faster than either twigs or roots (Middleton and McKee 2001). Albright (1976) and Van der Valk and Attiwill (1984) demonstrated that *Avicennia* spp. leaves decompose faster than roots of the same species. *Avicennia marina* leaves decomposed several times faster than twigs in an Australian mangrove forest (Mackey and Smail 1996). In a tropical mangrove forest in Australia, *Rhizophora* trunks required over 5 years to lose half of their original trunks and the half-life for branches was about 2 years (Robertson and Daniel 1989a), compared with a half-life below 1 year for *Rhizophora* leaves under different conditions (Robertson *et al.* 1992). However, wood decomposition in more tropical areas may be more rapid than that reported from Australia (Gong and Ong 1990).

Within a given category of litter (*e.g.*, leaves or stems), decomposition often varies by plant species. Both physiological and chemical differences among species are causes of these differences. Platt *et al.* (1965) saw variation in the decomposition rates of both stems and roots of different conifer species under laboratory conditions. Bocock and Gilbert

(1957) and Witkamp (1966) described differences in decay rates of leaf litter for several upland plants. In a third order hard-water stream in southwestern Michigan, *Carya glabra* leaves decomposed faster than leaves of *Quercus alba* (Suberkropp *et al.* 1976). Leaching rates, most important during the early decomposition phase, can also vary among species (Nykqvist 1961).

Odum *et al.* (1984) placed freshwater tidal marsh plants into two categories with respect to decomposition rates, attributing variations in those rates to chemical and physiological differences between the groups. One group, broad-leaved perennials such as *Pontedaria cordata* and *Nuphar luteum*, contains relatively high amounts of nitrogen and low concentrations of structural tissue such as lignin. The second group includes marsh grasses such as *Zizania aquatica*, and has low levels of nitrogen and contains much structural tissue, therefore decaying at slower rates than the first group. *Ludwigia leptocarpa* and *Typha angustifolia* leaves exhibited decomposition rates slower than *Nelumbo lutea* leaves but faster than *N. lutea* petioles (Hill 1985). In a third order hard-water stream in southwestern Michigan, *Carya glabra* leaves decomposed faster than leaves of *Quercus alba* (Suberkropp *et al.* 1976). Wrubleski *et al.* (1997) observed differences in decomposition rates of roots of four macrophytes, with *Phragmites australis* and *Scolochloa festucacea* decomposing faster than *Scirpus lacustris* and *Typha glauca*. They ascribed the variation in rates to structural differences (*e.g.*, hemicellulose and cellulose) among the species. Differences in morphology and resistance to biotic and abiotic fragmentation were theorized to be responsible for the variation in decay patterns of *Spartina alterniflora* compared to *Juncus roemarianus* (usually with *Spartina* having a faster decay rate) in three North Carolina salt marshes (McKee and Seneca 1982). Benner and Hodson (1985)

demonstrated that lignocellulose from *R. mangle* is less biodegradable than that of *Spartina alterniflora* or *Juncus roemarianus*.

Plant litter that contains tannins and other polyphenolic compounds can inhibit degradation by macro- and micro-detritivores (Handley 1954, Heath and King 1964) and microorganisms (Horner *et al.* 1988) and thereby control rates of decomposition. Neilsen *et al.* (1986) demonstrated that flavolins, a type of tannin, inhibited mangrove leaf litter consumption by sesarmid crabs in Australia.

In both New World (McKee and Faulkner 2000) and Old World (Robertson *et al.* 1992) mangrove forests, *Rhizophora* spp. leaves can decompose slower than *Avicennia* spp. leaves in similar environments. Twilley *et al.* (1986) attributes these differences in decomposition rate to higher C:N ratios in *Rhizophora* spp. leaves compared to *Avicennia* spp. leaves. However, it is also recognized that *Avicennia* spp. leaves usually have lower concentrations of tannins than *Rhizophora* spp. leaves (Robertson 1988, Camilleri 1989, Pelegri and Twilley 1998), which can affect decomposition rates. Newell *et al.* (1984) reported that *R. mangle* and *Thalassia testudinum* decomposed much faster than *Juncus roemarianus*, but this could partly be explained by location of decomposition bags relative to water (*e.g.*, subtidal vs. intertidal) and not differences among species. In a Belizean mangrove forest, while *A. germinans* leaves decomposed more rapidly than either *R. mangle* or *L. racemosa*, intertidal position (upper vs. lower) had a much greater effect on decomposition of mangrove leaves than species (Middleton and McKee 2001). Robertson (1988) attributed the relatively rapid decomposition rates of *Avicennia marina* to high initial nitrogen concentration, low C:N ratio and low tannin concentration, while slower decomposition rates for *R. stylosa* and *Ceriops tagal* were ascribed to low initial nitrogen, high C:N ratios and high tannin concentrations.

Decomposer Organisms

Decomposers of plant tissue can be placed into two general categories, primary and secondary saprotrophs (Swift *et al.* 1979). Primary saprotrophs, such as amphipods (Ladle 1974), gastropods (Mason 1974), insects (Meyer and O'Hop 1983), and crustaceans (Robertson 1986) tend to be larger and do the initial breakdown of litter, producing a wide array of resources (*e.g.*, smaller particles, feces). The snail *Littoraria irrorata* is important in the alteration of *Spartina alterniflora* from standing-dead biomass to fine particulate detritus (Kemp *et al.* 1990). The gastropods *Melampus bidentatus* and *Littoraria* spp. were important to the energy relationships due to litter consumption in a north Florida salt marsh (Subrahmanyam *et al.* 1976). These resources are then utilized by the secondary saprotrophs, including micro- and meso-fauna, fungi and bacteria. These categories are not absolute, since some organisms feed at both trophic levels either at different life stages or according to resource availability (Swift *et al.* 1979). Fell *et al.* (1975) described microbial populations associated with the decomposition of *Rhizophora mangle*. They found a wide variation in the patterns of use by fungi and meiofauna and associated increases in absolute nitrogen in leaves with increases in the standing crop of microorganisms.

Mangrove Leaf Litter Degradation

Early workers thought that the degradation of mangrove leaf material was mediated primarily by fungi and bacteria (Odum and Heald 1975). Thus, early work focused on factors controlling microbial decomposition (reviewed above) and used techniques specific to this purpose. Due to rapid leaching of nutrients from the leaves, consumption of leaf material by macrodetritivores was assumed to occur only in the first two weeks after leaf abscission. In addition, mangrove decomposition *in situ* was assessed with fine mesh bags that excluded macrodetritivores (Fell *et al.* 1975, Odum and Heald 1975, Twilley *et al.*

1986). Consequently, macrodetritivore processing was initially thought to be less important than breakdown by fungi and bacteria.

However, in the mid-1980's, the importance of macrodetritivores in processing mangrove litter was assessed. Fell *et al.* (1984) recognized the inherent problems of macrodetritivore exclusion when using litter bags. In a series of studies, Robertson (1986, 1988) and Robertson and Daniel (1989b) demonstrated that sesarmid crabs in Australia processed a significant portion of the litter fall before it could be exported by tidal action. Robertson (1986) stated that earlier work on mangrove detrital export in Australia overestimated export by at least 22% because leaf litter consumption by the crab *Sesarma messa* was overlooked. Sesarmid crab density was negatively correlated with mangrove leaf litter turnover rate in a Hong Kong tidal shrimp pond, indicating that consumption by the crustaceans had a significant impact on standing leaf litter (Lee 1989b). Based on feeding rates in laboratory experiments, *Sesarma meinerti* was estimated to consume 44% of *Avicennia marina* leaf fall from a South African mangrove estuary (Emmerson and McGwynne 1992). A significantly higher decomposition rate for tethered leaves compared to leaves in mesh bags within a Belizean mangrove forest was attributed to consumption by herbivorous crabs (Middleton and McKee 2001). Some mangrove crab species (*e.g.*, *Neosarmatium smithi*) carry leaf litter into burrows, which also reduces tidal export of leaf litter (Giddens *et al.* 1986). Middleton and McKee (2001) observed tethered mangrove leaves that had been pulled into *Ucides cordatus* burrows. Camilleri (1989, 1992) observed a suite of invertebrates (crabs, isopods, amphipods, and a polychaete) processing litter in an Australian mangrove forest and concluded that this would increase the retention of leaf material in the forest and reduce the amount exported to nearby open-water systems. Flores-

Verdugo *et al.* (1990) stated that resident crustacean populations must affect leaf degradation in a Mexican-Pacific estuary.

The importance of litter turnover by crabs can vary widely by mangrove forest type (Robertson *et al.* 1992). In Australia, high intertidal mangrove forests dominated by *Cerriops tagal* and *Brughiera exaristata*, crabs removed 71 and 79%, respectively, of the annual litter fall, while in high intertidal mangrove forests dominated by *Avicennia marina* crabs removed only 33% of the leaf litter (Robertson and Daniel 1989b). Leaf consumption by macrodetritivores was greater in a low intertidal zone compared to a high intertidal zone in a Belizean mangrove forest (Middleton and McKee 2001). Highest consumption of propagules by crustaceans occurred in a high intertidal Australian forest compared to low intertidal (Osborne and Smith 1990). Shredding and fragmentation of leaves and fecal production by crabs provided greater opportunity for smaller detritivores and microbial decomposers to utilize mangrove litter before it was tidally exported from Queensland forests (Camilleri 1992). In Hong Kong forests, the crab *Sesarma messa* was an important litter consumer and producer of fecal material that may form a caprophagous food chain for small invertebrates (Lee 1997). Since different litter processors break leaves down into different particle sizes, many extra niches for detritus particle consumers are created (Camilleri 1992). The action of these macrodetritivores thus results in a faster rate of decomposition and recycling of nutrients in mangrove forests (Robertson 1986).

Work conducted to date investigating the role of macrodetritivores in mangrove litter processing in Neotropical forests suggests that 1) they may have as great an impact on litter turnover as in Old World forests (Middleton and McKee 2001, Twilley *et al.* 1997) and 2) gastropods may play a more important role than crabs in some locations (Proffitt *et al.* 1993, McKee and Faulkner 2000). Mangrove crabs, *e.g.* *Ucides* spp., appeared to increase litter

turnover rates in an estuary in Ecuador (Twilley *et al.* 1997) and on mangrove islands in Belize (McKee and Feller 1992, Middleton and McKee 2001). Direct consumption and burial in burrows accounted for up to 100% of fallen litter in these forests. In contrast, the only consumption of mangrove leaf litter in southwest Florida was attributed to *Melampus coffeus*, the coffee bean snail (Proffitt *et al.* 1993, McIvor and Smith 1995, McKee and Faulkner 2000). However, several crustacean species known to be detritivores elsewhere do occur in Florida, especially in the Indian River Lagoon region. The primary food for *M. coffeus* is fresh and decaying mangrove leaf litter (Mook 1986), and a significant portion of mangrove litter may be assimilated by *M. coffeus* before export (Proffitt *et al.* 1993, McKee and Faulkner 2000). Other work also supports the role of gastropods and suggests their impact on litter turnover may vary geographically and with environmental conditions. In a Hong Kong tidal shrimp pond associated with the mangrove *Kandelia candel*, Lee (1989b) suggested that, where frequent inundation occurred, gastropods were more important to litter turnover than grapsid crabs. These findings together suggest that at high enough densities, snails may be more important than crabs to litter processing in some systems. The effect of macrodetritivores, particularly gastropods, on litter turnover needs to be examined in greater detail in Neotropical forests. More information is also needed as to how composition and size of the macrodetritivore community impacts litter turnover and carbon movement in mangrove ecosystems. A better understanding of macrodetritivore dynamics could provide a tool to analyze the functional success (or failure) of mangrove restoration projects.

Wetland Restoration

Current concerns regarding wetland restoration focus on restoring wetland function. Although the correct vegetation may be in place, nutrient cycling, wildlife and fishery utilization, water quality improvement, and other important wetland components that are not

readily assessed may not be working as in natural systems. The comparison of the functionality of restored to natural wetlands should be used as an opportunity to both improve future restorations and as a means for further understanding the natural systems themselves.

Between thirty and fifty percent of the United States' wetlands have been lost to anthropogenic 'reclamation' since the Mayflower landed on Plymouth Rock in 1620 (Mitsch and Gosselink 1986). Settlers and farmers harvested wetlands for timber and drained them for agriculture in an attempt to gain some value from what were perceived to be useless lands. They also filled swamps, fens, moors, and bogs to decrease the occurrence of various swamp diseases believed to be caused by the stagnant waters. Mandates for wetland development even came from the federal government when Congress gave millions of acres to various states in the mid-1800's with the expectation that they would be converted into more "productive" areas (Salveson 1990).

During the 1800's early scientists and environmentalists slowly identified some useful functions of wetlands, especially as wildlife habitat. We now recognize and more fully appreciate other values, such as storm buffers on coastlines, flood control, groundwater recharge, and water quality improvement. However, it was only in the 1960's, with a new interpretation of the River and Harbors Act of 1899 that the federal government (and specifically the U.S. Army Corps of Engineers) began to play a significant role in wetlands protection. Many federal and local agencies now expend considerable effort in the protection and restoration of wetlands.

Salveson (1990) described wetland restoration as both a science and an art. Wetlands vary widely in type, size, species composition, and functional value. Soil type,

plant species, hydrological structuring, and topography are only a few of the criteria that must be considered when attempting wetland mitigation (Cylinder *et al.* 1995).

Four types of generally recognized actions are: preservation, restoration, enhancement, and creation. Preservation, as the name implies, is simply where a functioning wetland is left intact, protected through different legal means such as purchase by a public or private entity for preservation or the acceptance of a conservation easement on a property. Enhancement generally indicates some minor improvement of a wetland site to increase specific functions (*e.g.*, the flood control capacity of a marsh). Areas that were previously wetlands but were subsequently altered for agriculture or other uses are candidates for restoration, which is returning them to approximately their pre-degraded conditions. Since the area was previously a wetland, re-creating the conditions (*e.g.*, hydrology) that originally existed at the area can be easier; consequently, restoration is a preferred method of mitigation. Creation of wetlands involves transforming an area that usually does not have any wetland characteristics (*e.g.*, hydrology, soil). Creation of wetlands is considered extremely difficult, has a poor success rate and is therefore losing favor (Redmond *et al.* 1996).

Much of the current tidal wetland restoration theory and practice centers on establishment of the correct hydrology of an area (Moy and Levin 1991, Ellison 2000). If there is a nearby viable seed source that has hydrologic access to the restoration site, mangrove propagules and seeds often have the ability to float in through the connection and re-vegetate the area as long as the tidal regime is correct (Blanchard and Prado 1995, Stevenson *et al.* 1999). Because of this, many mangrove restoration projects in southern Florida now install an intertidal salt-marsh grass (usually *Spartina alterniflora*) to stabilize

the shoreline after earthwork and then allow propagules and seeds from nearby mature mangrove forests to colonize the site.

Although the vegetative success of mangrove restoration efforts has been demonstrated fairly often (Proffitt and Devlin 1991, Stevenson *et al.* 1999), restoration of a natural substrate is less certain (McKee and Faulkner 2000). Assessment of macrodetritivores and their impact on the litter cycling process may provide a more accurate description of the functionality of habitat restoration projects.

Research Goals

Mangrove forests within mosquito impoundments in the Indian River Lagoon system near Fort Pierce, Florida, and natural and restored mangrove forests in the Rookery Bay National Estuarine Research Reserve and along Naples Bay in the city of Naples, Florida presented an opportunity to examine the role of macrodetritivores in mangrove systems and how their influence may be affected by a history of disturbance that has altered forest structure and hydrology. Comparison of natural basin and fringe forests allowed assessment of differences in hydrology and forest structure on macroinvertebrate populations.

Two major goals existed for this research: 1) to determine the role macrodetritivores play in initial litter processing in a Neotropical mangrove ecosystem; and 2) examine differences in macrodetritivore populations with a focus on *Melampus coffeus* and a suite of decapod crustaceans in natural and restored mangrove forests to assess their relative functioning with respect to carbon dynamics. The main questions to be addressed were: 1) What controls macrodetritivore composition and densities?; 2) How do macrodetritivore communities vary in types and abundance seasonally and among mangrove forests?; 3) What controls leaf litter consumption and turnover?; 4) How do leaf litter consumption rates

vary spatially and temporally in mangrove forests?; and 5) How do restored and natural forests differ in macrodetritivore abundance and activity?

Project Significance

Macrodetritivores play an important role in many estuarine systems (Bertness 1984, Kemp *et al.* 1990). Mangrove ecosystems have paradigmatically been viewed as sources of food for nearby fisheries (Robertson *et al.* 1992). Estimates of food export from mangroves are often based upon a measure of litter fall with no accounting for internal turnover (*e.g.*, Boto and Bunt 1981, Twilley *et al.* 1986). However, processes such as production, degradation, and tidal transport are all involved in litter dynamics. If macrodetritivores play an important role in litter turnover in Neotropical mangrove forests, as is the case in Australia (*e.g.*, Robertson 1986), then the amount of carbon (i.e. food) exported per areal unit of mangrove forest can be more accurately predicted through the incorporation of macrodetritivore activity in outwelling models (*e.g.*, Twilley *et al.* 1986). Rates of leaf litter production, microbial decomposition, and tidal action have been quantified in different Florida locations (*e.g.*, Twilley 1985, Twilley *et al.* 1986, Parkinson *et al.* 1999, McKee and Faulkner 2000). The role of macrodetritivore degradation of leaf litter in Florida has not been intensively investigated (Proffitt *et al.* 1993, McIvor and Smith 1995), but some work suggests that it may have a major influence on litter turnover (McKee and Faulkner 2000). This information is consistent with that reported for other locations in the neotropics (Twilley *et al.* 1997, Middleton and McKee 2001). However, details about spatial and temporal patterns of leaf consumption as well as how factors such as detritivore densities and environmental conditions influence leaf litter turnover have not been described.

CHAPTER TWO: METHODS AND MATERIALS

Study Sites

Several distinct types of mangrove forest, based on hydrological regime and species composition, are recognized: riverine, fringe, basin, and scrub/dwarf (Lugo and Snedaker 1974). This study focused on three of these, fringe, basin, and dwarf, representing intermediate-high, intermediate-low and low hydrologic energy. Basin forests in Florida are usually inundated several times each month by spring tides and have a mixed species composition, including *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa*. Fringe mangroves are generally dominated by *R. mangle* and are inundated by almost every tide. Dwarf forests are either perennially flooded or infrequently flooded (leading to hypersaline conditions) and are dominated by short (less than 2 m) *R. mangle*, *A. germinans* and *L. racemosa*. These differences in hydrology and mangrove species composition not only influence litter decomposition and turnover rates, but also affect macrodetritivores. Restored mangrove forests may differ from adjacent natural areas due to differences in factors such as hydrology, age, and mangrove species composition (as an artifact of species planted or successional stage).

Rookery Bay

The Rookery Bay National Estuarine Research Reserve (Rookery Bay, 26°3'N, 81°42'W) (Figure 1) is located along the southern shore of Henderson Creek. This site is in an area that was originally leveled and dredged for a fishing pond in 1972 (RBNERR 1993). The two-phased restoration (completed in 1992) included removal of exotic vegetation, reestablishment of the original elevation, excavation of flushing cuts to facilitate water movement, and planting of 7,600 *R. mangle* seedlings. Percent cover was about 94% in 1993 and dominated by pioneer *L. racemosa* interspersed with *R. mangle* and *A. germinans*

(RBNERR 1993). The reference forests, located adjacent to the restoration site, are a typical mixed basin forest of *R. mangle*, *A. germinans*, and *L. racemosa* and a fringe forest dominated by *R. mangle*. Coultas (1977) classified soils in Rookery Bay as Typic Sulfihemists-Typic Sulfaquents with thin (20-48 cm) organic deposits over fine sands to sandy clay loam. Aerial photography indicates that it has been undisturbed for at least 60 years (Proffitt, pers. comm. to McKee). Southwest Florida is microtidal (<1 m)(Odum *et al.* 1982), and Naples (including both Rookery Bay and Windstar, described next), receives an average of 53.6 cm rainfall annually, with more than 60% of that coming between June and September (Southeast Regional Climate Center 2004b).

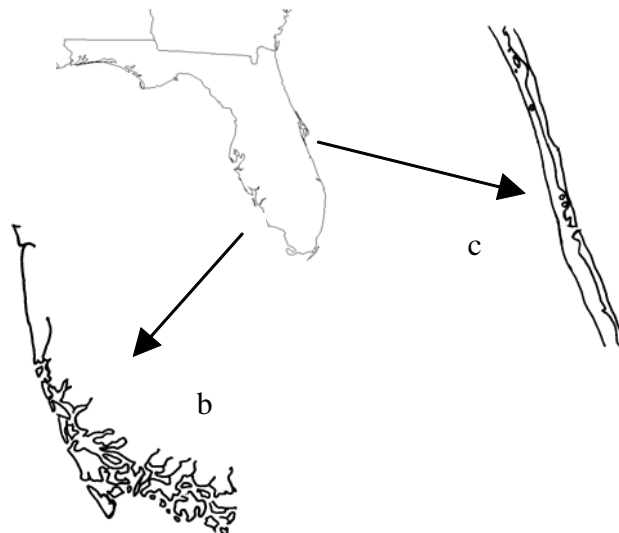


Figure 1. Map showing research locations: a. Windstar (Naples, Florida); b. Rookery Bay (Naples, Florida); c. Ft. Pierce, Florida.

Windstar

Deposition of dredge fill from the Intercoastal Waterway destroyed mangrove forest areas on the eastern side of Naples Bay prior to 1980. The Windstar Golf Course and Multi-Family Community (Windstar, 26°07'N, 81°47'W) (Figure 1) was constructed in 1982 on a 200 ha tract on the east side of Naples Bay and included over 40 ha of undisturbed

mangrove forest and the dredge spoil sites. Restoration of three dredge spoil sites (a total of 6 ha) was undertaken as mitigation for filling mosquito control ditches and destruction of existing *R. mangle* during construction of Windstar. The northernmost of the restoration areas, approximately 1.3 ha in area, was used for this study. After removal of vegetation (mostly *Schinus terebinthifolius*), restoration areas were graded to be completely flooded at mean high tide. More than 10,000 *R. mangle* propagules were collected nearby and planted in August, 1982, with a 97% initial survival rate (Stephen 1984). Subsequent to planting, numerous volunteer seedlings of *L. racemosa* and some *A. germinans* mangroves became established. At the time of this study, some rehabilitated areas were completely vegetated with closed canopies five to six meters in height. However, some sections remain unvegetated where standing water persists. The natural mangrove system adjacent to the mitigation site is a mixed basin forest with *R. mangle*, *A. germinans*, and *L. racemosa* and a fringe forest dominated by *R. mangle*. Aerial photographs from the 1940's (Proffitt and Devlin 1991) demonstrate the forest age is in excess of 50 years.

Ft. Pierce

Research on the east coast of Florida was conducted on North Hutchinson Island adjacent to Big Starvation Cove (Impoundment 33) on the Indian River Lagoon (Ft. Pierce, 27°32'N, 80°20'W) (Figure 1). The Ft. Pierce region is generally microtidal (< 1 m). Fort Pierce (located near North Hutchinson Island) receives an average of 53.7 cm rainfall annually, with more than 60% of that coming between June and October (Southeast Regional Climate Center 2004a). A sea level rise occurs in early fall that lasts approximately three months, after which water levels return to an early summer minimum (Provost 1973). This results in near continuous flooding in mangrove areas during the fall

months (late September to early December) and dry conditions from March to mid-September (except for flooding from heavy rainfall) (Rey *et al.* 1990a).

Officials of St. Lucie County, Florida, installed impoundment dikes with weirs on the Ft. Pierce site during the 1960's in an attempt to control mosquito populations. Impoundment management resulted in an alteration of the natural hydrology of the area by levee construction and control of water levels within the impoundments (Rey *et al.* 1990b). In addition, the exotic invader Brazilian pepper (*Schinus terebinthifolius*) encroached along the impoundment dikes. Active management of Impoundment 33 was halted in the late 1980's. Connections between Impoundment 33 and the Indian River Lagoon currently include a series of continuously open culverts and a 10-m breach on the north edge of the impoundment. Three distinct forest types were examined within this area: a basin forest dominated by *A. germinans* < 8 cm diameter at breast height, a *R. mangle* dominated fringe area across a small [3-5 meter] channel from the impoundment dike ranging between one and three meters wide, and a dwarf area dominated by *A. germinans*. No relatively undisturbed mangrove forest occurred nearby to be used as a reference.

Experimental Design

The basin and fringe sites at Rookery Bay and Windstar and the basin and dwarf sites at the Ft. Pierce had three plots randomly established on each of three transects parallel to the open water (a total of nine plots at each site). Nine fringe plots were established at random intervals 11-20 m apart approximately 3-4 m from the outside edge of the mangroves at Rookery Bay and Windstar, and 1-2 m from the outside edge of the mangroves on the inside of the impoundment at the Ft. Pierce site.

Methods

Forest Structure

The forest structure influences a number of variables including litter fall and macrodetritivore population characteristics. The point-centered quarter method (Cottam and Curtis 1956, Cintrón and Novelli 1984, Day *et al.* 1987) was used to estimate mangrove species composition, tree density, canopy height, basal area, and complexity index for trees over 4 cm Diameter at Breast Height (DBH) in all forests except the Ft. Pierce dwarf forest. Due to the absence of trees with a measurable DBH, nine (9) 10m x 10m plots were established and all trees within the Ft. Pierce dwarf forest plots were counted. These counts were then used to estimate the same parameters (*i.e.*, species composition, tree density, canopy height, basal area, and complexity index).

Environmental Factors

Environmental (*i.e.*, abiotic) factors were monitored at 3-month intervals to aid in interpretation of detritivore differences among seasons, sites and forest types. Interstitial water was collected from the soil with a sipper (McKee *et al.* 1988), and salinity was determined with a refractometer. Temperature was recorded with two (2) max-min thermometers at each site.

During the summer of 1999, four measurements of light levels were taken at each plot with a LiCor quantum radiometer at approximately 1.8 m above the soil surface. Light readings were taken at each site between 10 a.m. and 2 p.m. under clear conditions to ensure consistency among sites. These readings were referenced to values obtained in nearby open areas and are reported as percent of ambient light.

Litter Dynamics

Litter fall rate and standing litter crop, as indicators of productivity and total turnover rate (Olson 1963, Pool *et al.* 1975), were obtained, and composition (proportion of leaves, reproductive parts, and twigs) described. Litter was collected in 0.25 m² (50 x 50 cm) litter traps and retrieved at approximately monthly intervals. Standing litter crop was collected every 3 months approximately 2 m from each litter trap inside ~ 0.2 m² (42 x 42 cm) quadrats during low tide (to maximize soil surface exposure). To minimize impact on other seasonal collections, each standing litter collection area was rotated to a different position around the litter traps. Litter was dried to a constant mass at 70 °C, sorted by species into leaf and reproductive components, and weighed to 0.1 g (Brown 1984, Day *et al.* 1996). Wood was not sorted to species prior to weighing. Leaf fragments, insect frass and debris were summed together into a single category called “other”. Leaf turnover rate was estimated by dividing annual leaf fall rate by average standing stock of litter.

Macrodetritivore Dynamics

Melampus coffeus and crab burrow densities were estimated from the 42 cm x 42 cm standing litter quadrats used for standing litter surveys (*i.e.*, 3 month intervals at low tide). To minimize impact on other seasonal collections, each collection area was rotated to a different position around the litter traps. *Melampus coffeus* found during the initial litter collection were tabulated and released after the litter collection was complete. Since smaller *M. coffeus* are difficult to observe in the field due to cryptic coloration, individuals found during litter sorting (after the litter was oven dried) were also counted; snails without bleached shells were regarded as viable when collected. These two counts were added together to get an estimate for snail density. All *M. coffeus* were placed in 12 size classes by widest shell diameter. Other gastropods were collected and counted in a similar manner.

Leaf litter processing by macrodetritivores was examined in the field by leaf-tethering (Robertson 1986, Proffitt *et al.* 1993). Changes in leaf mass and structure without the influence of macrodetritivores were assessed with litter bag trials. Where possible, undamaged, senescent, non-abscised leaves were gathered from each mangrove species (*i.e.*, *R. mangle*, *A. germinans*, and *L. racemosa*). A high level of herbivory, as seen elsewhere (Johnstone 1981, Farnsworth and Ellison 1991), increased search time for useable leaves. Leaves were photocopied before processing, and photocopies were digitally scanned. Leaf area was determined with the MacFolia (Regent Instruments, Inc., Canada) area analysis software using the digitally scanned leaves. A subset of leaves from each species was used to determine initial leaf area to mass ratio (Figures 2-4). Leaves were then tethered in the field using light monofilament line tied between leaves and small flags.

Tethered leaves were collected from each plot at varying intervals for up to three weeks (Table 1). All foreign material (*e.g.*, soil) was gently washed off the leaves with tap water. Leaves were scored as damaged or undamaged by macrodetritivore type (*i.e.*, crustacean or gastropod) where possible. Leaves were then dried to constant mass and weighed to 0.01 g. Final weight was subtracted from original estimated weight to calculate biomass consumed, and percent mass loss per day was calculated using the series of leaves retrieved from each plot. To estimate mass loss due to leaching, mass change in tethered leaves not visibly damaged by macrodetritivores and leaves in mesh bags were compared with mass loss in damaged leaves.

Change in leaf nutritional content after abscission may have an effect on leaf consumption by macrodetritivores. Therefore, in Fall 1998 and Spring 1999 separate sets of leaves were tethered, retrieved after predetermined intervals (Table 1), washed with deionized water, freeze dried, ground with a Wiley mill (40 micron mesh), and analyzed

with a Leeman Labs Model CE440 CHN/O/S elemental analyzer (Leeman Labs Inc. 55 Technology Dr, Lowell, MA 08151) for carbon and nitrogen content.

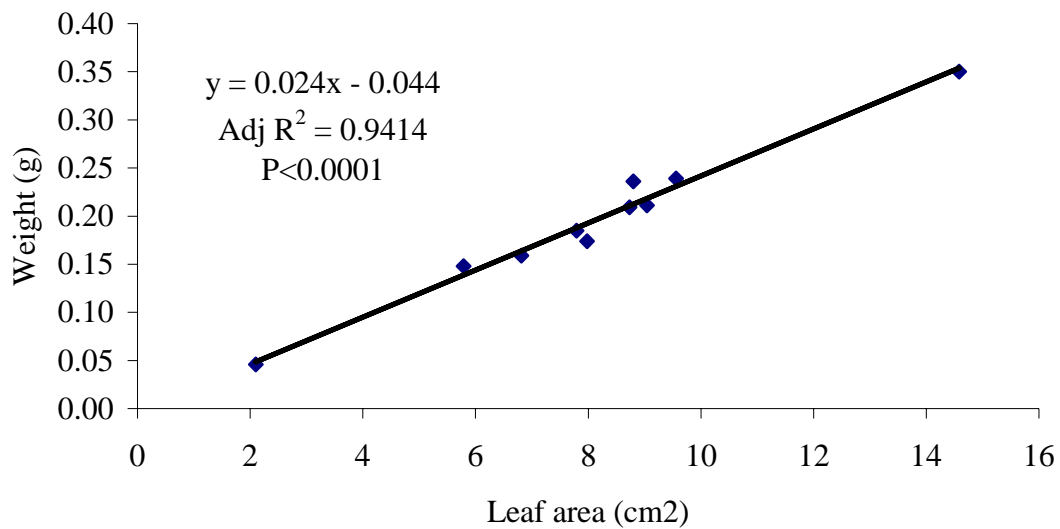


Figure 2. Regression of *A. germinans* leaf area on mass.

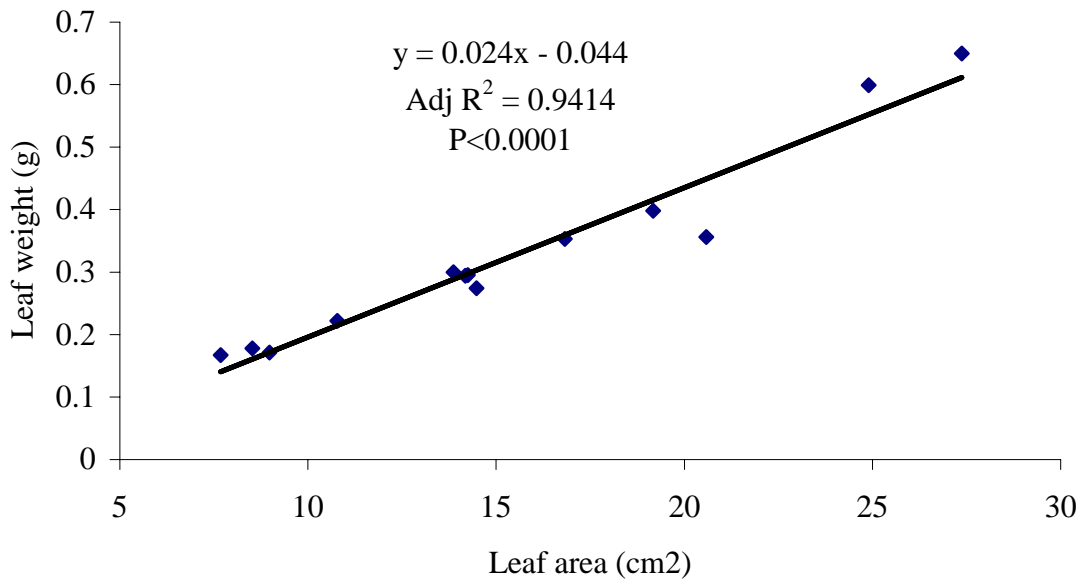


Figure 3. Regression of *L. racemosa* leaf area on mass.

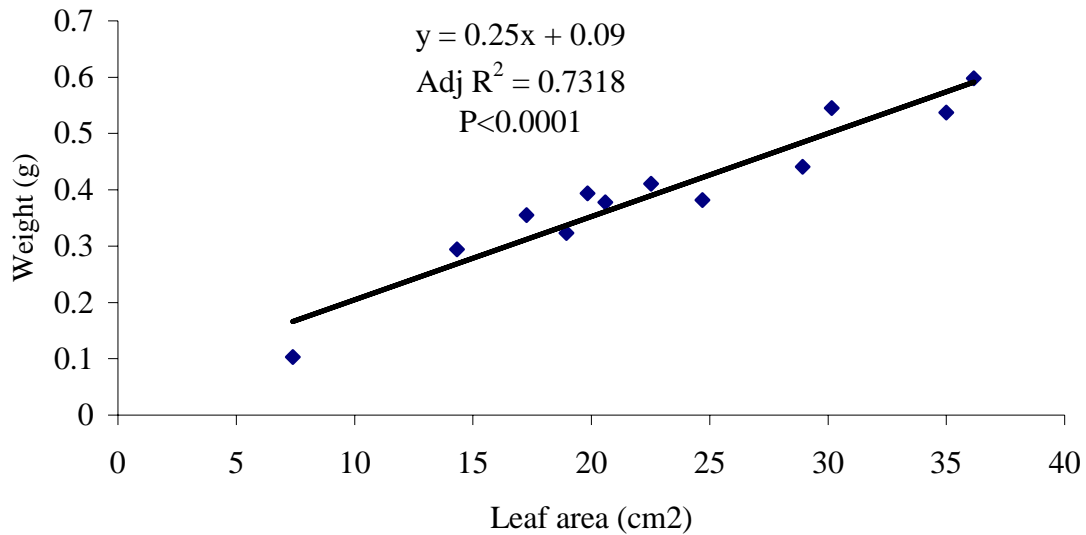


Figure 4. Regression of *R. mangle* leaf area on mass.

Feeding Trials

Captive snails (*M. coffeus*) between 5 and 12 mm shell width were used to determine preferences and feeding rates in the field and laboratory. Prior to all feeding trials, snails were starved for 24 hours. Intact, yellowing leaves from each mangrove species were collected and leaf wet weight was measured. Leaves were presented to replicate groups of snails held in aquaria (laboratory trials) and mesh cages (field trials) designed to exclude predators. To maintain different field conditions and to control snail density while excluding predators, 3 mesh cages containing 10 *M. coffeus* and 2 leaves of each mangrove species were placed at four sites (Rookery Bay basin, Rookery Bay restoration, Windstar Basin, and Windstar Restoration). Leaves were re-weighed after one week to determine biomass loss. To determine if salinity affects the snails' feeding habits, leaves (or leaf sections) of the preferred species (determined in previous experiments) were soaked for 24 hours in water with different salinities (saltwater created with Instant Ocean®) and

presented to four replicate groups of the snails in laboratory aquaria. Snail density in the aquaria was approximately 60 *M. coffeus* m⁻².

Table 1. Retrieval schedule for tethered leaves during detritivore study. Numbers indicate number of days after placement that leaves were retrieved. An “N” indicates leaves used in nutrient analysis were retrieved.

Season	Site	Days			
Fall 1998 (Leaves for nutrient analysis only)					
	Ft. Pierce	0, N	1, N	7, N	14, N
	Naples	0, N	1, N	8, N	14, N
Spring 1999					
	Ft. Pierce	1, N	3	8, N	16
	Naples	1	3, N	8, N	17
Summer 1999					
	Ft. Pierce	1	4	7	14
	Naples	1	4	7	14
Fall 1999					
	Ft. Pierce	1	4	7	14
	Naples	1	4	7	14
Winter 2000					
	Ft. Pierce	1	4	7	14
	Naples	1	4	7	14

Statistical Analysis

All statistical tests were conducted with SAS (SAS Institute 1993). For data gathered once (*e.g.*, tree density, light), simple analysis of variance (ANOVA) was used. A split-plot ANOVA using PROC MIXED was used to analyze seasonal changes in leaf biomass, salinity, standing litter, *M. coffeus* populations, crab burrows, attack rates, and litter degradation. A Tukey analysis was used with LSMEANS to test main effects (site, season,

and where applicable, species) and all interactions. Tests were run to examine differences between location (Rookery Bay vs. Windstar vs. Ft. Pierce), site history (natural vs. restored), and forest type in Naples (restored, basin and fringe) with CONTRAST statements. Correlation analyses were run with PROC CORR to examine relationships between environmental and response variables.

CHAPTER THREE: FOREST STRUCTURE, ENVIRONMENTAL CONDITIONS, AND LITTER DYNAMICS

Forest Structure

Rhizophora mangle was the dominant species in the basin and fringe mangrove forests in Naples (Table 2). Relative density of *R. mangle* at these sites ranged from 58.3% to 92.9%. The Rookery Bay restoration site was dominated by *L. racemosa*, and the Windstar restoration site had a mixture of *R. mangle* and *L. racemosa* that co-dominated the site. *Avicennia germinans* had the highest relative density in the Ft. Pierce basin (67.5%) and *L. racemosa* had the highest relative density in the Ft. Pierce fringe site. The Ft. Pierce dwarf site was nearly a monoculture of small (*i.e.*, < 2 m in height) *A. germinans* (relative density of 99.8%) with very few *L. racemosa* and no *R. mangle*.

Table 2. Mangrove forest structure from Rookery Bay, Windstar, and Ft. Pierce sites.

Location	Total Density (stems ha ⁻¹)	Dominant Tree(s)	% Relative Density	% Relative Dominance
Ft. Pierce Basin	7947	<i>A. germinans</i>	67.5	65.9
Ft. Pierce Fringe	16168	<i>L. racemosa</i>	46.4	44.2
Ft. Pierce Dwarf	17866	<i>A. germinans</i>	99.8	N/A
Rookery Bay Basin	2019	<i>R. mangle</i>	92.0	74.1
Rookery Bay Fringe	3986	<i>R. mangle</i>	92.9	70.1
Rookery Bay Restoration	10612	<i>L. racemosa</i>	92.9	86.3
Windstar Basin	2293	<i>R. mangle</i>	58.3	40.1
Windstar Fringe	5735	<i>R. mangle</i>	88.1	88.4
Windstar Restoration	6830	<i>R. mangle</i> / <i>L. racemosa</i>	43/48	53/46

The restoration sites in Naples and the basin and fringe sites on the Ft. Pierce have an important characteristic indicative of early regenerating forests: a high density of small diameter trees (Ball 1980, Blanchard and Prado 1995, McKee and Faulkner 2000). Also, *L. racemosa*, characterized as a shade-intolerant, early-successional species (Ball 1980), was

either dominant or co-dominant at the restoration sites although only *R. mangle* had been planted (Stephen 1983, McKee and Faulkner 1999). The Naples basin and fringe sites had trees with much greater basal diameter and height compared to all other sites, characteristic of mature mangrove forests. Both of the study areas within the Naples restoration sites, from their location within the landscape, may be expected to naturally support a basin-type forest, similar to the nearby reference forests. The Ft. Pierce dwarf mangrove forest, a nearly pure stand of short (< 2 m tall) *A. germinans* interspersed with *L. racemosa*, was unlike any other site within this study with regard to structure and species composition.

The restoration sites, with large number of small trees (primarily *L. racemosa*) may be acting like early successional areas (Stevenson *et al.* 1999). Personal observations indicate that small openings (as a result of single tree falls) in mature mangrove forests (on the order of > 0.1 ha) are generally re-populated by *R. mangle*, while the restoration sites in this study (areas greater than 0.5 ha) were colonized by *L. racemosa*.

Environmental Factors

Porewater Salinity

Porewater salinity varied both by site and season during the project (Figure 5). The Ft. Pierce dwarf forest had the highest overall porewater salinity mean of 63.6 ± 2.7 ppt and the Rookery Bay basin forest site had the lowest overall porewater salinity mean of 28.2 ± 1.3 ppt (Table 3). Fall 1999 had the lowest overall salinity mean (35.2 ± 2.0 ppt) and spring 1999 had the highest overall salinity mean (48.7 ± 1.5 ppt) (Figure 5). The lowest single-season porewater salinity mean occurred in the Rookery Bay basin forest during summer 1998 (20.6 ± 2.5 ppt). The highest single-season porewater salinity mean occurred in the Ft. Pierce dwarf forest during summer 1999 (82.3 ± 1.6 ppt). The single highest observed porewater salinity value (93 ppt) was from a Ft. Pierce dwarf forest plot during spring 1999.

The single lowest porewater salinity value (10 ppt) occurred summer 1999 in a Rookery Bay basin forest plot.

Seasonal patterns in porewater salinity differed among the sites (Table 3). Porewater salinity seasonal patterns were similar at Rookery Bay and Windstar, with highest values usually seen in fall or winter. Highest salinity values at the Ft. Pierce sites were during spring or summer. No differences in porewater salinity were observed among the Rookery Bay sites during a single season. However, seasonal variation occurred, with spring 1999 and winter 2000 higher than summer 1999 and fall 1999. Similar values and seasonal variations are reported elsewhere for the Rookery Bay and Windstar sites (Twilley *et al.* 1986, McKee 1993, McKee and Faulkner 2000). Rey *et al.* (1992) reported similar porewater salinities at a nearby Ft. Pierce site. Seasonality due to rainfall is not universal, as reports from other areas have shown no seasonal variation in porewater salinity, and tidal inundation may be a more important factor in these areas (*e.g.*, Day *et al.* 1996, Twilley *et al.* 1997). Dwarf or dying mangrove forests often have very high salinity values (Cintrón *et al.* 1978, Day *et al.* 1996, Cardona and Botero 1998), which, although not necessarily the only cause, are indicators of a stressed system.

Differences in porewater salinity also occurred among the areas (*i.e.*, Ft. Pierce, Rookery Bay, and Windstar) and forest types (Table 4). The basin and fringe sites at Ft. Pierce were higher in porewater salinity than the basin and fringe sites at both of the Naples (*i.e.*, Rookery Bay and Windstar) sites ($P \leq 0.001$). The Windstar sites had higher porewater salinity than the Rookery Bay sites ($P \leq 0.001$). Porewater salinity in the fringe sites was higher than in the nearby basin sites ($P \leq 0.05$). The Windstar restoration site usually had higher porewater salinity values compared to the Windstar basin site, while the Rookery Bay restoration and basin sites were very similar with respect to porewater salinity (Figure 5).

Table 3. Comparison of differences in porewater salinity (ppt) among nine mangrove forest sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.

Source	F	P	Porewater salinity (ppt)
Site	33.97	***	
Ft. Pierce Dwarf			63.6 ± 2.7^a
Ft. Pierce Basin			59.7 ± 1.8^a
Ft. Pierce Fringe			44.7 ± 0.8^b
Windstar Restoration			40.9 ± 2.1^{bc}
Windstar Basin			37.3 ± 1.9^{bcd}
Windstar Fringe			30.6 ± 1.2^{de}
Rookery Bay Restoration			29.8 ± 1.3^{de}
Rookery Bay Basin			29.1 ± 1.5^{de}
Rookery Bay Fringe			28.2 ± 1.3^e
Season	75.61	***	
Spring 1999			48.7 ± 1.5^a
Summer 1999			40.1 ± 2.0^b
Winter 2000			37.7 ± 1.1^b
Fall 1999			35.2 ± 2.0^c
Season x site	17.51	***	

Notes: Post-ANOVA Tukey analyses with F-ratio and P-value presented with mean \pm 1 SE. *** indicates $P \leq 0.0001$. Different superscripts within main effects indicate significant differences ($P \leq 0.05$).

Porewater salinity in the Ft. Pierce fringe site (44.7 ± 0.8 ppt) was significantly lower than both the basin (59.7 ± 1.8 ppt) and dwarf (63.6 ± 2.7 ppt) forests. Salinity differences among areas (*i.e.*, Rookery Bay, Windstar, and the Ft. Pierce) may be due at least in part to the difference in saline contributions of nearby water bodies to each mangrove forest. The Rookery Bay sites along Henderson Creek (a brackish-water creek) had the lowest mean salinities, the Windstar sites (adjoining Naples Bay, a water body with salinities reflecting the Gulf of Mexico) were intermediate, and the Ft. Pierce sites (situated on the Indian River Lagoon, a high-salinity water body) had the highest mean salinities. The isolated nature of

all of the Ft. Pierce sites (within a mosquito impoundment) may also decrease tidal exchange and allow evaporation to raise the salinity. The highly seasonal Florida rainfall (and resulting stormwater runoff) probably plays the largest role in the porewater salinity seasonality at the Naples sites while tidal inundation (occurring most frequently in the winter) may be the driving factor at the Ft. Pierce sites (Rey et al. 1992). The Naples sites had lowest salinity values in the summer and fall, the period of regular afternoon showers and frequent high rainfall events (Twilley *et al.* 1986).

Salinity in the Rookery Bay restoration site was very similar to the nearby basin site, while mean porewater salinity at the restoration site at Windstar was often more than 10 ppt

Table 4. Comparisons of differences in porewater salinity between different areas and forest types in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.

Source	F	P	Porewater Salinity (ppt)
Area			
Rookery Bay v. Windstar	25.50	***	
Ft. Pierce v. Rookery Bay	222.20	***	
Ft. Pierce v. Windstar	97.15	***	
Ft. Pierce			52.2 ± 1.3 ^a
Windstar			33.9 ± 1.6 ^b
Rookery Bay			28.6 ± 1.4 ^c
Forest type			
Naples Basin v. Restored	10.15	NS	
Naples Basin v. Fringe	5.71	*	
Naples Fringe v. Restored	7.68	**	
Naples Restored			35.3 ± 1.7 ^a
Naples Basin			33.2 ± 1.7 ^a
Naples Fringe			29.4 ± 1.2 ^b

Notes: Post-ANOVA Tukey analyses with F-ratio and P-value presented with mean ± 1 SE. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.0001$, NS = not significant at $P \leq 0.05$. Different superscripts within area and forest type comparisons indicate significant differences ($P \leq 0.05$).

higher than at the nearby basin site (Figure 5). This may or may not indicate that the hydrology of the restoration site at Rookery Bay could more closely match the natural conditions than the Windstar restoration site. McKee and Faulkner (2000) noted that soils in the Naples basin sites had a thicker peat layer than at the restoration sites. This could contribute to greater moisture retention, which would mean that other hydrological factors in the restoration site offset that difference. For example, the Rookery Bay restoration site could be flushed more frequently with brackish water from Henderson Creek if it is at a lower elevation (possibly due to construction activities during restoration) compared to the basin site. Several areas in the Windstar restoration site were consistently inundated with shallow standing water that could increase local porewater salinity through evaporation. Differences in porewater salinity between forest types (basin and fringe) followed similar patterns previously reported in other studies, with basin forests having higher salinity than fringe forests, generally attributed to the basin forests having less frequent tidal exchange than the fringe forests (*e.g.*, Lugo 1980, Twilley *et al.* 1986, Day *et al.* 1996). The extremely high porewater salinity values seen in the Ft. Pierce dwarf site could be partly attributed to the openness of the canopy and resulting high temperatures (see discussion below). This would lead to a more rapid evaporation rate than in the other study sites and elevate porewater salinity levels.

Light

Light levels at the Ft. Pierce dwarf site were significantly higher than at any other site (Table 5). Measures of leaf area index in Belize demonstrated the same situation with a *R. mangle* dwarf stand (Feller 1995). Mean corrected light values were less than 20% of the ambient light at all other sites.

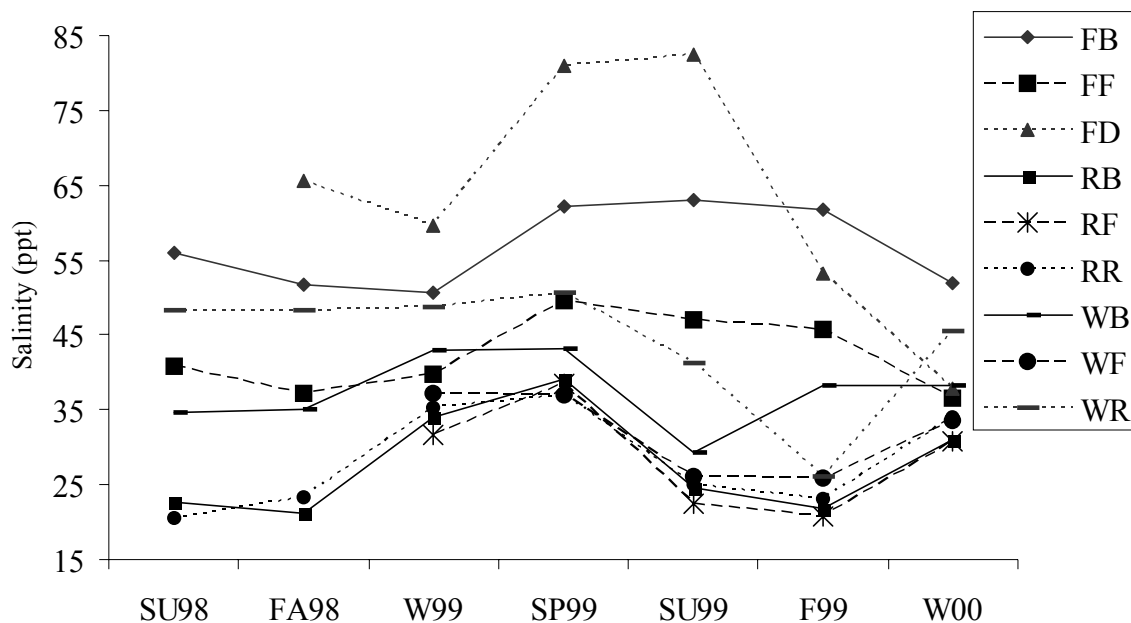


Figure 5. Porewater salinity values (ppt) for each site from Summer 1998 through Winter 2000 measured in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.

Temperature

The Ft. Pierce dwarf site usually exhibited the highest mean high temperature (Figure 6). The higher maximum temperatures seen in the Ft. Pierce dwarf site can be partly attributed to the higher light levels at that site as compared to all others (Figure 7). The high temperatures at the Ft. Pierce dwarf site may also be contributing to the high porewater salinity levels in that site (Figure 8) by increasing the evaporation rate relative to other sites. Temperatures greater than 40 °C occurred at four different sites (Ft. Pierce dwarf, Ft. Pierce basin, Windstar restoration, and Rookery Bay restoration) and during two sampling periods (spring 1999 and summer 1999). The temperature never went below 0 °C at any of the sites while being monitored (Figure 9). All of the lowest recorded temperatures (less than 10 °C) occurred during winter 2000.

Table 5. Light levels corrected for ambient light for nine sites in Southwest Florida, measured during summer 1999. Each value is based on nine plots, with 4 nearly simultaneous readings taken at each plot and referenced to readings taken in full light. Values are percentage of full light.

Area	Percent of Ambient Light
Rookery Bay	
Basin	17.5 ± 5.5^a
Fringe	6.3 ± 1.2^a
Restoration	5.8 ± 1.1^a
Windstar	
Basin	11.3 ± 1.6^a
Fringe	6.1 ± 0.7^a
Restoration	15.2 ± 5.1^a
Fort Pierce	
Basin	5.1 ± 1.2^a
Fringe	10.2 ± 2.3^a
Dwarf	72.4 ± 7.9^b
Notes: Tukey analyses with mean \pm 1 SE. Different superscripts indicate significant differences among sites ($P \leq 0.05$).	

Litter Dynamics

Litter Fall

Litter fall rates at the sites (Table 6) were within the range of that reported for mangroves in South Florida (*e.g.*, Twilley *et al.* 1986, McKee and Faulkner 2000), and in other regions of the world (*e.g.*, Robertson and Daniel 1989b, Day *et al.* 1996, Twilley *et al.* 1997, Wafar *et al.* 1997). The Ft. Pierce dwarf forest had a litter fall rate of $0.5 \pm 0.1 \text{ gm}^{-2} \text{ d}^{-1}$, less litter fall than at any other site, and litter fall at the other sites did not differ from one another. However, when considered together, litter fall from the set of three Rookery Bay

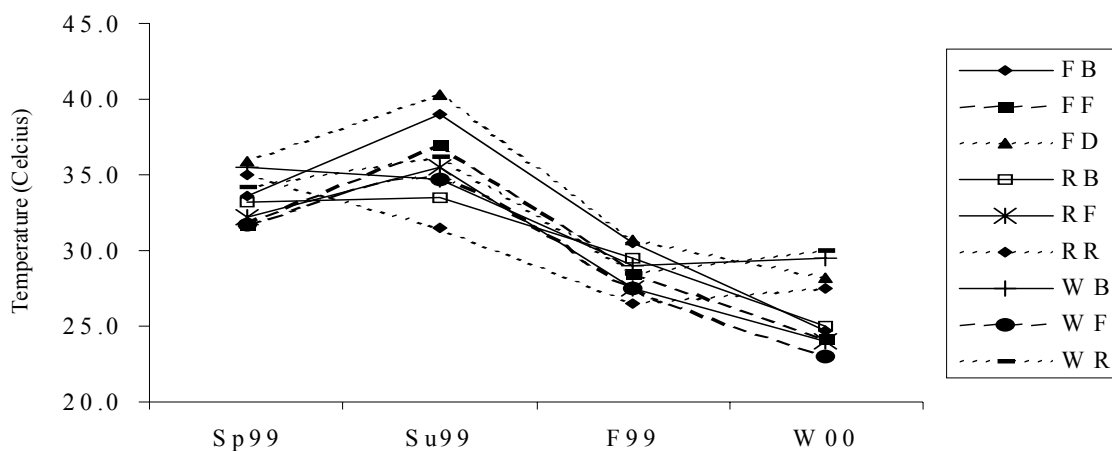


Figure 6. Mean maximum temperatures measured in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida, from Summer 1998 through Winter 2000. Values are °C. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.

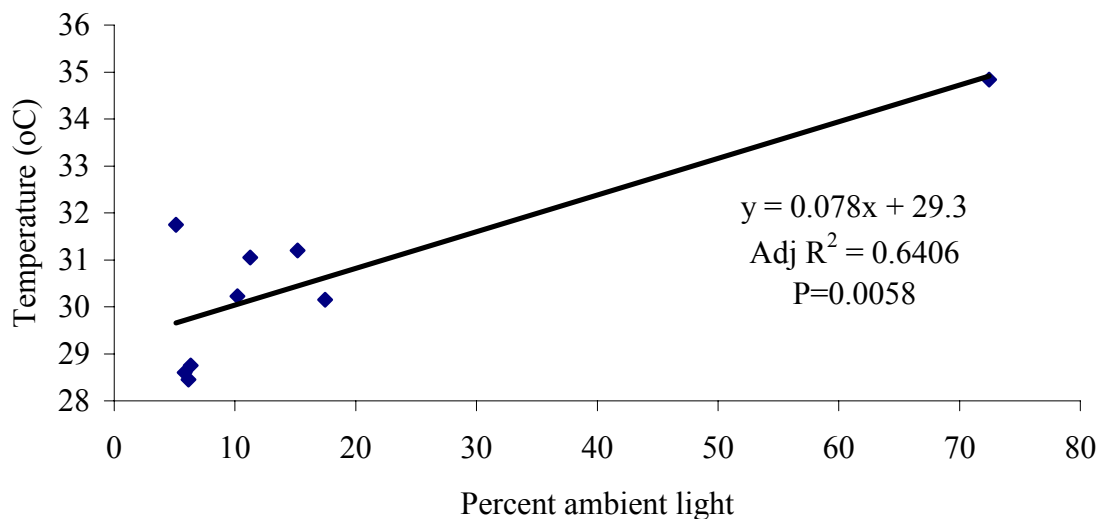


Figure 7. Regression of light and maximum temperature in nine mangrove forests in Naples and Fort Pierce, Florida.

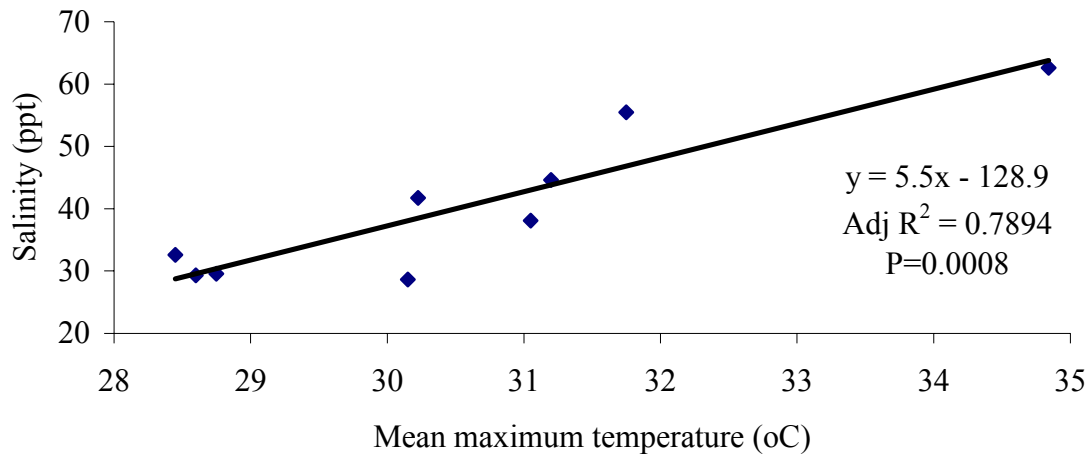


Figure 8. Regression of maximum temperature and salinity at nine sites in Naples and Fort Pierce, Florida.

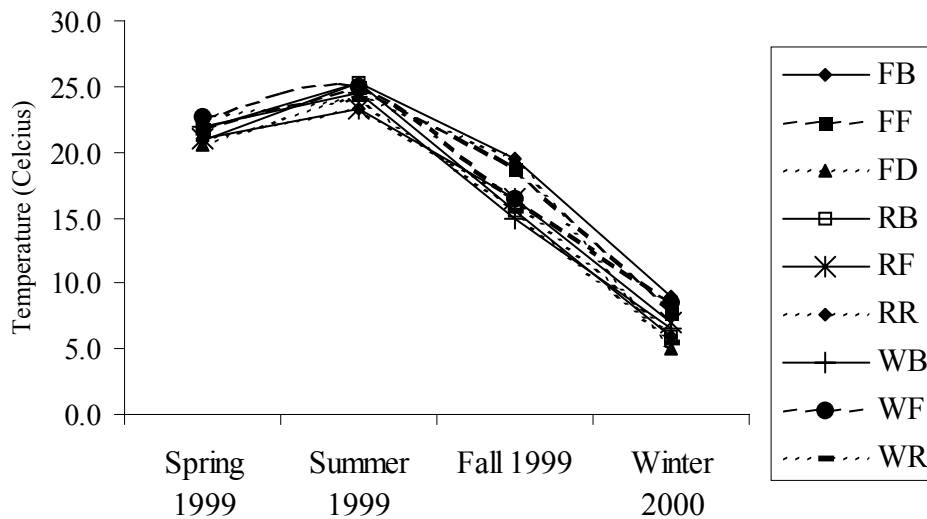


Figure 9. Average minimum temperatures measured in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida. Values are $^{\circ}\text{C}$. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.

sites (basin, fringe, and restoration) was higher than the set of Windstar sites (Table 6). Both the Rookery Bay and Windstar areas had greater amounts of litter fall than the Fort Pierce areas. No differences were observed among basin, fringe and restoration forest types in Naples (Table 7). Leaves from the three mangrove species accounted for more than 50% of the litter fall in all sites (Table 6). No other litter component (*i.e.*, reproductive tissues, wood, or frass) accounted for more than 25% of the litter fall at any given site. Leaf litter fall varied greatly among the different sites and was usually dominated by *R. mangle* (Table 6). The litter fall composition was comparable to that reported in other mangrove forests, with leaves usually making up the largest portion (*e.g.*, Clough *et al.* 2000, Day *et al.* 1996). Woody and reproductive components (*e.g.*, flowers and propagules) were highly seasonal and variable. Leaf litter fall and standing litter on most of the sites was a reflection of the dominant tree (or trees) at that site. Salinity was negatively correlated with litter fall (*e.g.*, Twilley *et al.* 1986, Day *et al.* 1996, McKee and Faulkner 2000) (Figure 10).

Litter Standing Stocks

The standing litter crop biomass varied widely within and among sites and ranged from 29.3 g m⁻² (in the Ft. Pierce dwarf site) to 559.3 g m⁻² (in the Windstar restoration site), with an overall mean of 269.0 g m⁻² (Table 8). This is higher than has previously been reported for Southwest Florida mangrove forests (Twilley *et al.* 1986, Twilley *et al.* 1997), but within the range of standing litter crops found elsewhere (*e.g.*, Lee 1989a, Day *et al.* 1996). Seasonal differences in standing litter crop did not occur (Table 9). Standing litter at the Windstar sites was higher than at the Rookery Bay and Ft. Pierce sites (Table 10).

Table 6. Components of litter fall from nine mangrove forest sites in Naples (Rookery Bay and Windstar) and Ft. Pierce, Florida. For Ft. Pierce sites sample period = 378 days (17 April 1999 through 30 April 2000), for Naples sites sample period = 368 days (31 March 1999 through 3 April 2000). *Rhizophora mangle* reproductive tissues include flowers, propagules,. *A. germinans* reproductive tissues include flowers and propagules. *L. racemosa* reproductive tissues include flowers and seeds. Miscellaneous includes unidentifiable leaf fragments, frass, and *R. mangle* stipules. N = 9 for all sites. Values are g dry weight m⁻² day⁻¹ ± 1 SE.

	Ft. Pierce Basin	Ft. Pierce Fringe	Ft. Pierce Dwarf
<i>R. mangle</i> leaves	0.2 ± 0.1	1.5 ± 0.1	0.0 ± 0.0
<i>R. mangle</i> reproductive tissues	0.0 ± 0.0	0.6 ± 0.1	0.0 ± 0.0
<i>A. germinans</i> leaves	1.0 ± 0.1	0.2 ± 0.0	0.3 ± 0.1
<i>A. germinans</i> reproductive tissues	0.1 ± 0.0	0.0 ± 0.0	0.1 ± 0.0
<i>L. racemosa</i> leaves	0.6 ± 0.3	0.3 ± 0.1	0.1 ± 0.0
<i>L. racemosa</i> reproductive tissues	0.3 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Wood	0.5 ± 0.1	0.2 ± 0.0	0.0 ± 0.0
Miscellaneous	0.1 ± 0.0	0.3 ± 0.0	0.1 ± 0.0
Total	2.8 ± 0.4	3.1 ± 0.2	0.5 ± 0.1

Table 6 (continued).

	Rookery Bay Basin	Rookery Bay Fringe	Rookery Bay Restoration
<i>R. mangle</i> leaves	1.3 ± 0.1	1.6 ± 0.1	0.5 ± 0.1
<i>R. mangle</i> reproductive tissues	0.7 ± 0.2	0.6 ± 0.1	0.2 ± 0.1
<i>A. germinans</i> leaves	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.0
<i>A. germinans</i> reproductive tissues	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
<i>L. racemosa</i> leaves	0.7 ± 0.2	0.6 ± 0.2	1.9 ± 0.2
<i>L. racemosa</i> reproductive tissues	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.0
Wood	0.3 ± 0.1	0.3 ± 0.1	0.4 ± 0.1
Miscellaneous	0.3 ± 0.0	0.3 ± 0.0	0.2 ± 0.0
Total	3.7 ± 0.4	3.6 ± 0.4	3.4 ± 0.2

Table 6 (continued).

	Windstar Basin	Windstar Fringe	Windstar Restoration
<i>R. mangle</i> leaves	0.9 ± 0.1	1.3 ± 0.1	1.0 ± 0.2
<i>R. mangle</i> reproductive	0.2 ± 0.1	0.6 ± 0.2	0.4 ± 0.2
<i>A. germinans</i> leaves	0.6 ± 0.1	0.0 ± 0.0	0.1 ± 0.1
<i>A. germinans</i> reproductive	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
<i>L. racemosa</i> leaves	0.7 ± 0.3	0.6 ± 0.2	0.7 ± 0.2
<i>L. racemosa</i> reproductive	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Wood	0.2 ± 0.0	0.2 ± 0.1	0.1 ± 0.0
Miscellaneous	0.4 ± 0.0	0.3 ± 0.0	0.3 ± 0.0
Total	3.0 ± 0.2	3.2 ± 0.2	2.6 ± 0.3

Table 7. Comparisons of litter fall between different areas and forest types in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.

Source	F	P	Litter Fall
Area			
Rookery Bay v. Windstar	6.01	*	
Ft. Pierce v. Rookery Bay	40.94	***	
Ft. Pierce v. Windstar	15.58	**	
Rookery Bay			3.2 ± 0.3^a
Windstar			2.7 ± 0.2^b
Ft. Pierce			2.4 ± 0.2^c
Forest Type			
Naples Basin v. Restored	1.60	NS	
Naples Basin v. Fringe	0.04	NS	
Naples Fringe v. Restored	2.15	NS	
Naples Fringe			3.0 ± 0.3^a
Naples Basin			2.9 ± 0.2^a
Naples Restoration			2.5 ± 0.3^a

Note: Post-ANOVA Tukey analyses with F-ratio and P-value presented with mean \pm 1 SE. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.0001$, NS = not significant at $P = 0.05$. Different superscripts within area and forest type comparisons indicate significant differences ($P \leq 0.05$).

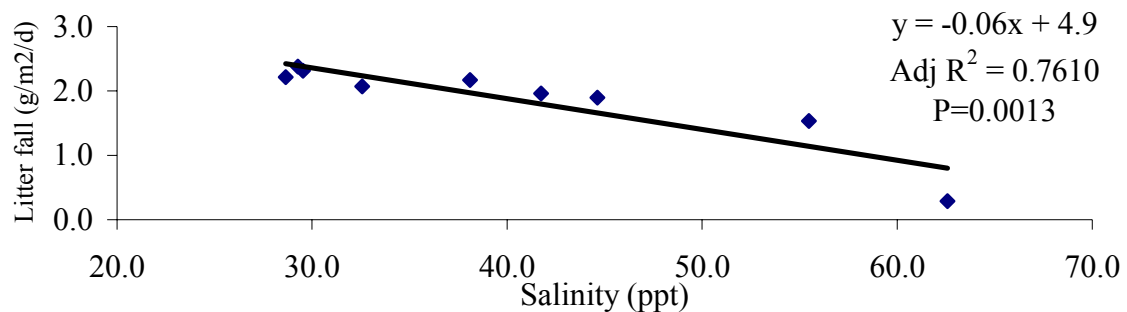


Figure 10. Regression of soil salinity and leaf litter fall at nine mangrove forest sites in Naples and Ft. Pierce, Florida.

Standing litter had a relatively large woody component at all sites. Wood contributed from 13.5% to 56.4% of the standing litter, and leaves contributed from 19.3% to 44.4% of the standing litter (Table 8). As reported elsewhere (McKee and Faulkner 2000), this is most likely due to the slow decomposition rates of the woody debris relative to other litter types. *Rhizophora mangle* leaves were usually a much greater component of the standing litter than either *A. germinans* or *L. racemosa* (Table 8). There was a slight relationship between litter fall and standing litter (Figure 11) at the nine sites. This indicates that leaf degradation or other factors such as tidal export play a differential role among the sites.

Leaf Turnover Rates

The leaf turnover ratio reflects the net effect of degradation, decomposition, and tidal export/import processes. A comparison of leaf litter turnover rate with leaf consumption by macrodetritivores will give an estimate of the impact of the latter process on litter dynamics at each site. Leaf turnover was usually higher in the fringe forests compared to other forest types (Figure 12).

Site-specific differences in leaf turnover rates between species occurred. For example, *A. germinans* had the highest turnover rate at both of the Naples fringe forests (*i.e.*, Windstar and Rookery Bay), and *L. racemosa* had the highest turnover rate at both of the Naples restoration forests (Figure 12). Calculated values were similar to those reported elsewhere (Pool et al. 1963, Day et al. 1996). The turnover rate generally decreased with increasing salinity levels (Figure 13).

Table 8. Components of standing litter fall from nine mangrove forest sites in Naples (Rookery Bay and Windstar) and Ft. Pierce, Florida. *Rhizophora mangle* reproductive tissues include flowers, propagules,. *A. germinans* reproductive tissues include flowers and propagules. *L. racemosa* reproductive tissues include flowers and seeds. Miscellaneous includes unidentifiable leaf fragments, frass, and *R. mangle* stipules. N = 36 for all sites. Values are g dry weight m⁻² ± 1 SE.

	Ft. Pierce Basin	Ft. Pierce Fringe	Ft. Pierce Dwarf
<i>R. mangle</i> leaves	8.6 ± 2.9	56.6 ± 8.6	0.0 ± 0.0
<i>R. mangle</i> reproductive tissues	20.2 ± 7.1	64.7 ± 11.5	0.0 ± 0.0
<i>A. germinans</i> leaves	23.5 ± 2.3	7.1 ± 1.0	22.4 ± 3.6
<i>A. germinans</i> reproductive tissues	3.0 ± 1.0	0.2 ± 0.2	1.2 ± 0.5
<i>L. racemosa</i> leaves	32.2 ± 9.0	13.4 ± 2.2	5.5 ± 1.5
<i>L. racemosa</i> reproductive tissues	4.9 ± 1.6	1.3 ± 0.6	0.6 ± 0.2
Wood	131.1 ± 26.3	97.2 ± 11.2	2.9 ± 1.1
Miscellaneous	16.8 ± 2.3	17.9 ± 1.7	16.3 ± 2.3

Table 8 (continued).

	Rookery Bay Basin	Rookery Bay Fringe	Rookery Bay Restoration
<i>R. mangle</i> leaves	84.7 ± 10.0	54.6 ± 8.8	35.6 ± 4.2
<i>R. mangle</i> reproductive tissues	77.6 ± 12.2	95.1 ± 24.4	60.3 ± 9.9
<i>A. germinans</i> leaves	6.6 ± 1.5	2.0 ± 0.7	3.4 ± 1.1
<i>A. germinans</i> reproductive tissues	0.3 ± 0.2	0.2 ± 0.1	0.1 ± 0.1
<i>L. racemosa</i> leaves	24.3 ± 6.4	13.2 ± 2.5	50.1 ± 6.2
<i>L. racemosa</i> reproductive tissues	2.9 ± 0.8	13.5 ± 9.5	0.8 ± 0.2
Wood	186.6 ± 31.9	157.7 ± 34.3	129.6 ± 20.7
Miscellaneous	28.8 ± 4.5	18.2 ± 4.1	15.7 ± 1.8

Table 8 (continued).

	Windstar Basin	Windstar Fringe	Windstar Restoration
R. mangle leaves	119.0 ± 17.2	60.7 ± 7.0	192.2 ± 30.0
R. mangle reproductive tissues	57.5 ± 11.1	29.8 ± 7.6	43.4 ± 8.2
A. germinans leaves	17.6 ± 2.9	0.7 ± 0.3	14.4 ± 4.0
A. germinans reproductive tissues	0.0 ± 0.0	0.4 ± 0.4	0.0 ± 0.0
L. racemosa leaves	32.1 ± 7.8	11.4 ± 2.6	38.5 ± 6.8
L. racemosa reproductive tissues	0.1 ± 0.0	3.0 ± 2.9	0.1 ± 0.0
Wood	209.9 ± 38.2	53.5 ± 16.5	120.7 ± 18.2
Miscellaneous	38.2 ± 7.5	11.5 ± 2.1	40.1 ± 8.2

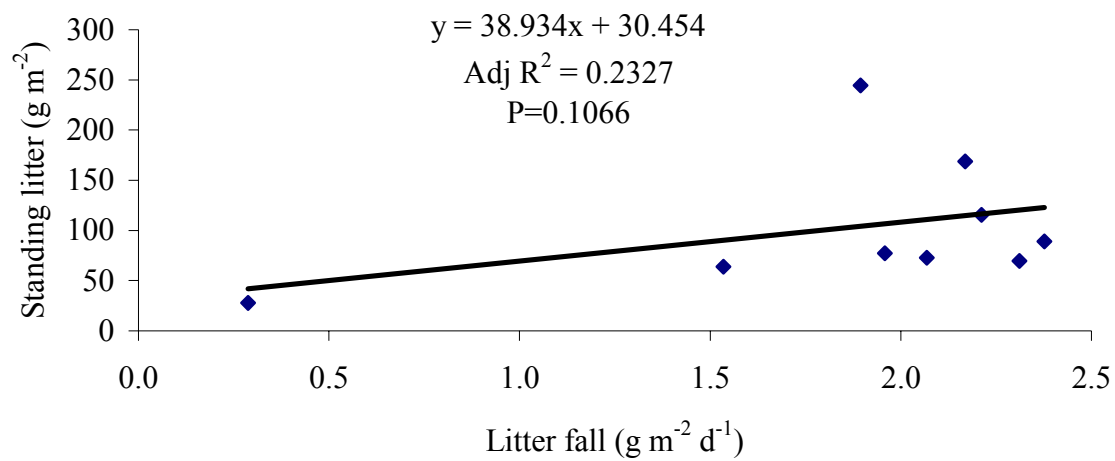


Figure 11. Regression of litter fall and standing litter at nine mangrove forest sites in Naples and Fort Pierce, Florida.

Table 9. Comparison of differences in standing litter for main effects and interaction between sites and seasons in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida from spring 1999 through winter 2000.

Source	F	P	Standing litter (g m ⁻²)
Site	11.49	***	
Windstar Basin			513.2 ± 48.8 ^a
Windstar Restoration			558.2 ± 68.2 ^a
Rookery Bay Basin			450.9 ± 49.7 ^{ab}
Ft. Pierce Fringe			390.4 ± 53.1 ^{bc}
Rookery Bay Fringe			321.7 ± 62.1 ^{abc}
Rookery Bay Restoration			299.0 ± 32.1 ^{bc}
Ft. Pierce Basin			196.3 ± 25.1 ^{bc}
Windstar Fringe			174.9 ± 26.8 ^{cd}
Ft. Pierce Dwarf			28.3 ± 3.9 ^d
Season	0.07	NS	
Fall 1999			301.5 ± 30.5 ^a
Summer 1999			301.1 ± 29.4 ^a
Spring 1999			295.3 ± 33.9 ^a
Winter 2000			286.2 ± 34.0 ^a
Season x site	1.58	*	

Notes: Post-ANOVA Tukey analyses with F-ratio and P-value presented with Mean ± 1 SE. * $P \leq 0.05$, *** $P \leq 0.0001$, NS = no significance at $P = 0.05$. Different superscripts within main effects indicate significant differences ($P \leq 0.05$).

Table 10. Comparisons of differences in standing litter between different areas and forest types in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.

Source	F	P	Standing litter (g m ⁻²)
Area			
Rookery Bay v. Windstar	2.05	NS	
Ft. Pierce v. Rookery Bay	11.18	**	
Ft. Pierce v. Windstar	3.66	NS	
Rookery Bay			386.3 ± 55.9 ^a
Windstar			344.1 ± 37.8 ^{ab}
Ft. Pierce			293.4 ± 39.1 ^b
Forest type			
Naples Basin v. Restored	2.86	NS	
Naples Basin v. Fringe	18.82	***	
Naples Fringe v. Restored	7.01	*	
Naples Basin			482.1 ± 49.3 ^a
Naples Restored			428.6 ± 50.2 ^a
Naples Fringe			248.3 ± 44.4 ^b
Note: Post-ANOVA Tukey analyses with F-ratio and P-value presented with mean ± 1 SE. * $P \leq 0.05$, ** $P \leq 0.001$, *** $P \leq 0.0001$, NS = not significant at $P = 0.05$. Different superscripts within area and forest type comparisons indicate significant differences ($P \leq 0.05$).			

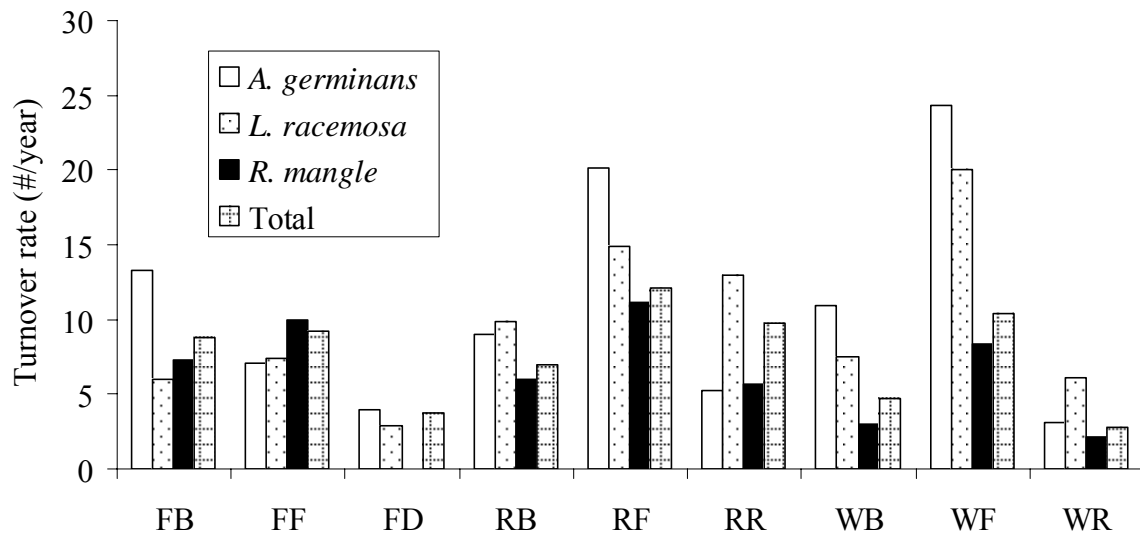


Figure 12. Mangrove leaf turnover rates for nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida. Values are number of times leaves turn over in 1 year. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.

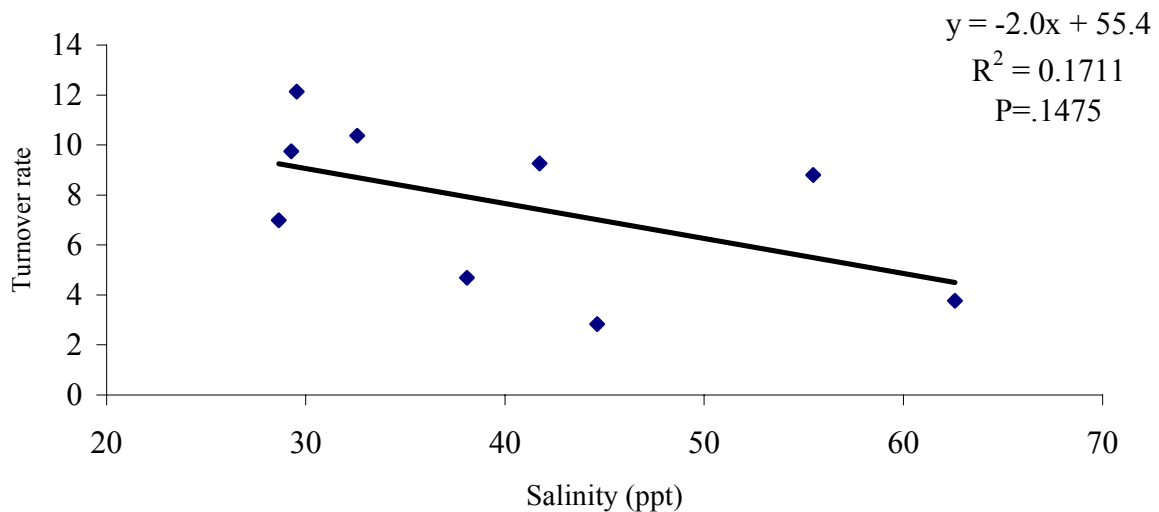


Figure 13. Regression of porewater salinity and turnover rate at nine mangrove forest sites in Naples and Fort Pierce, Florida.

CHAPTER FOUR: MACRODETRITIVORE DYNAMICS

Macrodetritivore Densities

Melampus coffeus Densities

As with other estimates of gastropod populations (Holle and Dineen 1957, Mook 1973, Joyce and Weisberg 1986, Donnay and Beissinger 1993, Peck *et al.* 1994), *M. coffeus* densities at these sites were patchy and variable (Table 11). *Melampus coffeus* occurred in relatively high numbers at all Rookery Bay sites. The highest densities were observed at the Windstar restoration site (128.8 ± 43.0 *M. coffeus* m⁻²), although relatively few *M. coffeus* were observed in the other Windstar sites (Figure 14). Densities of *M. coffeus* were within the range of other studies for this genus (Mook 1973, Price 1980).

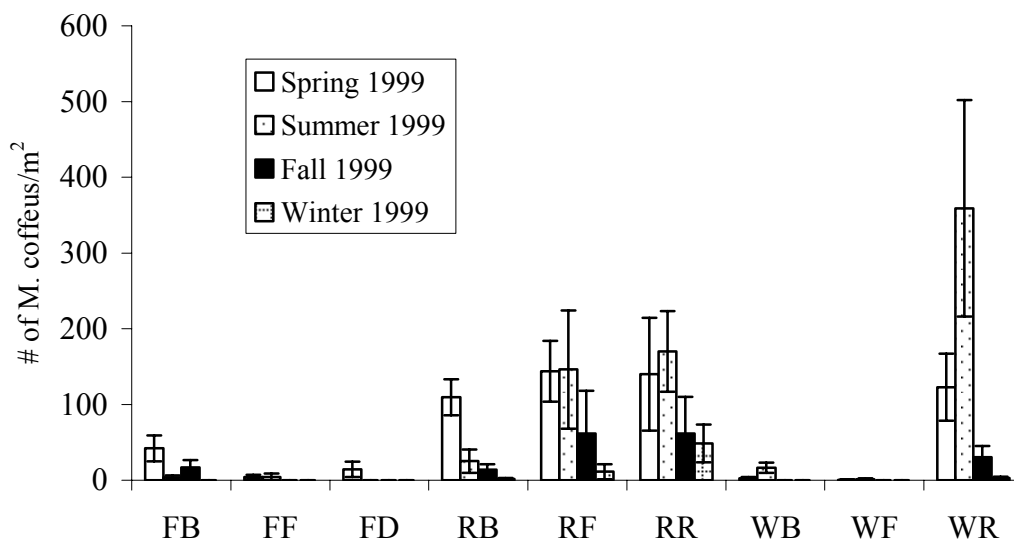


Figure 14. *Melampus coffeus* densities (# of *M. coffeus* m⁻²) at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.

Table 11. *Melampus coffeus* densities (Number of *M. coffeus* m⁻²) comparison for sites and seasons in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.

Source	F	P	No. of <i>M. coffeus</i> m ⁻²
Site	8.07	***	
Windstar Restoration			128.8 ± 43.0 ^a
Rookery Bay Restoration			105.0 ± 26.8 ^{ab}
Rookery Bay Fringe			90.7 ± 26.8 ^{abc}
Rookery Bay Basin			37.6 ± 10.0 ^{bcd}
Ft. Pierce Basin			15.7 ± 5.5 ^{cd}
Windstar Basin			4.7 ± 2.0 ^d
Ft. Pierce Dwarf			3.6 ± 2.6 ^d
Ft. Pierce Fringe			2.2 ± 1.3 ^d
Windstar Fringe			0.5 ± 0.3 ^d
Season	8.56	***	
Summer 1999			64.5 ± 12.5 ^a
Spring 1999			80.7 ± 22.3 ^a
Fall 1999			20.5 ± 8.5 ^b
Winter 2000			7.2 ± 3.3 ^b
Season x site	2.52	**	

Notes: Post-ANOVA Tukey analyses with F-ratio and P-value presented with mean ± 1 SE. *** $P \leq 0.0001$, ** $P \leq 0.001$. Different superscripts within main effects indicate significant differences ($P = 0.05$).

Melampus coffeus densities (number of *M. coffeus* per m²) varied widely within and among sites and seasons (Figure 14). *Melampus coffeus* were observed in all sites during the study. The Rookery Bay sites (basin, fringe, and restoration) had higher densities of *M. coffeus* compared to all sites except the Windstar restoration site (Table 9). Higher densities of *M. coffeus* generally occurred in spring and summer 1999 compared to fall 1999 and winter 2000 (Table 9). In the four sites with the highest mean *M. coffeus* densities (*i.e.*, all of the Rookery Bay sites and the Windstar restoration site), seasonal differences in *M.*

coffeus densities were extremely pronounced (Figure 14). *Melampus coffeus* densities varied among areas and forest type (Table 12). Excluding the restoration sites in Naples and the dwarf site in the Ft. Pierce (to enable a comparison of like sites), the Rookery Bay *M. coffeus* density was greater than either that of Windstar or the Ft. Pierce. Within the Naples study areas (*i.e.* Rookery Bay and Windstar), the restoration sites had higher *M. coffeus* than either the basin or fringe sites (Table 12).

Table 12. *Melampus coffeus* densities compared among different locations and forest types in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.

Source	F	P	Density
Area			
Rookery Bay v. Windstar	11.79	***	
Ft. Pierce v. Rookery Bay	9.48	**	
Ft. Pierce v. Windstar	0.13	NS	
Rookery Bay			64.2 ± 14.6 ^a
Ft. Pierce			9.0 ± 2.9 ^b
Windstar			2.6 ± 1.1 ^b
Forest type			
Naples Basin v. Restored	28.52	***	
Naples Basin v. Fringe	1.85	NS	
Naples Fringe v. Restored	15.83	***	
Naples Restored			116.9 ± 25.2 ^a
Naples Fringe			45.6 ± 14.4 ^b
Naples Basin			21.2 ± 5.4 ^b

Notes: Post-ANOVA Tukey analyses with F-ratio and P-value presented with mean ± 1 SE. ** $P \leq 0.01$, *** $P \leq 0.001$, NS = not significant. Different superscripts within area and forest type comparisons indicate significant differences ($P \leq 0.05$).

Crab Burrow Densities

The density of crab burrows, as an index of crustacean activity (Lee 1989a, Knott *et al.* 1997, Twilley *et al.* 1997) varied by site but not season (Table 13). The Windstar fringe site had the largest number of crab burrows and the lowest number of burrows was seen at the Ft. Pierce dwarf site. Within the Ft. Pierce sites, the fringe area had the highest number of crab burrows (Figure 15).

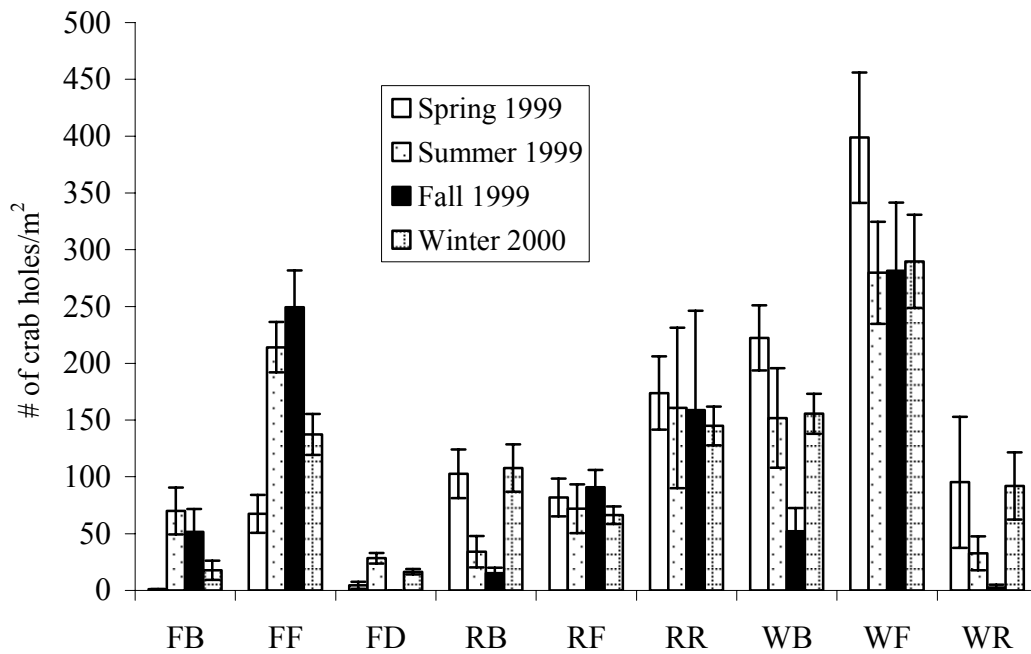


Figure 15. Crab burrows (Mean \pm 1 SE) at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.

Table 13. Crustacean burrow density comparison for sites and seasons in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.

Source	F	P	No. of burrows m ⁻²
Site	5.05	***	
Windstar Fringe			312.4 ± 50.8 ^a
Ft. Pierce Fringe			167.1 ± 22.2 ^a
Rookery Bay Restoration			159.5 ± 51.9 ^a
Windstar Basin			145.5 ± 27.6 ^{ab}
Rookery Bay Fringe			77.6 ± 15.3 ^{ab}
Rookery Bay Basin			64.9 ± 15.3 ^{ab}
Windstar Restoration			55.6 ± 26.2 ^b
Ft. Pierce Basin			35.1 ± 16.4 ^b
Ft. Pierce Dwarf			16.4 ± 3.3 ^b
Season	0.48	NS	
Fall 1999			143.3 ± 29.2 ^a
Winter 2000			126.2 ± 19.3 ^a
Spring 1999			121.6 ± 29.6 ^a
Summer 1999			121.5 ± 31.8 ^a
Season x site	2.52	**	

Notes: Post-ANOVA Tukey analyses with F-ratio and P-value presented with mean ± 1 SE. ** $P \leq 0.01$, *** $P \leq 0.001$, NS = not significant. Different superscripts within main effects indicate significant differences ($P \leq 0.05$).

Leaf Consumption by Macrodetritivores

Direct (watching detritivore activity) and indirect (examining attacked leaves) observations of detritivory indicated that leaves at the Naples sites were almost always consumed by *Melampus coffeus* (pers. obs.), while decapod crustaceans appeared to be the primary consumers of leaves at the Ft. Pierce fringe site (Figure 16). As seen in other regions (Lee 1989b, Robertson and Daniel 1989b), in several cases less than 24 hours passed before leaves were completely skeletonized, consumed, or pulled into crab burrows. In the Ft. Pierce basin site, both *M. coffeus* and decapod crustaceans consumed tethered leaves.

A total of 528 out of 4120 tethered leaves were attacked (12.8 %) during the study. The Ft. Pierce fringe site had the highest mean attack rate ($29.6 \pm 2.1\%$), and decapod crustaceans (primarily *Sesarma cinereum*, *Goniopsis cruentata*, and *Pachygrapsus gracilis*) were responsible for the majority of the consumption occurring at that site. *Melampus coffeus* was the most important macrodetritivore at all other sites. The Windstar basin (1.7 ± 0.6) and the Ft. Pierce dwarf ($2.0 \pm 0.6\%$) sites had the lowest overall mean attack rates (Table 17).

Attack rates varied by site among seasons (Figure 17) and species (Figure 18). The highest mean seasonal attack rate occurred in spring 1999 ($22.2 \pm 1.3\%$) and the lowest mean seasonal attack rate occurred in winter 2000 ($1.2 \pm 0.4\%$) (Table 14). *Avicennia*

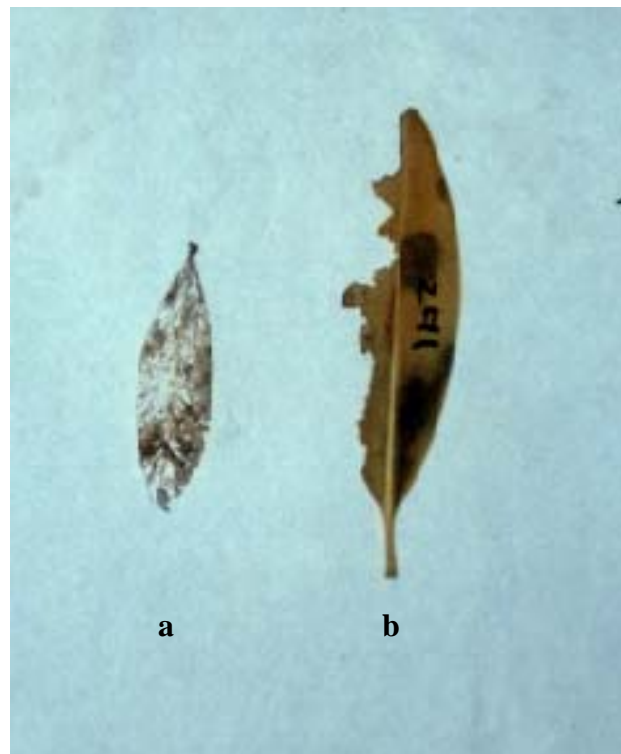


Figure 16. Example of partially consumed a) *A. germinans* and b) *R. mangle* leaves. (a) is typical of *M. coffeus* consumption, while (b) is typical of crustacean feeding activity.

Table 14. Comparison of percentage of leaves “attacked” (defined by visible evidence of consumption) by macrodetritivores between sites, seasons, and species in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida during seasonal sampling from spring 1999 to winter 2000.

Source	F	P	Percent attacked
Site	38.12	***	
Fort Pierce Fringe			29.6 ± 2.1% ^a
Rookery Bay Restoration			18.6 ± 1.8% ^b
Rookery Bay Fringe			18.5 ± 1.8% ^b
Rookery Bay Basin			15.1 ± 1.7% ^{bc}
Fort Pierce Basin			14.8 ± 1.7% ^{bc}
Windstar Restoration			8.8 ± 1.3% ^{cd}
Windstar Fringe			6.5 ± 1.2% ^{de}
Fort Pierce Dwarf			2.0 ± 0.6% ^e
Windstar Basin			1.7 ± 0.6% ^e
Season	101.81	***	
Spring 1999			22.2 ± 1.3% ^a
Summer 1999			17.4 ± 1.2% ^b
Fall 1999			8.5 ± 0.9% ^c
Winter 1999			1.2 ± 0.4% ^d
Species	15.10	***	
<i>Avicennia germinans</i>			16.7 ± 1.0% ^a
<i>Rhizophora mangle</i>			12.0 ± 0.9% ^b
<i>Laguncularia racemosa</i>			9.8 ± 0.8% ^b
Season x site	11.04	***	
Site x species	4.52	***	
Season x species	9.90	***	
Season x site x species	1.40	*	

Notes: Post-ANOVA Tukey analyses with F-ratio and P-value presented with mean ± 1 SE.
 * $P \leq 0.05$, *** $P \leq 0.001$. Different superscripts within main effects indicate significant differences ($P \leq 0.05$).

germinans leaves were attacked more often ($16.7 \pm 1.0\%$) than either *Rhizophora mangle* ($12.0 \pm 0.9\%$) or *Laguncularia racemosa* ($9.8 \pm 0.8\%$) (Table 14). The Ft. Pierce basin and fringe sites had a significantly higher attack rate than the Rookery Bay basin and fringe sites ($p = 0.0004$), and the Rookery Bay basin and fringe sites had a significantly higher attack rate than the Windstar basin and fringe sites ($p < 0.0001$). The rate of attack in the Naples basin sites (*i.e.* Rookery Bay Basin and Windstar Basin) was lower than in Naples fringe (*i.e.* Rookery Bay Fringe and Windstar Fringe, $p < 0.0001$) and the Naples restoration sites (*i.e.* Rookery Bay Restoration and Windstar Restoration, $p = 0.0375$). The Naples fringe and restoration sites were not different (Table 15)

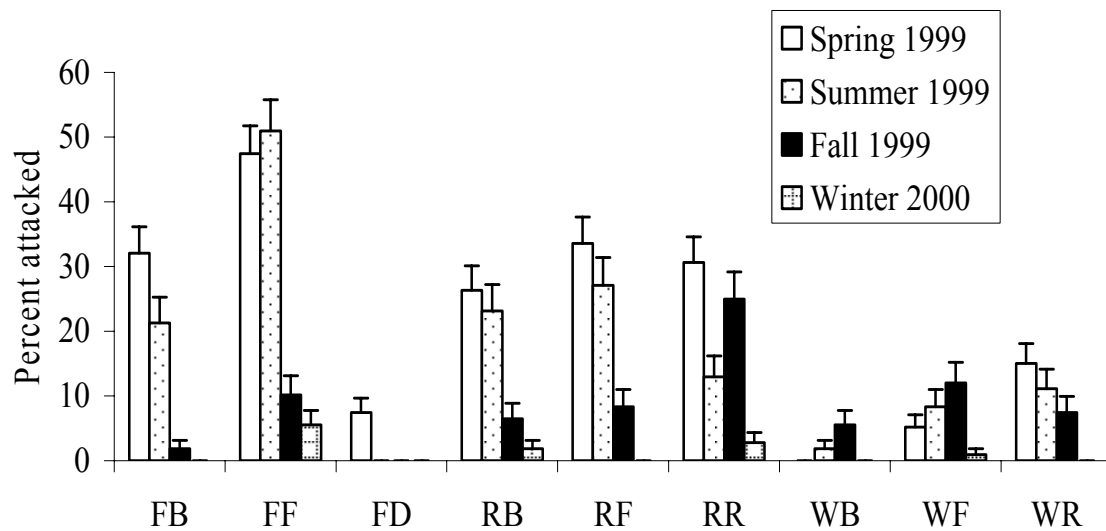


Figure 17. Attack of leaves by site and season at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida. Values are mean percentage \pm 1 SE of tethered leaves that were visibly damaged by macrodetritivores. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.

Seasonal patterns of leaf attack varied by site (Figure 17). The Ft. Pierce fringe site, during summer 1999, had the greatest mean attack rate within one season ($50.9 \pm 4.8\%$). With the exception of the Windstar basin and Windstar fringe sites, spring 1999 or summer 1999 had the highest seasonal mean attack rates within each site. Winter 2000 had the lowest seasonal mean attack rates within all sites and was less than 6% at every site during that season. Attack rates at the Ft. Pierce dwarf site, Windstar basin site, and Windstar fringe site did not vary significantly among the seasons. In four sites (Ft. Pierce basin, Ft. Pierce fringe, Rookery Bay basin, and Rookery Bay fringe), both the spring and summer 1999 attack rates were more than twice as high as in fall 1999 and winter 2000 (Figure 17).

Summer 1999 had the largest variation in attack rates among the nine sites, ranging from $0.0 \pm 0.0\%$ (Ft. Pierce dwarf) to $50.9 \pm 4.8\%$ (Ft. Pierce fringe). The mean attack rate in winter 2000 ranged from 0.0 ± 0.0 (5 sites) to 5.6 ± 2.2 (Ft. Pierce fringe). The Ft. Pierce fringe site had the highest seasonal variation of any of the sites, ranging from $5.6 \pm 2.2\%$ (winter 2000) to $50.9 \pm 4.8\%$ (summer 1999). The Windstar basin site exhibited the lowest variation by season of attack rate, ranging from $0.0 \pm 0.0\%$ to $5.6 \pm 2.2\%$.

Attack rates also differed by mangrove species depending upon the site (Figure 18). Several of these attack rates (*L. racemosa* and *R. mangle* in the Ft. Pierce dwarf site, all three species in the Windstar basin site, *A. germinans* in the Windstar fringe site, and *R. mangle* in the Windstar restoration site) did not significantly differ from zero. *Rhizophora mangle* in the Ft. Pierce fringe site had the highest mean attack rate ($39.9 \pm 4.0\%$). Either spring 1999 or summer 1999 had the highest seasonal mean attack rates for each species. Winter 2000 had the lowest seasonal mean attack rates within each species ($p < 0.05$).

Rhizophora mangle had the largest variation in attack rates among the different sites, ranging from $0.0 \pm 0.0\%$ (Ft. Pierce dwarf) to $39.9 \pm 4.0\%$ (Ft. Pierce fringe). The mean

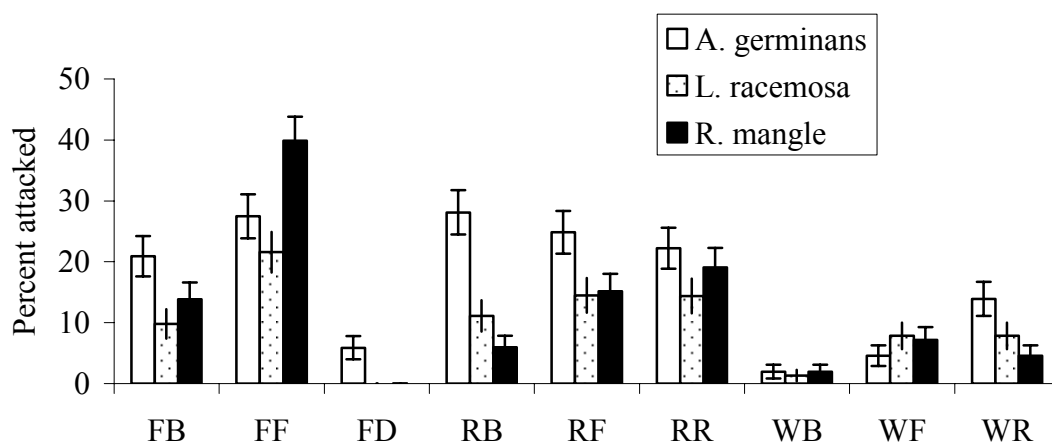


Figure 18. Attack of leaves by species and site at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida. Values are mean percentage \pm 1 SE of tethered leaves that were visibly damaged by macrodetritivores. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.

attack rate for *L. racemosa* ranged 14.5% and ranged 26.1% for *A. germinans*. The Rookery Bay basin site had the widest variation among species attack rates (22.1%) and the Windstar basin site had the narrowest variation among species attack rates (0.7%).

Leaf consumption of the three mangrove species by macrodetritivores varied differentially by season (Figure 19). No attack rates during winter 2000 were significantly different from zero. The *A. germinans* spring 1999 had the greatest mean attack rate ($32.8 \pm 2.3\%$) for any combination of season and species. Either spring 1999 or summer 1999 had the highest seasonal mean attack rates for each species. Winter 2000 had the lowest seasonal mean attack rates within each species ($p < 0.05$).

Spring 1999 had the largest variation in attack rates among the three species, ranging from $13.9 \pm 1.7\%$ (*L. racemosa*) to $32.8 \pm 2.3\%$ (*A. germinans*), a difference of 18.9%. The mean attack rates in fall 1999 and winter 2000 ranged approximately two (2) percent.

Avicennia germinans had the highest seasonal variation in attack rate of the species, ranging

Table 15. Differences in percentage of leaves “attacked” (defined by visible evidence of consumption) by macrodetritivores in different areas and forest types in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.

Source	F	P	Percent attacked
Area			
Rookery Bay v. Windstar	92.79	***	
Ft. Pierce v. Rookery Bay	12.80	**	
Ft. Pierce v. Windstar	145.51	***	
Ft. Pierce			22.2 ± 1.9 ^a
Rookery Bay			16.8 ± 1.8 ^b
Windstar			4.1 ± 0.9 ^c
Forest type			
Naples Basin v. Restored	12.69	**	
Naples Basin v. Fringe	8.47	**	
Naples Fringe v. Restored	0.42	NS	
Naples Restoration			13.7 ± 1.6 ^a
Naples Fringe			12.5 ± 1.5 ^{ab}
Naples Basin			8.4 ± 1.1 ^c

Notes: Post-ANOVA Tukey analyses with F-ratio and P-value presented with mean ± 1 SE. ** $P \leq 0.01$, *** $P \leq 0.001$, NS = not significant at $P \leq 0.05$). Different superscripts within area and forest type indicate significant differences ($P \leq 0.05$).

from $0.0 \pm 0.0\%$ (winter 2000) to $32.8 \pm 2.3\%$ (spring 1999), a difference of 32.8%.

Laguncularia racemosa exhibited the lowest variation by season of attack rate, ranging from

1.5 ± 0.7 (winter 2000) to $13.9 \pm 1.7\%$ (spring 1999), a difference of 12.4%.

Sites with high attack rates also had high consumption rates (Figure 20). However, the

Windstar restoration site, which had the highest *M. coffeus* density, did not have the highest observed leaf attack rate. This may in part be due to the high amount of standing leaf litter at the Windstar restoration site, which affected consumption of tethered leaves. Therefore, leaf consumption in areas with high standing leaf litter could have been underestimated.

Standing leaf litter was not removed from the substrate before tethering the leaves because

this would alter the macrodetritivore habitat. Alternatively, the high standing litter mass seen in several sites may reduce the necessity for rapid consumption of leaf material due to changes in leaf nutritional quality that can impact choice by macrodetritivores (Lee 1989b). *Rhizophora mangle* dominated the standing leaf litter in six of the sites (Table 8). In most sites, the attack rate by macrodetritivores on *A. germinans* (Figure 18) was high with respect to its natural occurrence on the forest floor. *I.e.*, macrodetritivores consumed *A. germinans* leaves at a higher rate than the background level. Macrodetritivores also consumed *L. racemosa* leaves at relatively high rates in several sites, although not as high as those of *A. germinans*. This pattern suggests that the order of preference for mangrove leaves by *M. coffeus* in these systems is: *A. germinans* > *L. racemosa* > *R. mangle*. Previous work in southwest Florida indicated that *M. coffeus* leaf preference varied, and that all three species are consumed (McKee and Faulkner 1999, Proffitt *et al.* 1993). However, in the Ft. Pierce Fringe site, the only site where much of the consumption was done by crustaceans (pers. obs) and leaves were often pulled into crab burrows, *R. mangle* was preferred at higher levels than either *A. germinans* or *L. racemosa* (Figure 18).

Leaf Degradation Rates

Initial rates of leaf degradation (mass loss per unit time), which combine consumption and shredding by macrodetritivores and leaching of soluble compounds, were compared across site and season. Degradation of leaves differed by site and season (Figure 23). The Ft. Pierce fringe site ($2.9 \pm 0.3\% \text{ day}^{-1}$) had the highest overall mean degradation rate (Table 16). The Windstar basin site ($0.8 \pm 0.1\% \text{ day}^{-1}$) had the lowest mean degradation rate (although not significantly different from the Windstar fringe, Ft. Pierce dwarf, Windstar restoration, or Rookery Bay basin sites). Significantly higher leaf

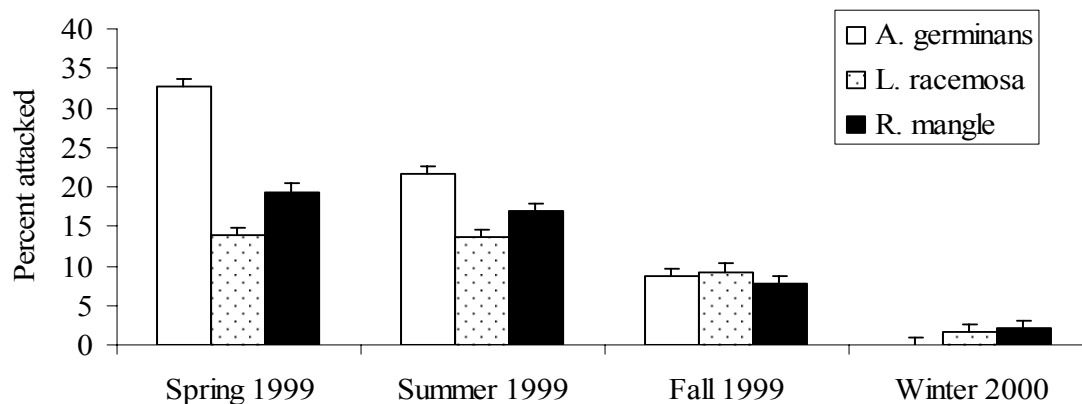


Figure 19. Attack of leaves by species and season at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration. Values are mean percentage \pm 1 SE of tethered leaves that were visibly damaged by macrodetritivores.

degradation rates occurred in spring 1999 ($2.0 \pm 0.1\% \text{ day}^{-1}$) and summer 1999 ($2.4 \pm 0.1\% \text{ day}^{-1}$) compared to fall 1999 ($1.2 \pm 0.1\% \text{ day}^{-1}$) and winter 2000 ($0.8 \pm 0.1\% \text{ day}^{-1}$). The leaf degradation rate in winter 2000 was lower than the other seasons ($p < 0.0001$ compared to spring 1999 and summer 1999, and $p = 0.0141$ compared to fall 1999) (Table 16).

Leaves that were attacked during the study period lost $51.7 \pm 1.1\%$ of their mass, while those not attacked or in mesh bags lost $27.7 \pm 0.4\%$. These leaf decomposition rates are comparable to those of other mangrove forests (Tam *et al.* 1998) and more rapid than some other areas (*e.g.*, Heath and King 1964, Minderman 1968). The number of leaves attacked in any particular site was directly related to the consumption rate (Figure 20).

Consistent seasonal patterns of leaf degradation within the sites did not occur (Figure 21). The Ft. Pierce fringe site summer 1999 had the greatest mean degradation rate ($4.9 \pm 0.5\% \text{ day}^{-1}$) ($p < 0.05$ except compared to Ft. Pierce basin site spring 1999, $p = 0.0752$). With

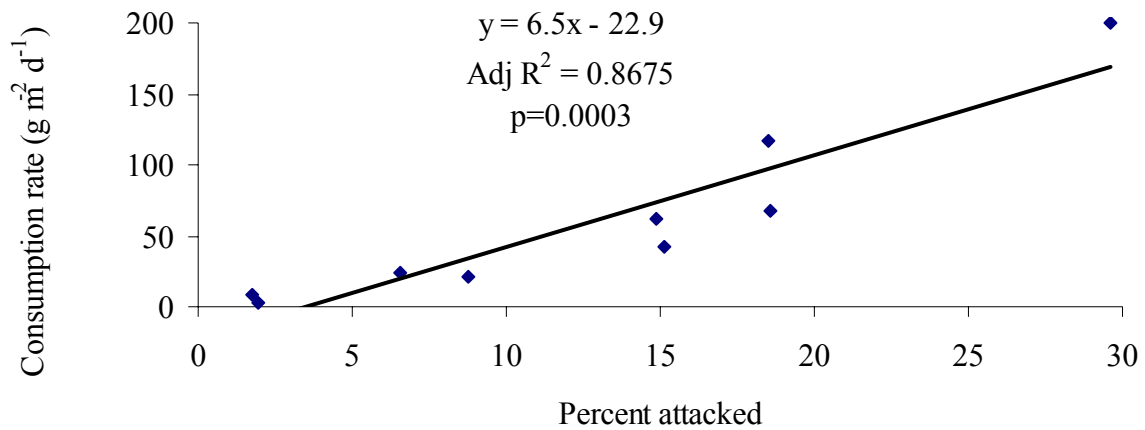


Figure 20. Regression of percent of leaves attacked to annual consumption rates of mangrove leaves at eight sites in at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida (excludes Ft. Pierce fringe, where crustaceans were the primary consumers of leaf litter).

two exceptions (Ft. Pierce Basin and Ft. Pierce Dwarf), winter 2000 had the lowest seasonal mean degradation rates within each site (although not always statistically significant). The highest leaf degradation rates for each site occurred in either spring 1999 or summer 1999. Summer 1999 was the only season within which the degradation rate at one site (Ft. Pierce fringe, $4.9 \pm 0.5\% \text{ day}^{-1}$) was significantly higher than all other sites (Table 16). The degradation rates at the individual sites did not vary between fall 1999 and winter 2000 and were usually lower than spring 1999 or summer 1999. Excluding the dwarf and restoration sites, Ft. Pierce had the highest mean degradation rates and Windstar had the lowest degradation rates (Table 17). Degradation rates in the Naples basin sites (*i.e.* Rookery Bay and Windstar basin sites) were significantly slower than in Naples fringe sites (*i.e.* Rookery Bay and Windstar fringe sites, $p < 0.0001$) and the Naples restoration sites (*i.e.*, Rookery Bay and Windstar restoration sites, $p = 0.0264$) (Table 17). Mean degradation rates for the Naples fringe sites were higher than the Naples restoration sites ($p = 0.0697$).

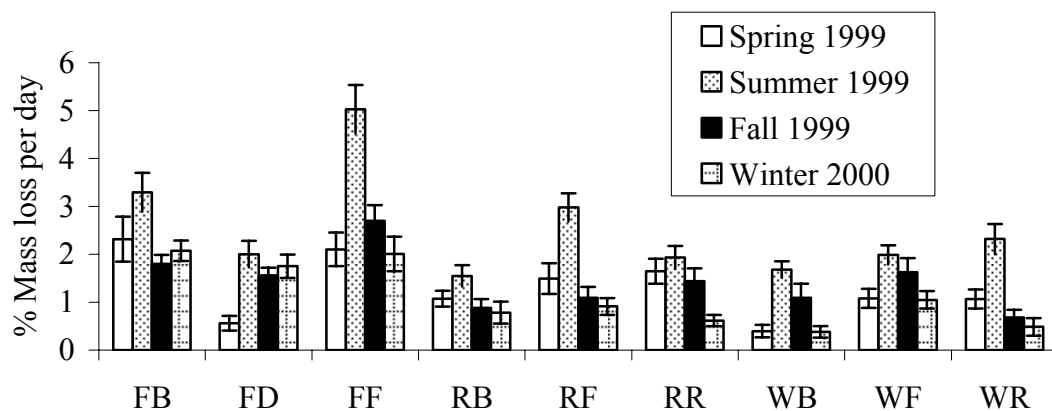


Figure 21. Degradation of leaves by site and season at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida. Values are % mass loss day⁻¹ ± 1 SE. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.

Leaf Nutrients

Avicennia germinans leaves exhibited the highest and *L. racemosa* exhibited the lowest initial mean percent nitrogen during the two seasons nutrients were sampled (Table 18). Initial nitrogen content ranged from 0.37 to 1.54 percent. The highest value is slightly higher than what has been reported elsewhere (Feller *et al.* 1999, Pelegri and Twilley 1998, Lee 1989b), but the other nitrogen values concur with previous research. Leaves taken from the Rookery Bay site had the highest initial nitrogen content and those from the Ft. Pierce site had the lowest initial nitrogen content. No seasonal differences in initial nitrogen content occurred. Percent nitrogen within each site increased over the two to three week periods when leaves were tethered during both Fall 1998 and Spring 1999. Increases in percent nitrogen were seen regardless of species during both Fall 1998 and Spring 1999. Rates of increase in percent nitrogen were similar for all sites and species.

Table 16. Comparison of degradation rates (percent mass loss day⁻¹) for main effects and interaction between sites, seasons, and species in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.

Source	F	P	Percent mass loss day ⁻¹
Site	26.26	***	
Ft. Pierce Fringe			3.0 ± 0.2 ^a
Ft. Pierce Basin			2.4 ± 0.2 ^{ab}
Rookery Bay Fringe			1.6 ± 0.2 ^{bc}
Rookery Bay Restoration			1.4 ± 0.1 ^{cd}
Ft. Pierce Dwarf			1.5 ± 0.1 ^{cde}
Windstar Fringe			1.4 ± 0.1 ^{cde}
Windstar Restoration			1.1 ± 0.1 ^{de}
Rookery Bay Basin			1.1 ± 0.1 ^{de}
Windstar Basin			0.9 ± 0.1 ^e
Season	52.93	***	
Summer 1999			2.5 ± 0.1 ^a
Fall 1999			1.4 ± 0.1 ^b
Spring 1999			1.3 ± 0.1 ^{bc}
Winter 1999			1.1 ± 0.1 ^c
Species	8.04	**	
<i>L. racemosa</i>			1.8 ± 0.1 ^a
<i>A. germinans</i>			1.6 ± 0.1 ^{ab}
<i>R. mangle</i>			1.4 ± 0.1 ^b
Season x site	2.99	***	
Site x species	1.29	NS	
Season x species	1.77	NS	
Season x site x species	1.88	**	

Notes: Post-ANOVA Tukey analyses with F-ratio and P-value presented with mean ± 1 SE. * $P \leq 0.01$, *** $P \leq 0.001$, NS = not significant at $P \leq 0.05$. Different superscripts within main effects indicate significant differences ($P \leq 0.05$).

The initial percent carbon content was similar among all three areas and during the two seasons sampled and ranged from 41.6 to 48.3 (Table 18). These values are similar to what has been seen in other mangrove forests (*e.g.*, Camilleri 1989, Hemminga *et al.* 1994, Wafar 1997). The initial percent carbon content was lower in *L. racemosa* leaves compared to the other two mangrove species (Table 18). Percent carbon in the mangrove leaves slightly increased over the observation periods in all sites and all three species.

As a result of increasing nitrogen and slightly increasing carbon concentrations in the leaves, the carbon:nitrogen ratio generally decreased during both Fall 1998 (Figure 22) and Spring 1999 (Figure 23) at all sites. The lowest initial carbon:nitrogen (C:N) ratio was seen in *A. germinans* leaves during the study, and the highest C:N ratio occurred in *L. racemosa* (Table 18). The Ft. Pierce leaves exhibited the highest and Rookery Bay the lowest C:N ratio among the sites. The C:N ratio in the two seasons was similar. Changes in the C:N ratio also decreased within all species over both seasons, and *A. germinans* had the lowest ratio at all times examined during both Fall 1998 (Figure 24) and Spring 1999 (Figure 25). These changes in nitrogen and carbon concentrations and C:N ratios agree with Pelegri *et al.* (1997) who found similar results when comparing fresh and aged mangrove leaves.

Macrodetritivore Feeding Trials

During the laboratory feeding trials *M. coffeus* exhibited preferences for leaves of the three mangrove species tested: *L. racemosa* > *A. germinans* > *R. mangle* (Figure 26). Approximately three times the amount of *L. racemosa* leaf material was consumed compared to *R. mangle*. No differences in consumption rates were seen among *L. racemosa* leaves soaked in water of 0 ppt salinity compared to those soaked in water of 40 ppt salinity. Initial

consumption of mangrove leaves occurred slower during the laboratory trials than during the field tethering trials. The field feeding trials were unsuccessful due to dessication of the cages, and results are not reported here.

Table 17. Comparisons of degradation rates between different areas and forest types in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.

Source	F	P	Percent mass loss day ⁻¹
Area			
Rookery Bay v. Windstar	2.12	NS	
Ft. Pierce v. Rookery Bay	104.85	***	
Ft. Pierce v. Windstar	137.77	***	
Ft. Pierce			2.3 ± 0.1 ^a
Rookery Bay			1.4 ± 0.1 ^{bc}
Windstar			1.2 ± 0.1 ^c
Forest Type			
Naples Basin v. Restored	5.34	*	
Naples Basin v. Fringe	18.37	***	
Naples Fringe v. Restored	3.94	*	
Naples Fringe			1.5 ± 0.1 ^a
Naples Restored			1.3 ± 0.1 ^b
Naples Basin			1.0 ± 0.1 ^c

Notes: Post-ANOVA Tukey analyses with F-ratio and P-value presented with mean ± 1 SE. ** $P \leq 0.01$, *** $P \leq 0.001$, NS = not significant at $P \leq 0.05$. Different superscripts within Area and Forest Type indicate significant differences ($P \leq 0.05$).

Table 18. Comparison of the initial percent nitrogen, percent carbon and carbon:nitrogen ratio of leaves among sites, seasons, and species in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.

Source	Percent Nitrogen (mean \pm 1 SE)	Percent Carbon (mean \pm 1 SE)	C:N Ratio (mean \pm 1 SE)
Species			
<i>A. germinans</i>	0.95 \pm 0.08	48.29 \pm 0.75	52.36 \pm 3.98
<i>L. racemosa</i>	0.47 \pm 0.03	41.60 \pm 1.40	89.79 \pm 5.15
<i>R. mangle</i>	0.78 \pm 0.15	47.30 \pm 0.57	67.98 \pm 7.89
Site			
Fort Pierce	0.61 \pm 0.07	45.45 \pm 1.47	78.66 \pm 8.43
Rookery Bay	0.89 \pm 0.18	45.35 \pm 1.94	59.97 \pm 9.19
Windstar	0.73 \pm 0.10	47.02 \pm 1.12	69.65 \pm 7.72
Season			
Fall 1998	0.76 \pm 0.13	44.98 \pm 1.44	70.51 \pm 8.61
Spring 1999	0.74 \pm 0.07	47.08 \pm 0.80	67.05 \pm 4.84

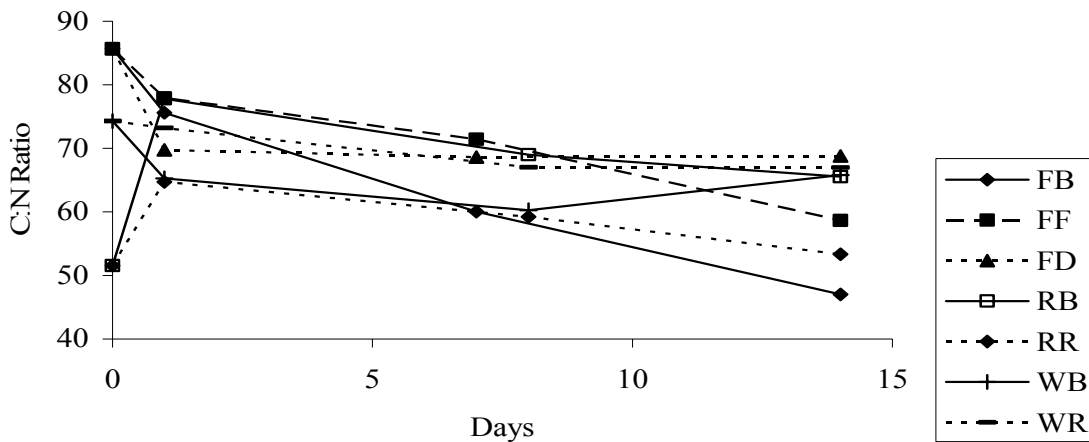


Figure 22. Carbon:nitrogen ratio for seven mangrove sites in at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida during Fall 1998. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.

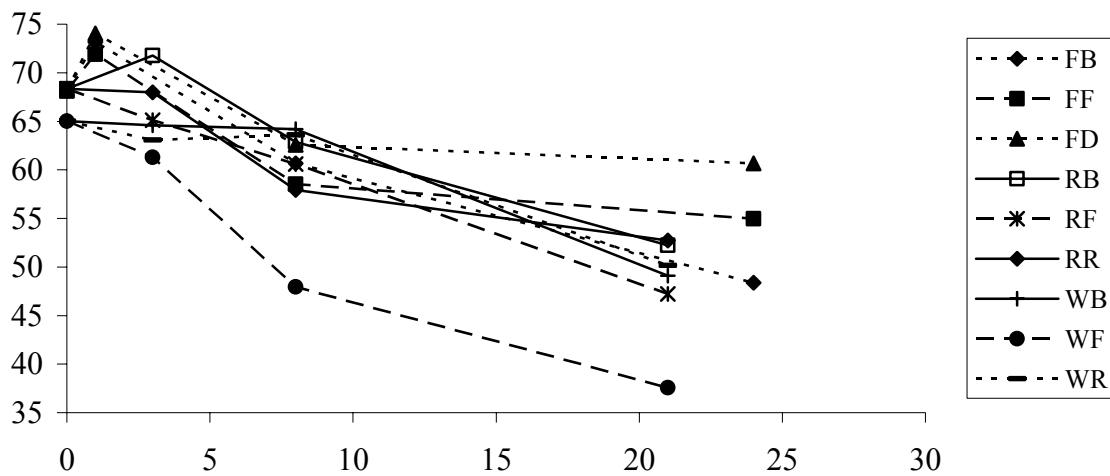


Figure 23. Carbon:nitrogen ratio for nine mangrove sites in at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida during Spring 1999. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.

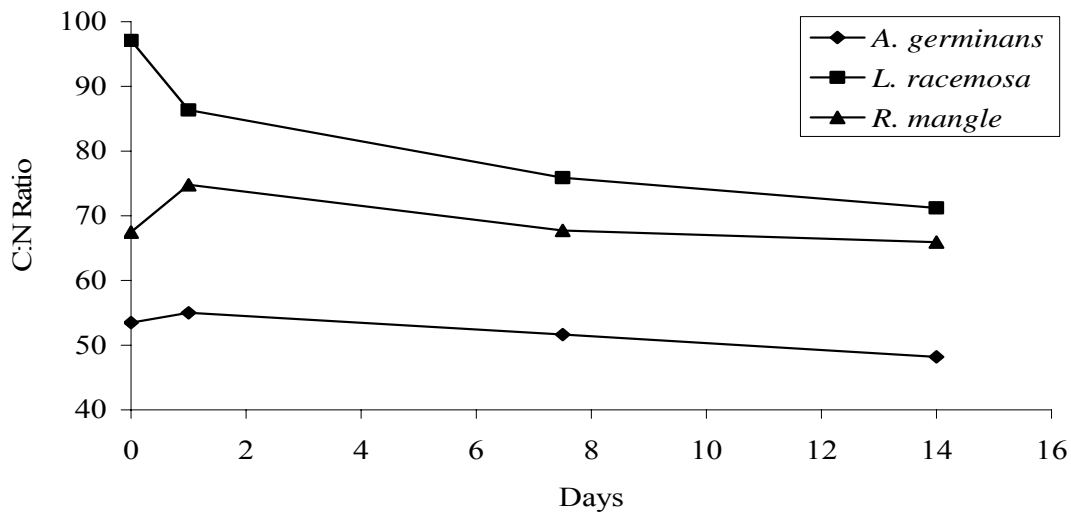


Figure 24. Changes in the carbon:nitrogen ratio of three mangrove species at nine sites in at nine sites in Naples and Fort Pierce, Florida during Fall 1998.

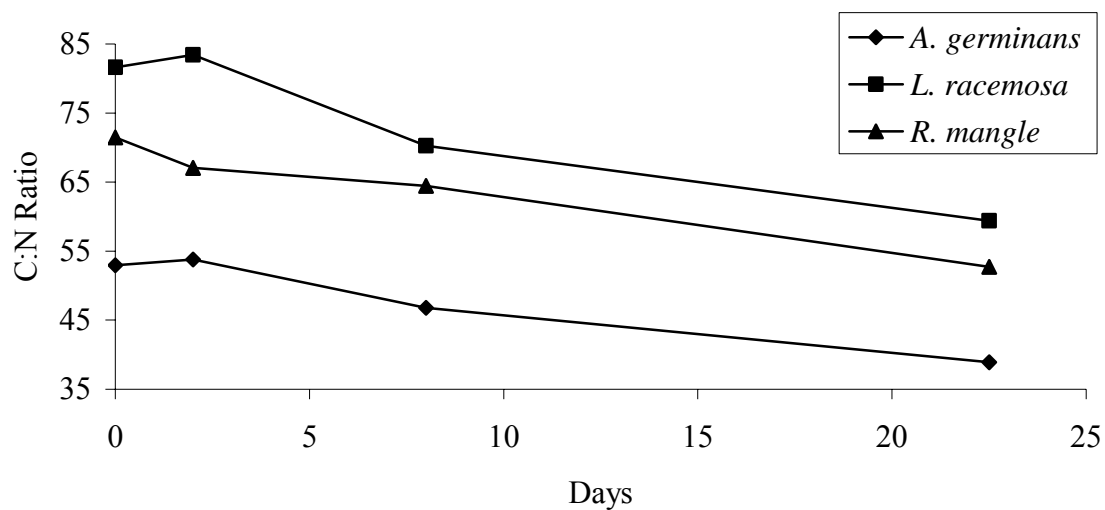


Figure 25. Changes in the carbon:nitrogen ratio of three mangrove species at nine sites in at nine sites in Naples and Fort Pierce, Florida during Spring 1999.

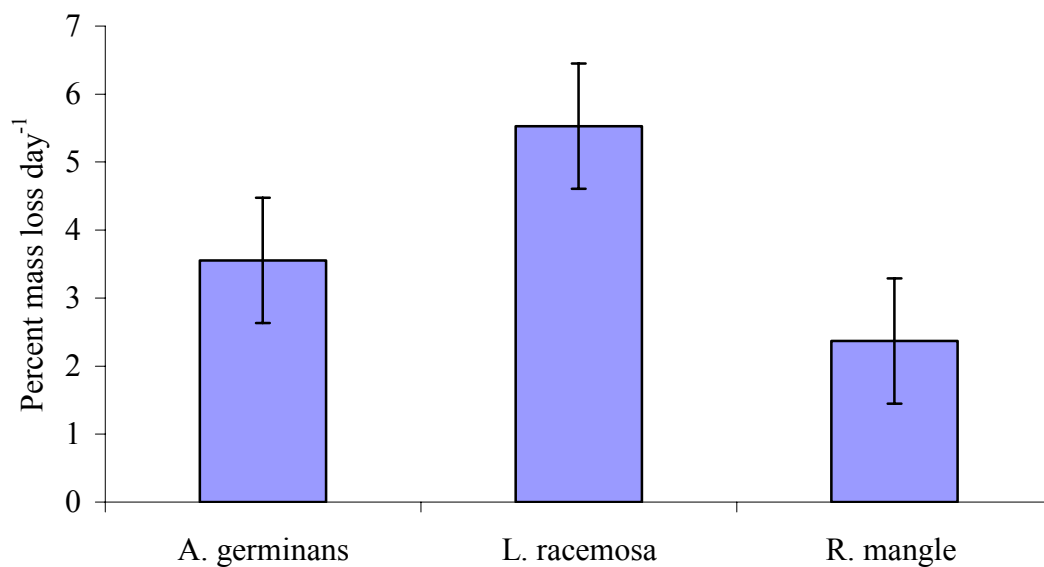


Figure 26. Mass loss of mangrove leaf species during laboratory feeding trials with *M. coffeus*.

CHAPTER 5: SUMMARY AND DISCUSSION

Note: This section is intended for submission to a scientific journal and therefore contains an introduction, methods and materials, results, and discussion sections.

Introduction

Mangrove forest ecosystems are important as sources of energy and nursery areas for fisheries and wildlife (Odum and Heald 1972, Rodelli *et al.* 1984, John and Lawson 1990), timber production (Noakes 1955, Clough and Scott 1989), and storm protection (Teas 1977, Christensen 1978). Detrital export from mangrove forests is a source of nutrients and energy to nearby ecosystems such as Biscayne Bay, Florida (Fleming *et al.* 1990), the Great Barrier Reef of Australia (Alongi 1990), Gazi Bay, Kenya (Hemminga *et al.* 1994) and the Guayas River Estuary Ecosystem of Ecuador (Cifuentes *et al.* 1996). Coastal-oriented development, mangrove timber harvesting, and shrimp pond mariculture will continue to put pressure on these mangrove forests (Boto *et al.* 1984, Rodelli *et al.* 1984). Our understanding of how these systems function in their natural state must be enhanced to improve attempts at restoration in disturbed sites or the creation of new mangrove forests in legal mitigation processes. Knowledge of mangrove litter dynamics is crucial in understanding the energetic links between mangrove forests and adjacent aquatic systems (Twilley *et al.* 1997, Wafar *et al.* 1997, Gong and Ong 1990).

Primary saprotrophs, such as amphipods (Ladle 1974), gastropods (Mason 1974), insects (Meyer and O'Hop 1983), and crustaceans (Robertson 1986) can do initial breakdown of litter, producing a wide array of resources (*e.g.*, smaller particles, feces). These resources are then utilized by the secondary saprotrophs, including micro- and meso-fauna, fungi and

bacteria. These categories are not absolute, since some organisms feed at both trophic levels either at different life stages or according to resource availability (Swift *et al.* 1979).

Early mangrove litter cycling research focused on factors controlling microbial decomposition and used techniques specific to this purpose. In addition, mangrove decomposition *in situ* was assessed with fine mesh bags that excluded macrodetritivores (Fell *et al.* 1975, Odum and Heald 1975, Twilley *et al.* 1986). Consequently, macrodetritivore processing was initially thought to be less important than breakdown by fungi and bacteria.

However, beginning in the mid-1980's, the importance of macrodetritivores in processing mangrove litter was assessed. Robertson (1986, 1988) and Robertson and Daniel (1989b) demonstrated that sesarmid crabs in Australia processed a significant portion of the litter fall before it could be exported by tidal action. Sesarmid crab density was negatively correlated with mangrove leaf litter turnover rate in a Hong Kong tidal shrimp pond (Lee 1989b). *Sesarma meinerti* was estimated to consume 44% of *Avicennia marina* leaf fall from a South African mangrove estuary (Emmerson and McGwynne 1992). A significantly higher decomposition rate for tethered leaves compared to leaves in mesh bags within a Belizean mangrove forest was attributed to consumption by herbivorous crabs (Middleton and McKee 2001). Some mangrove crab species transport litter into burrows, which also reduces tidal export of leaf litter (Giddens *et al.* 1986, Robertson and Daniel 1989b, Middleton and McKee 2001).

The importance of macrodetritivore litter consumption can vary widely by mangrove forest type (Robertson and Daniel 1989b, Robertson *et al.* 1992, Middleton and McKee 2001). Since different litter processors break leaves down into different particle sizes, many extra

niches for detritus particle consumers are created (Camilleri 1992). The action of these macrodetritivores thus results in a faster rate of decomposition and recycling of nutrients in mangrove forests (Robertson 1986).

Work conducted to date investigating the role of macrodetritivores in mangrove litter processing in Neotropical forests suggests that 1) they may have as great an impact on litter turnover as in Old World forests (Middleton and McKee 2001, Twilley *et al.* 1997) and 2) gastropods may play a more important role than crabs in some locations (Proffitt *et al.* 1993, McKee and Faulkner 2000). Mangrove crabs, *e.g.* *Ucides* spp., appeared to increase litter turnover rates in an estuary in Ecuador (Twilley *et al.* 1997) and on mangrove islands in Belize (McKee and Feller 1992, Middleton and McKee 2001). Direct consumption and burial in burrows accounted for up to 100% of fallen litter in these forests. In contrast, the only consumption of mangrove leaf litter in southwest Florida was attributed to *Melampus coffeus*, the coffee bean snail (Proffitt *et al.* 1993, McIvor and Smith 1995, McKee and Faulkner 2000). However, several crustacean species known to be detritivores elsewhere do occur in Florida, especially in the Indian River Lagoon region. The primary food for *M. coffeus* is fresh and decaying mangrove leaf litter (Mook 1986), and a significant portion of mangrove litter may be assimilated by *M. coffeus* before export (Proffitt *et al.* 1993, McKee and Faulkner 2000). Other work also supports the role of gastropods and suggests their impact on litter turnover may vary geographically and with environmental conditions (Lee 1989b).

If macrodetritivores play an important role in litter turnover in Neotropical mangrove forests, as is the case in Australia (*e.g.*, Robertson 1986), then the amount of carbon (i.e. food) exported per areal unit of mangrove forest can be more accurately predicted through the

incorporation of macrodetritivore activity in outwelling models (*e.g.*, Twilley *et al.* 1986). Rates of leaf litter production, microbial decomposition, and tidal action have been quantified in different Florida locations (*e.g.*, Twilley 1985, Twilley *et al.* 1986, Parkinson *et al.* 1999, McKee and Faulkner 2000). The role of macrodetritivore degradation of leaf litter in Florida has not been intensively investigated (Proffitt *et al.* 1993, McIvor and Smith 1995), but some work suggests that it may have a major influence on litter turnover (McKee and Faulkner 2000). However, details about spatial and temporal patterns of leaf consumption as well as how factors such as detritivore densities and environmental conditions influence leaf litter turnover have not been described. Two major goals existed for this research: 1) to determine the role macrodetritivores play in initial litter processing in a Neotropical mangrove ecosystem; and 2) examine differences in macrodetritivore populations with a focus on *Melampus coffeus* and a suite of decapod crustaceans in natural and restored mangrove forests to assess their relative functioning with respect to carbon dynamics.

Methods and Materials

Study Sites

The Rookery Bay National Estuarine Research Reserve (Rookery Bay, 26°3'N, 81°42'W) is located along the southern shore of Henderson Creek in Naples, Florida. This site is in an area that was originally leveled and dredged for a fishing pond in 1972 (RBNERR 1993). The two-phased restoration (completed in 1992) included removal of exotic vegetation, reestablishment of the original elevation, excavation of flushing cuts to facilitate water movement, and planting of *R. mangle* seedlings. Reference forests, located adjacent to the restoration site, are a typical mixed basin forest of *R. mangle*, *A. germinans*, and *L.*

racemosa and a fringe forest dominated by *R. mangle*. Aerial photography indicates that it has been undisturbed for at least 60 years (Hopkins, pers. comm. to McKee).

Deposition of dredge fill from the Intercoastal Waterway destroyed mangrove forest areas on the eastern side of Naples Bay prior to 1980. The Windstar Golf Course and Multi-Family Community (Windstar, 26°7'N, 81°47'W) was constructed in 1982 on a 200 ha tract on the east side of Naples Bay and included over 40 ha of undisturbed mangrove forest and the dredge spoil sites. Restoration of three dredge spoil sites (a total of 6 ha), including exotic plant removal, mechanical grading, and planting *R. mangle* seedlings, was undertaken as mitigation for filling mosquito control ditches and destruction of existing *R. mangle* during construction of Windstar. The natural mangrove system adjacent to the mitigation site is a mixed basin forest with *R. mangle*, *A. germinans*, and *L. racemosa* and a fringe forest dominated by *R. mangle*. Aerial photographs from the 1940's (Proffitt and Devlin 1991) demonstrate the forest age is in excess of 50 years.

Officials of St. Lucie County, Florida, installed impoundment dikes with weirs within mangroves forests on North Hutchinson Island (Ft. Pierce, 27°32'N, 80°20'W) during the 1960's in an attempt to control mosquito populations. Impoundment management resulted in an alteration of the natural hydrology of the area by levee construction and control of water levels within the impoundments (Rey *et al.* 1990b). Active management was halted in the late 1980's. Connections between Impoundment 33 and the Indian River Lagoon currently include a series of continuously open culverts and a 10-m breach on the north edge of the impoundment. Three distinct forest types were examined within this area: a basin forest dominated by *A. germinans* < 8 cm diameter at breast height, a *R. mangle* dominated fringe

area across a small (3-5 meter) channel from the impoundment dike ranging between one and three meters wide, and a dwarf area dominated by *A. germinans*. No relatively undisturbed mangrove forest occurred nearby to be used as a reference.

Experimental Design

The basin and fringe sites at Rookery Bay and Windstar and the basin and dwarf sites at the Ft. Pierce had three plots randomly established on each of three transects parallel to the open water (a total of nine plots at each site). Nine fringe plots were established at random intervals 11-20 m apart approximately 3-4 m from the outside edge of the mangroves at Rookery Bay and Windstar, and 1-2 m from the outside edge of the mangroves on the inside of the impoundment at the Ft. Pierce site.

Forest Structure

The forest structure influences a number of variables including litter fall and macrodetritivore population characteristics. The point-centered quarter method (Cottam and Curtis 1956, Cintrón and Novelli 1984, Day *et al.* 1987) was used to estimate mangrove species composition, tree density, canopy height, basal area, and complexity index for trees over 4 cm Diameter at Breast Height (DBH) in all forests except the Ft. Pierce dwarf forest. Due to the absence of trees with a measurable DBH, nine (9) 10m x 10m plots were established and all trees within the Ft. Pierce dwarf forest plots were counted. These counts were then used to estimate the same parameters (*i.e.*, species composition, tree density, canopy height, basal area, and complexity index).

Environmental Factors

Environmental (*i.e.*, abiotic) factors were monitored at 3-month intervals to aid in interpretation of detritivore differences among seasons, sites and forest types. Interstitial water was collected from the soil with a sipper (McKee *et al.* 1988), and salinity was determined with a refractometer. Temperature was recorded with two (2) max-min thermometers at each site.

During the summer of 1999, four measurements of light levels were taken at each plot with a LiCor quantum radiometer at approximately 1.8 m above the soil surface. Light readings were taken at each site between 10 a.m. and 2 p.m. under clear conditions to ensure consistency among sites. These readings were referenced to values obtained in nearby open areas and are reported as percent of ambient light.

Litter Dynamics

Litter fall rate and standing litter crop, as indicators of productivity and total turnover rate (Olson 1963, Pool *et al.* 1975), were obtained, and composition (proportion of leaves, reproductive parts, and twigs) described. Litter was collected in 0.25 m² (50 x 50 cm) litter traps and retrieved at approximately monthly intervals. Standing litter crop was collected every 3 months approximately 2 m from each litter trap inside ~ 0.2 m² (42 x 42 cm) quadrats during low tide (to maximize soil surface exposure). To minimize impact on other seasonal collections, each standing litter collection area was rotated to a different position around the litter traps. Litter was dried to a constant mass at 70 °C, sorted by species into leaf and reproductive components, and weighed to 0.1 g (Brown 1984, Day *et al.* 1996). Wood was not sorted to species prior to weighing. Leaf fragments, insect frass and debris were summed

together into a single category called “other”. Leaf turnover rate was estimated by dividing annual leaf fall rate by average standing stock of litter.

Macrodetritivore Dynamics

Melampus coffeus and crab burrow densities were estimated from the 42 cm x 42 cm standing litter quadrats used for standing litter surveys (*i.e.*, 3 month intervals at low tide). To minimize impact on other seasonal collections, each collection area was rotated to a different position around the litter traps. *Melampus coffeus* found during the initial litter collection were tabulated and released after the litter collection was complete. Since smaller *M. coffeus* are difficult to observe in the field due to cryptic coloration, individuals found during litter sorting (after the litter was oven dried) were also counted; snails without bleached shells were regarded as viable when collected. These two counts were added together to get an estimate for snail density. All *M. coffeus* were placed in 12 size classes by widest shell diameter. Other gastropods were collected and counted in a similar manner.

Leaf litter processing by macrodetritivores was examined in the field by leaf-tethering (Robertson 1986, Proffitt *et al.* 1993). Changes in leaf mass and structure without the influence of macrodetritivores were assessed with litter bag trials. Where possible, undamaged, senescent, non-abscised leaves were gathered from each mangrove species (*i.e.*, *R. mangle*, *A. germinans*, and *L. racemosa*). A high level of herbivory, as seen elsewhere (Johnstone 1981, Farnsworth and Ellison 1991), increased search time for useable leaves. Leaves were photocopied before processing, and photocopies were digitally scanned. Leaf area was determined with the MacFolia (Regent Instruments, Inc., Canada) area analysis software using the digitally scanned leaves. A subset of leaves from each species was used to

determine initial leaf area to mass ratio. Leaves were then tethered in the field using light monofilament line tied between leaves and small flags.

Tethered leaves were collected from each plot at varying intervals for up to three weeks. All foreign material (*e.g.*, soil) was gently washed off the leaves with tap water. Leaves were scored as damaged or undamaged by macrodetritivore type (*i.e.*, crustacean or gastropod) where possible. Leaves were then dried to constant mass and weighed to 0.01 g. Final weight was subtracted from original estimated weight to calculate biomass consumed, and percent mass loss per day was calculated using the series of leaves retrieved from each plot. To estimate mass loss due to leaching, mass change in tethered leaves not visibly damaged by macrodetritivores and leaves in mesh bags were compared with mass loss in damaged leaves.

Change in leaf nutritional content after abscission may have an effect on leaf consumption by macrodetritivores. Therefore, in Fall 1998 and Spring 1999 separate sets of leaves were tethered, retrieved after predetermined intervals, washed with deionized water, freeze dried, ground with a Wiley mill (40 micron mesh), and analyzed with a Leeman Labs Model CE440 CHN/O/S elemental analyzer (Leeman Labs Inc. 55 Technology Dr, Lowell, MA 08151) for carbon and nitrogen content.

Feeding Trials

Captive snails (*M. coffeus*) between 5 and 12 mm shell width were used to determine preferences and feeding rates in the laboratory. Prior to all feeding trials, snails were starved for 24 hours. Intact, yellowing leaves from each mangrove species were collected and leaf wet weight was measured. Leaves were presented to replicate groups of

snails held in aquaria (laboratory trials). Leaves were re-weighed after one week to determine biomass loss. To determine if salinity affects the snails' feeding habits, leaves (or leaf sections) of the preferred species (determined in previous experiments) were soaked for 24 hours in water with different salinities (saltwater created with Instant Ocean®) and presented to four replicate groups of the snails in laboratory aquaria. Snail density in the aquaria was approximately 60 *M. coffeus* m⁻².

Statistical Analysis

All statistical tests were conducted with SAS (SAS Institute 1993). For data gathered once (e.g., tree density, light), simple analysis of variance (ANOVA) was used. A split-plot ANOVA using PROC MIXED was used to analyze seasonal changes in leaf biomass, salinity, standing litter, *M. coffeus* populations, crab burrows, attack rates, and litter degradation. A Tukey analysis was used with LSMEANS to test main effects (site, season, and where applicable, species) and all interactions. Tests were run to examine differences between location (Rookery Bay vs. Windstar vs. Ft. Pierce), site history (natural vs. restored), and forest type in Naples (restored, basin and fringe) with CONTRAST statements. Correlation analyses were run with PROC CORR to examine relationships between environmental and response variables.

Results

Forest Structure

Rhizophora mangle was the dominant species in the basin and fringe mangrove forests in Naples (Table 19). Relative density of *R. mangle* at these sites ranged from 58.3% to 92.9%. The Rookery Bay restoration site was dominated by *L. racemosa*, and the Windstar

restoration site had a mixture of *R. mangle* and *L. racemosa* that co-dominated the site.

Avicennia germinans had the highest relative density in the Ft. Pierce basin (67.5%) and *L.*

racemosa had the highest relative density in the Ft. Pierce fringe site. The Ft. Pierce dwarf site was nearly a monoculture of small (*i.e.*, < 2 m in height) *A. germinans*.

Table 19. Mangrove forest structure from Rookery Bay, Windstar, and Ft. Pierce sites.

Location	Total Density (stems ha ⁻¹)	Dominant Tree(s)	% Relative Density	% Relative Dominance
Ft. Pierce Basin	7947	<i>A. germinans</i>	67.5	65.9
Ft. Pierce Fringe	16168	<i>L. racemosa</i>	46.4	44.2
Ft. Pierce Dwarf	17866	<i>A. germinans</i>	99.8	N/A
Rookery Bay Basin	2019	<i>R. mangle</i>	92.0	74.1
Rookery Bay Fringe	3986	<i>R. mangle</i>	92.9	70.1
Rookery Bay Restoration	10612	<i>L. racemosa</i>	92.9	86.3
Windstar Basin	2293	<i>R. mangle</i>	58.3	40.1
Windstar Fringe	5735	<i>R. mangle</i>	88.1	88.4
Windstar Restoration	6830	<i>R. mangle</i> / <i>L. racemosa</i>	43/48	53/46

Abiotic Factors

Porewater salinity varied both by site and season during the project. The Ft. Pierce dwarf forest had the highest porewater salinity and the Rookery Bay basin forest site had the lowest porewater salinity (Table 20). Fall 1999 had the lowest seasonal porewater salinity (35.2 ± 2.0 ppt) and spring 1999 had the highest seasonal porewater salinity (48.7 ± 1.5 ppt).

Porewater salinity seasonal patterns were similar at Rookery Bay and Windstar, with highest values usually seen in fall or winter while highest salinity values at the Ft. Pierce sites were during spring or summer. Differences in porewater salinity also occurred among the areas (*i.e.*, Ft. Pierce, Rookery Bay, and Windstar) and forest types (Table 20). The basin and fringe sites at Ft. Pierce were higher in porewater salinity than the basin and fringe sites at

Table 20. Environmental variables from nine mangrove forest sites in Naples and Ft. Pierce, Florida.

	Ft. Pierce			Rookery Bay			Windstar		
	Basin Restoration	Fringe	Dwarf	Basin	Fringe	Restoration	Basin	Fringe	
Forest density (number ha ⁻¹)	7947	16168	17866	2019	3986	10612	2293	5735	6830
Salinity (ppt)	60	45	64	29	28	30	37	31	41
Leaf litter fall (g m ⁻² yr ⁻¹)	560	715	105	807	844	867	792	755	691
Standing leaf litter (g m ⁻²)	64	77	28	116	70	89	169	73	245
<i>M. coffeus</i> density (number m ⁻²)	16	2	4	38	91	105	5	1	129
Crab burrows (number. m ⁻²)	35	167	16	65	78	160	146	312	56

both of the Naples (*i.e.*, Rookery Bay and Windstar) sites ($P \leq 0.001$). The Windstar sites had higher porewater salinity than the Rookery Bay sites ($P \leq 0.001$). Differences in porewater salinity between forest types (basin and fringe) followed similar patterns previously reported in other studies, with basin forests having higher salinity than fringe forests, generally attributed to the basin forests having less frequent tidal exchange than the fringe forests (*e.g.*, Lugo 1980, Twilley *et al.* 1986, Day *et al.* 1996). The Windstar restoration site usually had higher porewater salinity values compared to the Windstar basin site, while the Rookery Bay restoration and basin sites were very similar with respect to porewater salinity (Table 20). Porewater salinity in the Ft. Pierce fringe site was significantly lower than both the basin and dwarf forests. The Rookery Bay sites along Henderson Creek (a brackish-water creek) had the lowest mean salinities, the Windstar sites (adjoining Naples Bay, a water body with salinities reflecting the Gulf of Mexico) were intermediate, and the Ft. Pierce sites (situated on the Indian River Lagoon, a high-salinity water body) had the highest mean salinities. The isolated nature of all of the Ft. Pierce sites (within a mosquito impoundment) may also decrease tidal exchange and allow evaporation to raise the salinity. Salinity in the Rookery Bay restoration site was very similar to the nearby basin site, while mean porewater salinity at the restoration site at Windstar was often more than 10 ppt higher than at the nearby basin site. The extremely high porewater salinity values seen in the Ft. Pierce dwarf site could be partly attributed to the openness of the canopy and resulting high temperatures (see discussion below). This would lead to a more rapid evaporation rate than in the other study sites and elevate porewater salinity levels.

Light levels at the Ft. Pierce dwarf site were significantly higher than at any other site (Table 20). Measures of leaf area index in Belize demonstrated the same situation with a *R.*

mangle dwarf stand (Feller 1995). Mean corrected light values were less than 20% of the ambient light at all other sites.

The Ft. Pierce dwarf site usually exhibited the highest mean high temperature (Table 20). The temperature never went below 0 °C at any of the sites while being monitored. All of the lowest recorded temperatures (less than 10 °C) occurred during winter 2000.

Litter Dynamics

The Ft. Pierce dwarf forest had a litter fall rate of $0.5 \pm 0.1 \text{ g m}^{-2} \text{ d}^{-1}$, less litter fall than at any other site, and litter fall at the other eight sites did not differ from one another (Table 20). However, when considered together, litter fall from the set of three Rookery Bay sites (basin, fringe, and restoration) was higher than the set of Windstar sites. Both the Rookery Bay and Windstar areas had greater amounts of litter fall than the Fort Pierce areas. No differences were observed among basin, fringe and restoration forest types in Naples. Leaves from the three mangrove species accounted for more than 50% of the litter fall in all sites, and no other component accounted for more than 25% of the litter fall at any site. Leaf litter fall varied greatly among the different sites and was usually dominated by *R. mangle*. Woody and reproductive components (*e.g.*, flowers and propagules) were highly seasonal and variable.

The standing leaf litter biomass varied widely within and among sites and ranged from 28 g m^{-2} (in the Ft. Pierce dwarf site) to 245 g m^{-2} (in the Windstar restoration site), (Table 20). Seasonal differences in standing litter crop did not occur. Standing litter at the Windstar sites was higher than at the Rookery Bay and Ft. Pierce sites. Wood contributed from 13.5% to 56.4% of the standing litter, and leaves contributed from 19.3% to 44.4% of the standing litter. *Rhizophora mangle* leaves were usually a much greater component of the standing litter than either *A. germinans* or *L. racemosa*.

Leaf turnover was usually higher in the fringe forests compared to other forest types (Table 21). Site-specific differences in leaf turnover rates between species occurred. For example, *A. germinans* had the highest turnover rate at both of the Naples fringe forests (i.e., Windstar and Rookery Bay), and *L. racemosa* had the highest turnover rate at both of the Naples restoration forests.

No seasonal variation was observed in standing litter even though seasonal variation in litter fall occurred. This was probably related to seasonal variation in leaf detritivory and degradation rates that occurred during this study. Leaf fall was highest in Spring and Summer 1999, the same period when both leaf detritivory and degradation rates were at their peak.

Macrodetritivore Densities

As with other estimates of gastropod populations (Holle and Dineen 1957, Mook 1973, Joyce and Weisberg 1986, Donnay and Beissinger 1993, Peck *et al.* 1994), *M. coffeus* densities at these sites were patchy and variable (Table 20). *Melampus coffeus* occurred in relatively high numbers at all Rookery Bay sites. The highest densities were observed at the Windstar restoration site (128.8 ± 43.0 *M. coffeus* m⁻²), although relatively few *M. coffeus* were observed in the other Windstar sites (Table 20). The Rookery Bay sites (basin, fringe, and restoration) had higher densities of *M. coffeus* compared to all sites except the Windstar restoration site (Table 20). Higher densities of *M. coffeus* generally occurred in spring and summer 1999 compared to fall 1999 and winter 2000. Excluding the restoration sites in Naples and the dwarf site in the Ft. Pierce (to enable a comparison of like sites), the Rookery Bay *M. coffeus* density was greater than either that of Windstar or the Ft. Pierce. Within the Naples study areas (i.e. Rookery Bay and Windstar), the restoration sites had higher *M. coffeus* than either the basin or fringe sites (Table 20).

The density of crab burrows, as an index of crustacean activity (Lee 1989a, Knott et al. 1997, Twilley et al. 1997) varied by site (Table 20). The Windstar fringe site had the largest number of crab burrows and the lowest number of burrows was seen at the Ft. Pierce dwarf site. Within the Ft. Pierce sites, the fringe area had the highest number of crab burrows.

Macrodetritivore Leaf Consumption

Direct (watching detritivore activity) and indirect (examining attacked leaves) observations of detritivory indicated that leaves at the Naples sites were almost always consumed by *Melampus coffeus* (pers. obs.), while decapod crustaceans appeared to be the primary consumers of leaves at the Ft. Pierce fringe site (Figure 27). As seen in other regions (Lee 1989b, Robertson and Daniel 1989b), in several cases less than 24 hours passed before leaves were completely skeletonized, consumed, or pulled into crab burrows. The Ft. Pierce fringe site had the highest mean attack rate, and decapod crustaceans (primarily *Sesarma cinereum*, *Goniopsis cruentata*, and *Pachygrapsus gracilis*) were responsible for the majority of the consumption occurring at that site. In the Ft. Pierce basin site, both *M. coffeus* and decapod crustaceans consumed tethered leaves. *Melampus coffeus* was the most important macrodetritivore at all other sites. The Windstar basin and the Ft. Pierce dwarf sites had the lowest attack rates (Figure 28).

Attack rates varied by site both among seasons and species. The highest mean seasonal attack rate occurred in spring 1999 ($22.2 \pm 1.3\%$) and the lowest mean seasonal attack rate occurred in winter 2000 ($1.2 \pm 0.4\%$). *Avicennia germinans* leaves were attacked more often ($16.7 \pm 1.0\%$) than either *Rhizophora mangle* ($12.0 \pm 0.9\%$) or *Laguncularia racemosa* ($9.8 \pm 0.8\%$). The Ft. Pierce basin and fringe sites had a significantly higher attack rate than the Rookery Bay basin and fringe sites ($p = 0.0004$), and the Rookery Bay basin and fringe sites had a significantly higher attack rate than the Windstar basin and fringe sites ($p <$

a



b



c



Figure 27. Example of partially consumed a) *A. germinans*, b) *L. racemosa*, and c) *R. mangle* leaves.

0.0001). The rate of attack in the Naples basin sites (*i.e.* Rookery Bay Basin and Windstar Basin) was lower than in Naples fringe (*i.e.* Rookery Bay Fringe and Windstar Fringe, $p < 0.0001$) and the Naples restoration sites (*i.e.* Rookery Bay Restoration and Windstar Restoration, $p = 0.0375$). The Naples fringe and restoration sites were not different.

With the exception of the Ft. Pierce dwarf, Windstar basin and Windstar fringe sites, spring 1999 or summer 1999 had the highest seasonal mean attack rates within each site. Winter 2000 had the lowest seasonal mean attack rates within all sites and was less than 6% at every site during that season. Attack rates at the Ft. Pierce dwarf site, Windstar basin site, and Windstar fringe site did not vary significantly among the seasons. In four sites (Ft. Pierce basin, Ft. Pierce fringe, Rookery Bay basin, and Rookery Bay fringe), both the spring and summer 1999 attack rates were more than twice as high as in fall 1999 and winter 2000 (Figure 28).

Attack rates also differed by mangrove species depending upon the site (Figure 29). *Rhizophora mangle* had the largest variation in attack rates among the different sites, ranging from $0.0 \pm 0.0\%$ (Ft. Pierce dwarf) to $39.9 \pm 4.0\%$ (Ft. Pierce fringe). The mean attack rate for *L. racemosa* ranged 14.5% and ranged 26.1% for *A. germinans*. The Rookery Bay basin site had the widest variation among species attack rates (22.1%) and the Windstar basin site had the narrowest variation among species attack rates (0.7%).

In most sites, the attack rate by macrodetritivores on *A. germinans* was high with respect to its natural occurrence on the forest floor. Macrodetritivores also consumed *L. racemosa* leaves at relatively high rates in several sites, although not as high as those of *A. germinans*. This pattern suggests that the order of preference for mangrove leaves by *M. coffeus* in these systems is: *A. germinans* > *L. racemosa* > *R. mangle*. Previous work in southwest Florida indicated that *M. coffeus* leaf preference varied, and that all three species

are consumed (McKee and Faulkner 1999, Proffitt *et al.* 1993). However, in the Ft. Pierce Fringe site, the only site where much of the consumption was done by crustaceans (pers. obs) and leaves were often pulled into crab burrows, *R. mangle* was preferred at higher levels than either *A. germinans* or *L. racemosa*.

Leaf Degradation Rates

The Ft. Pierce fringe site ($2.9 \pm 0.3\% \text{ day}^{-1}$) had the highest overall mean degradation rate (Table 21). The Windstar basin site ($0.8 \pm 0.1\% \text{ day}^{-1}$) had the lowest mean degradation rate. Significantly higher leaf degradation rates occurred in spring 1999 ($2.0 \pm 0.1\% \text{ day}^{-1}$) and summer 1999 ($2.4 \pm 0.1\% \text{ day}^{-1}$) compared to fall 1999 ($1.2 \pm 0.1\% \text{ day}^{-1}$) and winter 2000 ($0.8 \pm 0.1\% \text{ day}^{-1}$). The leaf degradation rate in winter 2000 was lower than the

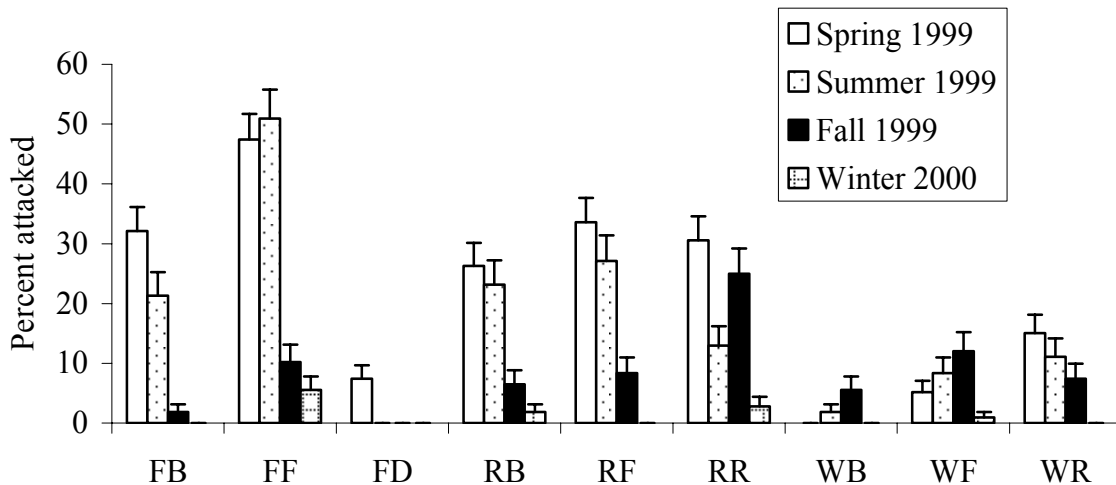


Figure 28. Attack of leaves by site and season at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida. Values are mean percentage ± 1 SE of tethered leaves that were visibly damaged by macrodetritivores. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.

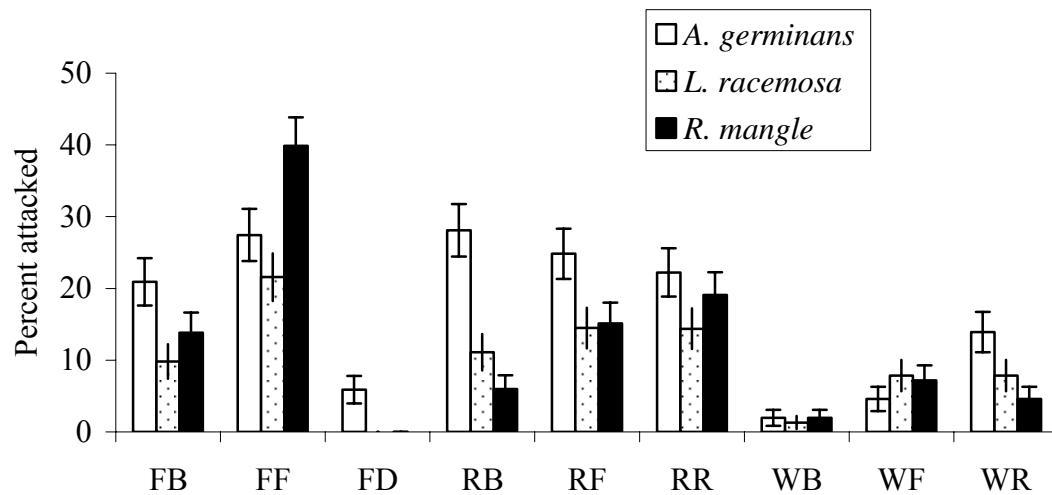


Figure 29. Attack of leaves by species and site at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida. Values are mean percentage \pm 1 SE of tethered leaves that were visibly damaged by macrodetritivores. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.

other seasons ($p < 0.0001$ compared to spring 1999 and summer 1999, and $p = 0.0141$ compared to fall 1999). Degradation rates in the Naples basin sites (*i.e.* Rookery Bay and Windstar basin sites) were significantly slower than in Naples fringe sites (*i.e.* Rookery Bay and Windstar fringe sites, $p < 0.0001$) and the Naples restoration sites (*i.e.*, Rookery Bay and Windstar restoration sites, $p = 0.0264$). Mean degradation rates for the Naples fringe sites were higher than the Naples restoration sites ($p = 0.0697$).

Leaf Consumption Rates

Leaf consumption rates, which combined percent of leaves attacked with leaf litter fall and degradation rates without leaching, varied by significantly by site, season, species and all interactions (Table 21). The Ft. Pierce Fringe site had the highest annual consumption rate

Table 21. Comparison of leaf consumption by macrodetritivores between sites, seasons, and species in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida during seasonal sampling from spring 1999 to winter 2000.

Source	F	P	Consumption rate (g m ⁻² d ⁻¹)(Mean ± 1 SE)
Site	14.36	***	
Fort Pierce Fringe			0.55 ± 0.13 ^a
Rookery Bay Fringe			0.32 ± 0.08 ^b
Rookery Bay Restoration			0.19 ± 0.05 ^{bc}
Fort Pierce Basin			0.17 ± 0.05 ^{bc}
Rookery Bay Basin			0.11 ± 0.04 ^c
Windstar Fringe			0.07 ± 0.02 ^c
Windstar Restoration			0.06 ± 0.02 ^c
Windstar Basin			0.02 ± 0.02 ^c
Fort Pierce Dwarf			0.009 ± 0.004 ^c
Season	25.77	***	
Summer 1999			0.32 ± 0.06 ^a
Spring 1999			0.28 ± 0.05 ^a
Fall 1999			0.07 ± 0.02 ^b
Winter 2000			0.002 ± 0.001 ^b
Species	11.78	***	
<i>L. racemosa</i>			0.08 ± 0.02 ^a
<i>R. mangle</i>			0.06 ± 0.01 ^a
<i>A. germinans</i>			0.02 ± 0.00 ^b
Season x site	7.42	***	
Site x species	9.47	***	
Season x species	7.33	***	
Season x site x species	4.62	***	

Notes: Post-ANOVA Tukey analyses with F-ratio and P-value presented with mean ± 1 SE.
*** $P \leq 0.001$. Different superscripts within main effects indicate significant differences ($P \leq 0.05$).

(200 g m⁻² yr⁻¹) and the Ft. Pierce Dwarf site had the lowest annual consumption rate (3 g m⁻² yr⁻¹). Consumption rates during Spring 1999 and Summer 1999 were greater than during Fall 1999 and Winter 2000. Mangrove leaf species consumption rates were greatest for *R. mangle*, intermediate in *L. racemosa* and lowest for *A. germinans*. Consumption in the Ft. Pierce sites was higher than the other two sites, while the Rookery Bay sites had higher consumption rates than the Windstar sites.

Leaf Nutrients

Avicennia germinans leaves exhibited the highest and *L. racemosa* exhibited the lowest initial mean percent nitrogen (Table 22). Leaves taken from the Rookery Bay site had the highest initial nitrogen content and those from the Ft. Pierce site had the lowest initial nitrogen content. Percent nitrogen increased for all species at all sites over the two to three week periods when leaves were tethered. The initial percent carbon content was lower in *L. racemosa* leaves compared to the other two mangrove species (Table 22). Percent carbon in the mangrove leaves slightly increased over the observation periods in all sites and all three species. As a result of increasing nitrogen and slightly increasing carbon concentrations in the leaves, the carbon:nitrogen (C:N) ratio generally decreased during the study at all sites. The lowest initial C:N ratio was seen in *A. germinans* leaves during the study, and the highest C:N ratio occurred in *L. racemosa* (Table 22). The Ft. Pierce leaves exhibited the highest and Rookery Bay the lowest C:N ratio among the sites. The C:N ratio in the two seasons was similar. Changes in the C:N ratio also decreased within all species (Figure 30), and *A. germinans* had the lowest ratio at all times. These changes in nitrogen and carbon concentrations and C:N ratios agree with Pelegri *et al.* (1997) who found similar results when comparing fresh and aged mangrove leaves.

Table 22. Comparison of the initial percent nitrogen, percent carbon and carbon:nitrogen ratio of leaves among sites, seasons, and species in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida.

Source	Percent Nitrogen (mean \pm 1 SE)	Percent Carbon (mean \pm 1 SE)	C:N Ratio (mean \pm 1 SE)
Species			
<i>A. germinans</i>	0.95 \pm 0.08	48.29 \pm 0.75	52.36 \pm 3.98
<i>L. racemosa</i>	0.47 \pm 0.03	41.60 \pm 1.40	89.79 \pm 5.15
<i>R. mangle</i>	0.78 \pm 0.15	47.30 \pm 0.57	67.98 \pm 7.89
Site			
Fort Pierce	0.61 \pm 0.07	45.45 \pm 1.47	78.66 \pm 8.43
Rookery Bay	0.89 \pm 0.18	45.35 \pm 1.94	59.97 \pm 9.19
Windstar	0.73 \pm 0.10	47.02 \pm 1.12	69.65 \pm 7.72
Season			
Fall 1998	0.76 \pm 0.13	44.98 \pm 1.44	70.51 \pm 8.61
Spring 1999	0.74 \pm 0.07	47.08 \pm 0.80	67.05 \pm 4.84

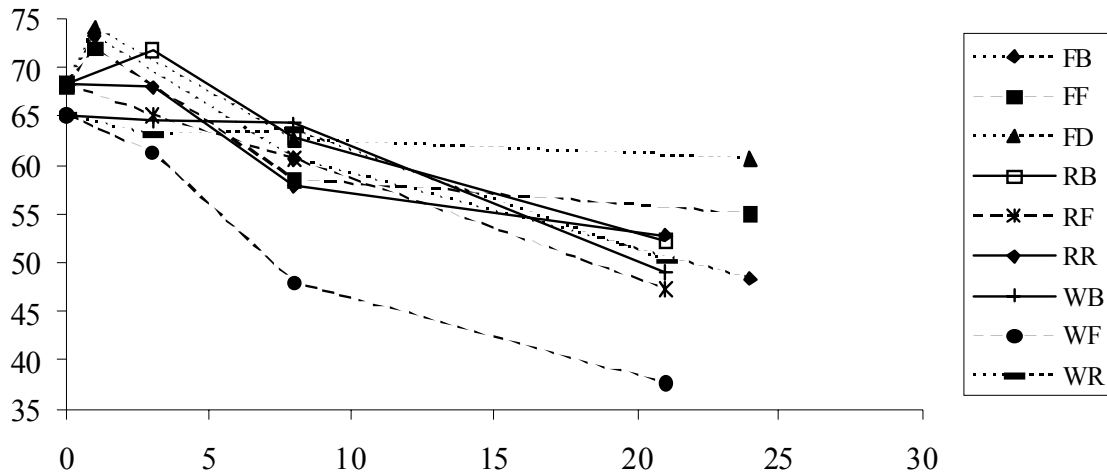


Figure 30. Carbon:nitrogen ratio for nine mangrove sites in at nine sites in Naples, Florida (Rookery Bay and Windstar) and Fort Pierce, Florida during Spring 1999. FB is Ft. Pierce Basin, FF is Ft. Pierce Fringe, FD is Ft. Pierce Dwarf, RB is Rookery Bay Basin, RF is Rookery Bay Fringe, RR is Rookery Bay Restoration, WB is Windstar Basin, WF is Windstar Fringe, and WR is Windstar Restoration.

Macrodetritivore Feeding Trials

During the laboratory feeding trials *M. coffeus* exhibited preferences for leaves of the three mangrove species tested: *L. racemosa* > *A. germinans* > *R. mangle* (Figure 31).

Approximately three times the amount of *L. racemosa* leaf material was consumed compared to *R. mangle*. No differences in consumption rates were seen between *L. racemosa* leaves soaked in water of 0 ppt salinity and 40 ppt salinity. Initial consumption of mangrove leaves occurred slower during the laboratory trials than during the field tethering trials.

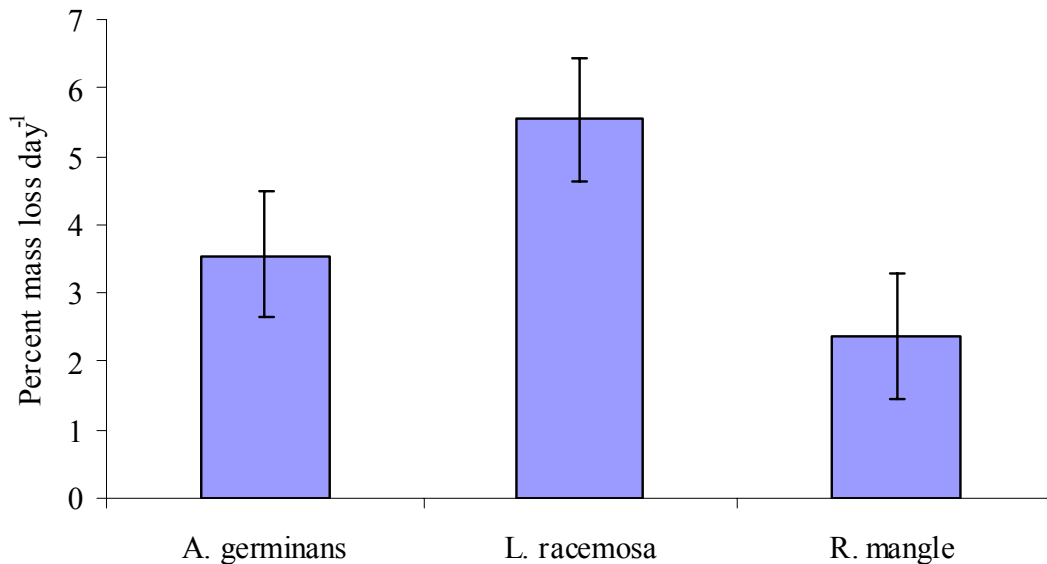


Figure 31. Mass loss of mangrove leaf species during laboratory feeding trials with *M. coffeus*.

Discussion

Macrodetritivore Community Variation

During this study, at most sites higher densities for both *M. coffeus* densities and crustacean burrows occurred in warmer seasons (spring and summer). Since these organisms hatch in the early spring months, the largest densities occur in the spring and summer, and

then decrease due to predation and other causes of mortality during the remainder of the year.

Also, as the year progresses, a shift in relative numbers in the size classes is expected, as the number of adults increases and the number of juveniles decreases (Mook 1973). Since invertebrate activity is generally higher in warmer months (due to their ectothermic metabolism) some of the extra burrows in spring and summer could be from the same number of crustaceans digging extra burrows. One reason for site-to-site variation in crustacean density could be ease of burrow creation. In areas with less impediments to digging (*e.g.*, forest floors with softer soils or less root material), crustaceans may have an easier time creating burrows and therefore either have a higher survival rate (from creation of more burrows for refugia) or expend less energy creating burrows. For example, the restoration sites generally had very rocky soil, which could impede digging efforts (Knott *et al.* 1997). Since the Rookery Bay restoration site had a relatively high number of crab burrows, this is not the driving factor at that site. Comparing within the Ft. Pierce sites, the basin and fringe seem to have similar soils, but the pneumatophores appear to be denser in the basin site (personal observation), and there are significantly fewer crab burrows at that site (Table 20).

In Ft. Pierce area, crustaceans were most active in the lower intertidal fringe forest while *M. coffeus* was the more important macrodetritivore in the upper intertidal basin forest. Several studies describe variations of important macrodetritivores by forest type and ascribe differences to factors such as amount of moisture (Lee 1989b, Slim *et al.* 1997) and sediment characteristics (Frusher *et al.* 1994).

Many factors control the community structure of macrodetritivores (as well as all other organisms). Environmental conditions, food availability, birth and growth rates, nearby communities, and predation all impact macrodetritivore populations.

Environmental conditions such as salinity, temperature, exposure, and forest structure (Table 20) provide one context within which macrodetritivores exist. Salinity, often a limiting factor in population coverage, appeared to have mixed relevance to *M. coffeus*. The Windstar restoration site, despite having the highest porewater salinity of any of the Naples sites, also had the highest *M. coffeus* densities. The other Windstar sites (basin and fringe), with slightly lower porewater salinities were relatively depauperate of *M. coffeus*. Densities at the Rookery Bay basin and fringe sites were much higher than at the corresponding Windstar sites. Salinities were high and *M. coffeus* densities low at all three Ft. Pierce sites. High temperatures and increased exposure (as measured by percent of ambient light) are highly correlated with increased porewater salinities and may increase dessication rates, which could decrease macrodetritivore populations (Lee 1989b, Slim *et al.* 1997). Forest structure provides both refugia from predators and acts as a food source.

The types, amounts, and accessibility of primary food sources also play an important role in macrodetritivore population control. Different life stages of invertebrates often require different food sources (Armitage 2004). For example, the veliger stage of *M. coffeus* probably consumes dissolved organic matter, while juvenile (< 5 mm) *M. coffeus* consume particulate organic matter, and the adults (> 5 mm) consume leaf litter. The question of whether standing litter or litter fall is more important probably depends on rates of litter fall in combination with decomposition, leaching and export rates, since this will determine the litter composition. The concentrations and relative amounts of nutrients, tannins, lignins and softer tissues in leaves can also influence macrodetritivore populations by providing more or less nutritional value.

Species life cycles, including fecundity and growth rates are both a result of success or failure of the previous cycle's population as well as an indicator of the future population. In

areas that may have an unsuitable substrate for egg-laying, the availability of nearby populations with a mobile age class that could act to supply new individuals can be important, especially for areas that may not naturally hold self-maintaining populations of their own, such as new restoration sites (Levin *et al.* 1996, Armitage and Fong 2004).

Predation on adults, juveniles and eggs also controls population structure (Joyce and Weisberg 1986, Zimmer *et al.* 2002), so it is important to understand predator avoidance capabilities of organisms and what may control predators and predation. Defenses against predation include armor, cryptic coloration, and movement. The focal species of this study (*M. coffeus* and gastropod crustaceans) are armored (with a shell and carapace, respectively) and camouflaged. Easily obtained prey would be preferable due to lower energy expenditures for capture. Ease of attainment may mean a large population, areas where prey is more vulnerable by lack of hiding places, or slow-moving populations. Predators must be able to maneuver through a site with relative ease. This would be partially related to the speed and maneuverability of the prey and partially related to the speed and maneuverability of the predator.

Several different predators feed upon *M. bidentatus*, the salt marsh snail and congeners of *M. coffeus*, including small fishes (Joyce and Weisberg 1986) and marsh birds (Hausman 1932). In what appears to be a subtidal predator avoidance response, slow-moving adult *M. coffeus* avoid inundation before high tide events by climbing up tree trunks or prop roots (Golley 1960, Mook 1973). This response occurs regardless of the actual high tide level (pers. obs.), so this may be responding to the gravitational influence of the moon as an indicator of an oncoming high tide. Therefore, *M. coffeus* appear to be more responsive to the possibility of sub-tidal predators than supra-tidal predators. Avian predators (*e.g.*, wading birds) would be around all the time, regardless of high tides. In fact, the tidal response should

make them easier targets for avian predators, because *M. coffeus* often cluster together when they are on prop roots or tree trunks, which should make the group more obvious. For gastropod crustaceans, different responses are observed. Some species retreat into burrows while others climb well into the canopy. Regardless of method, the responses to sudden nearby movements are rapid.

The restoration sites in this study had higher *M. coffeus* populations than nearby basin forests (Table 20). A lack of predation on eggs or veliger stages could be an important factor in contributing to the higher densities seen in the restoration sites (compared to nearby natural forests), since they have a much less ‘mature’ soil surface. This could prevent the existence of many of the organisms that would consume juvenile forms of *M. coffeus* in mature mangrove forests. Additionally, a lack of complex habitat structure (often found in newly-restored areas) may decrease the existing predator complex (Langellotto and Denno 2004).

Variation in Leaf Litter Consumption Rates

Leaf litter consumption should largely be a reflection of the macrodetritivore community in a particular area. However, as seen in this study, macrodetritivore consumption can vary widely within and among forest types. In Ft. Pierce, higher consumption by crustaceans occurred in the fringe area (a site with relatively high tidal activity), while *M. coffeus* was the primary consumer in the basin area (a site with lower tidal activity than the fringe site). Additionally, very little consumption occurred in the dwarf forest (a site with very irregular inundation, resulting in long periods of either no inundation or complete inundation). Macrodetritivore populations, as well as consumption rates, exhibited seasonal variations during this study. *M. coffeus* densities, crab burrows, and leaf litter consumption rates were all higher during the Spring 1999 and Summer 1999 as compared to Fall 1999 and Winter 2000.

The consumption of leaf litter by macrodetritivores affects the litter cycling process, and ultimately the amount available for export or further decomposition by physical processes or other organisms (Figure 32). For example, although litter fall in the Ft. Pierce fringe site was higher than at the nearby basin site, the amount of leaf litter available for export or accumulation after two weeks was very similar due to macrodetritivore consumption of the leaf litter (Table 23). Leaf litter fall at the Rookery Bay sites was higher than at the Windstar sites, but lower macrodetritivore leaf litter consumption rates combined with slower leaching resulted in the availability of more leaf litter for accumulation or export at the Windstar sites (Table 23). Robertson and Daniel (1989b) estimated a leaf consumption rate from 580 to 1022 g m⁻² yr⁻¹, while all other estimates have been considerably lower (Table 24). These results show the role macrodetritivores play in litter processing can vary widely within different mangrove forest types in close proximity.

Several important effects of different macrodetritivore species are visible immediately upon retrieval of leaves from tethering. Skeletonization of leaves, as seen with *A. germinans* consumption by *M. coffeus* in this study (Figure 27), leaves the more refractory petiole, midrib and veins in place. The remaining leaf components have a higher lignin content and slower decomposition rate than the blade tissue (Minderman 1968, Horner *et al.* 1988). The cutting action of crustaceans' claws often results in small pieces of leaves not being eaten but rather falling to the forest floor or decomposing within burrows (Robertson 1986, Camilleri 1989). Camilleri (1992) showed that this "sloppy feeding" increases the amount of food available for smaller decomposer organisms in Australian mangrove forests. The "screen door" appearance on leaves in mesh bags from *M. coffeus* scraping epidermal layers off of *A. germinans*, as described by Proffitt *et al.* (1993), also appeared several times during this work. As reported for other areas (Robertson 1986, Middleton and McKee 2001), crustaceans at the

Table 23. Litter cycling data from nine mangrove forest sites in Naples and Ft. Pierce, Florida.

	Ft. Pierce			Rookery Bay			Windstar		
	Basin	Fringe	Dwarf	Basin	Fringe	Restoration	Basin	Fringe	Restoration
Degradation rate (Percent mass loss d ⁻¹)	2	3	2	1	2	1	1	1	1
Consumption by macrodetritivores (g m ⁻² yr ⁻¹)	62	200	3	42	117	68	9	24	21
Leaching (g m ⁻² yr ⁻¹)	228	191	35	332	331	349	188	227	154
Available for accumulation or export (g m ⁻² yr ⁻¹)	270	324	67	433	396	450	595	504	516

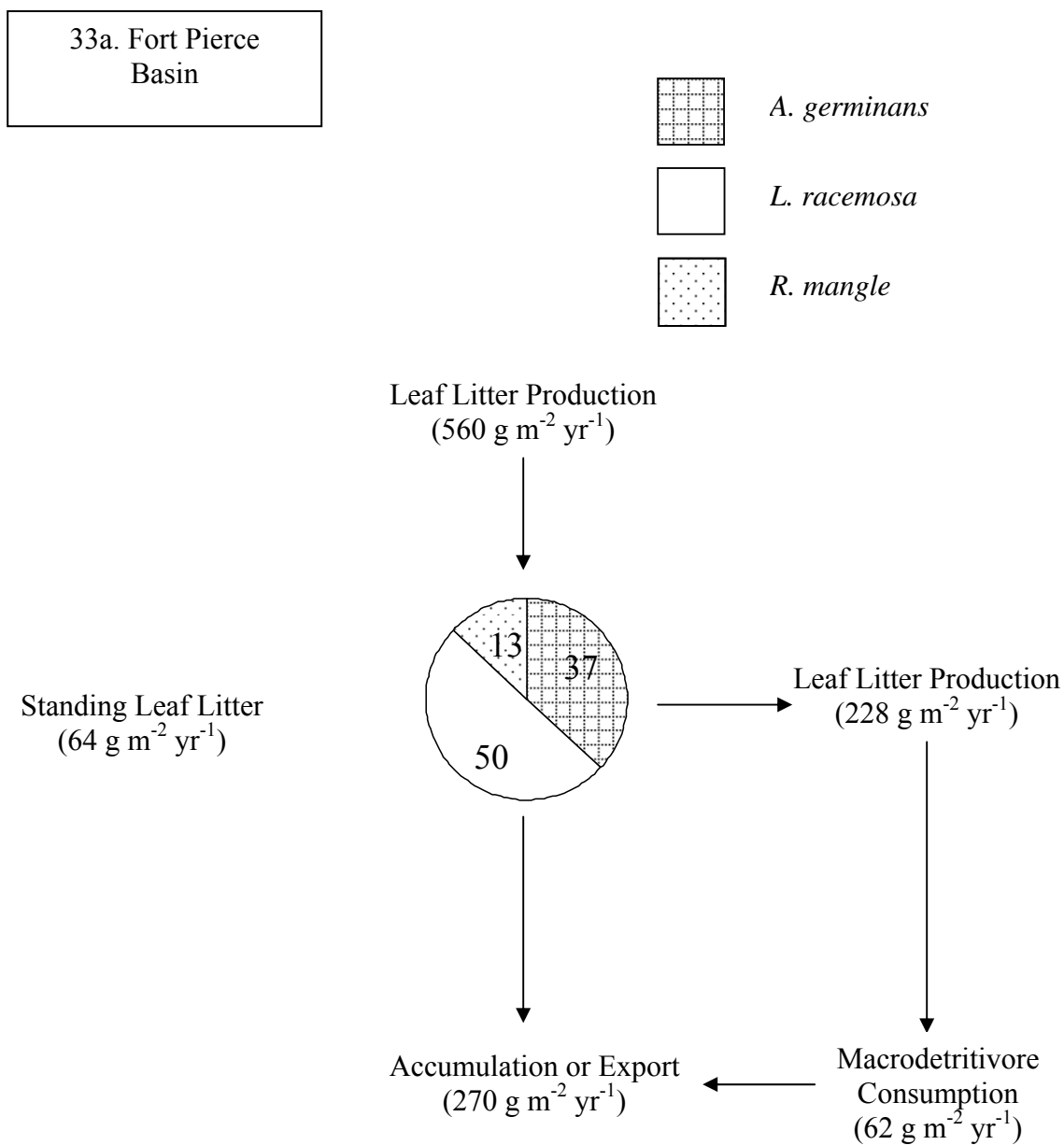


Figure 32. Cycling of matter within nine mangrove forests in Naples and Ft. Pierce, Florida. Pie charts represent relative amounts of standing litter and numbers within pie charts are percentages of standing leaf litter.

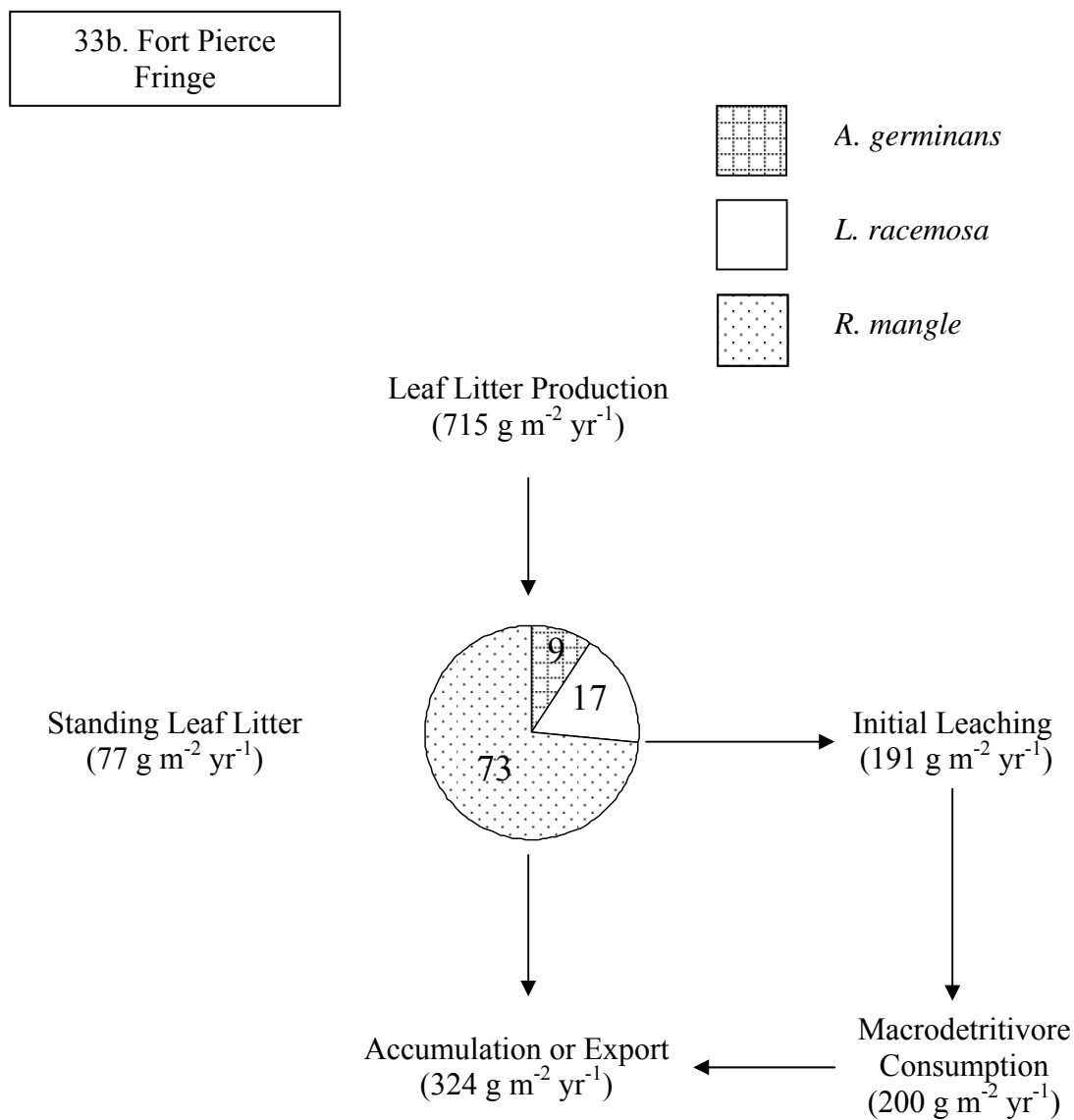


Figure 32 (continued).

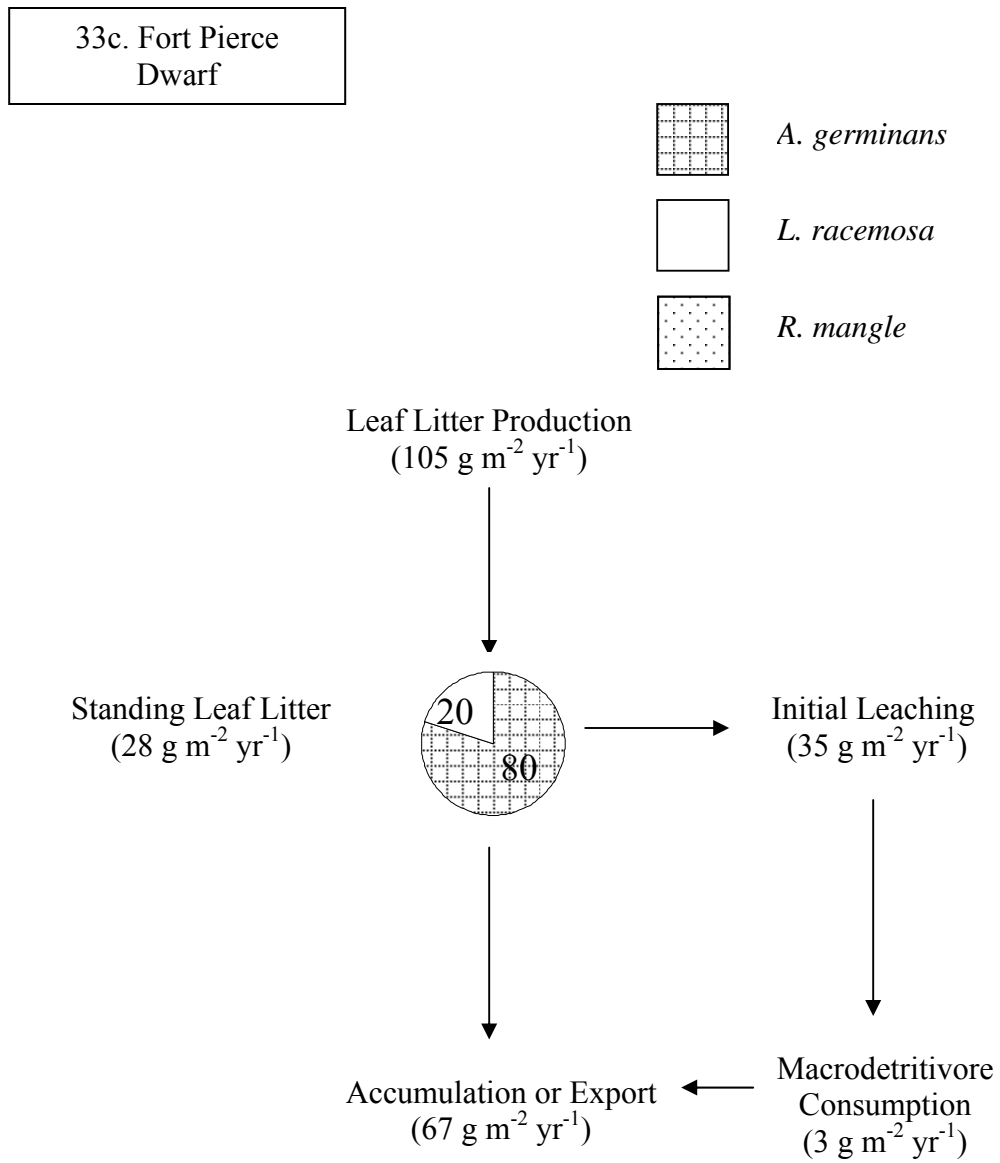


Figure 32 (continued).

33d. Rookery Bay
Basin

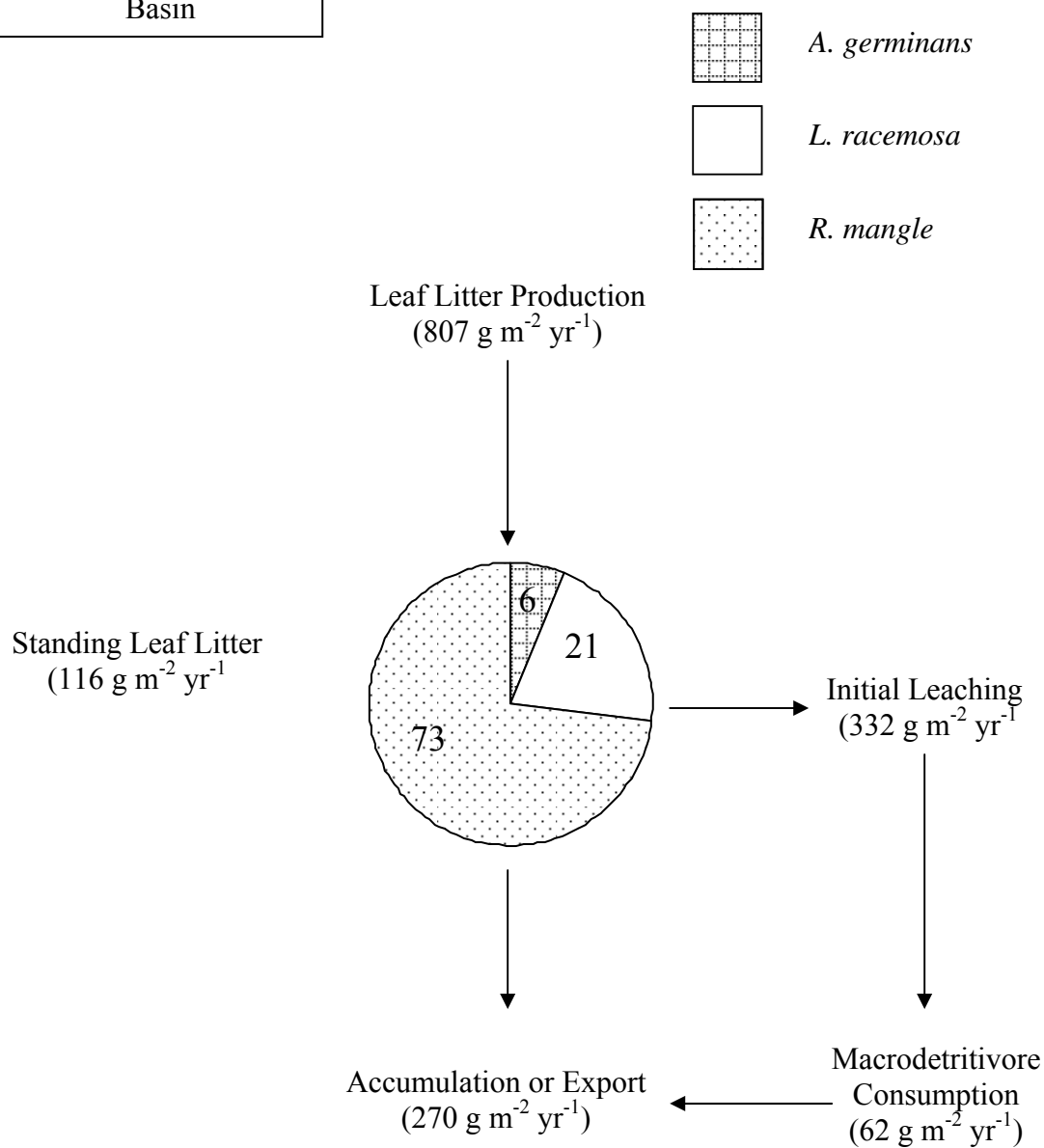


Figure 32 (continued).

33e. Rookery Bay
Fringe



A. germinans



L. racemosa



R. mangle

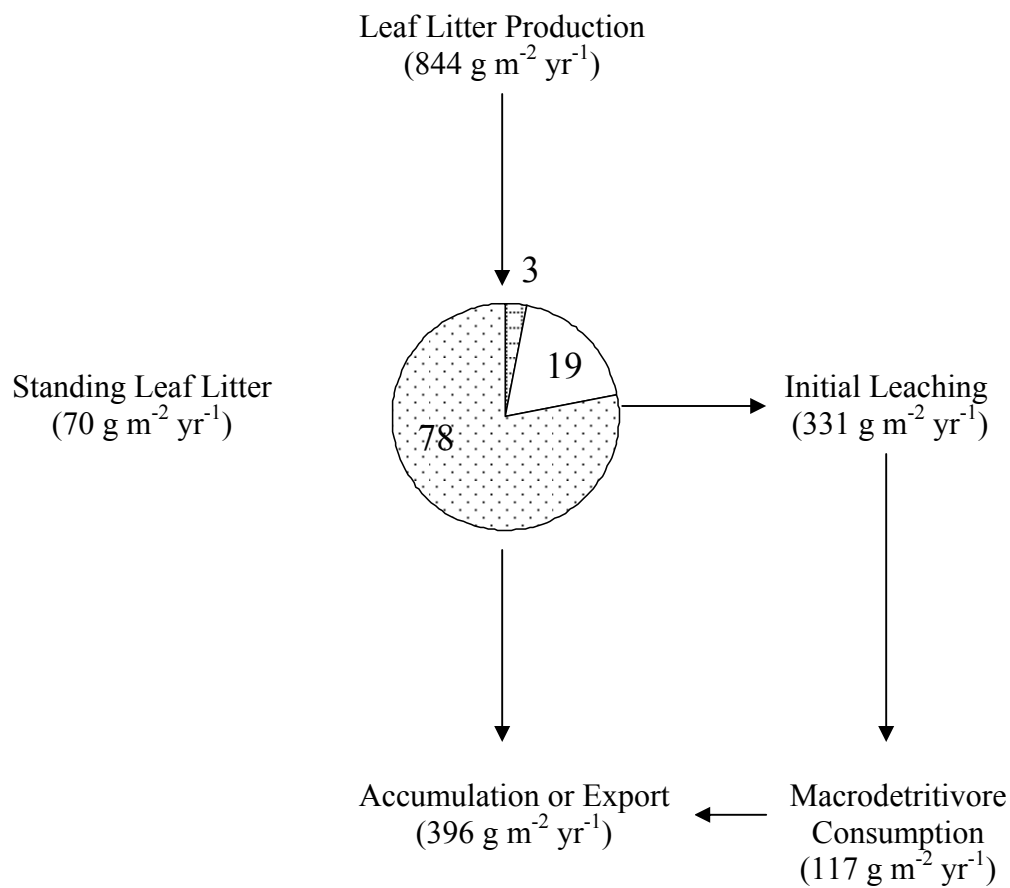


Figure 32 (continued).

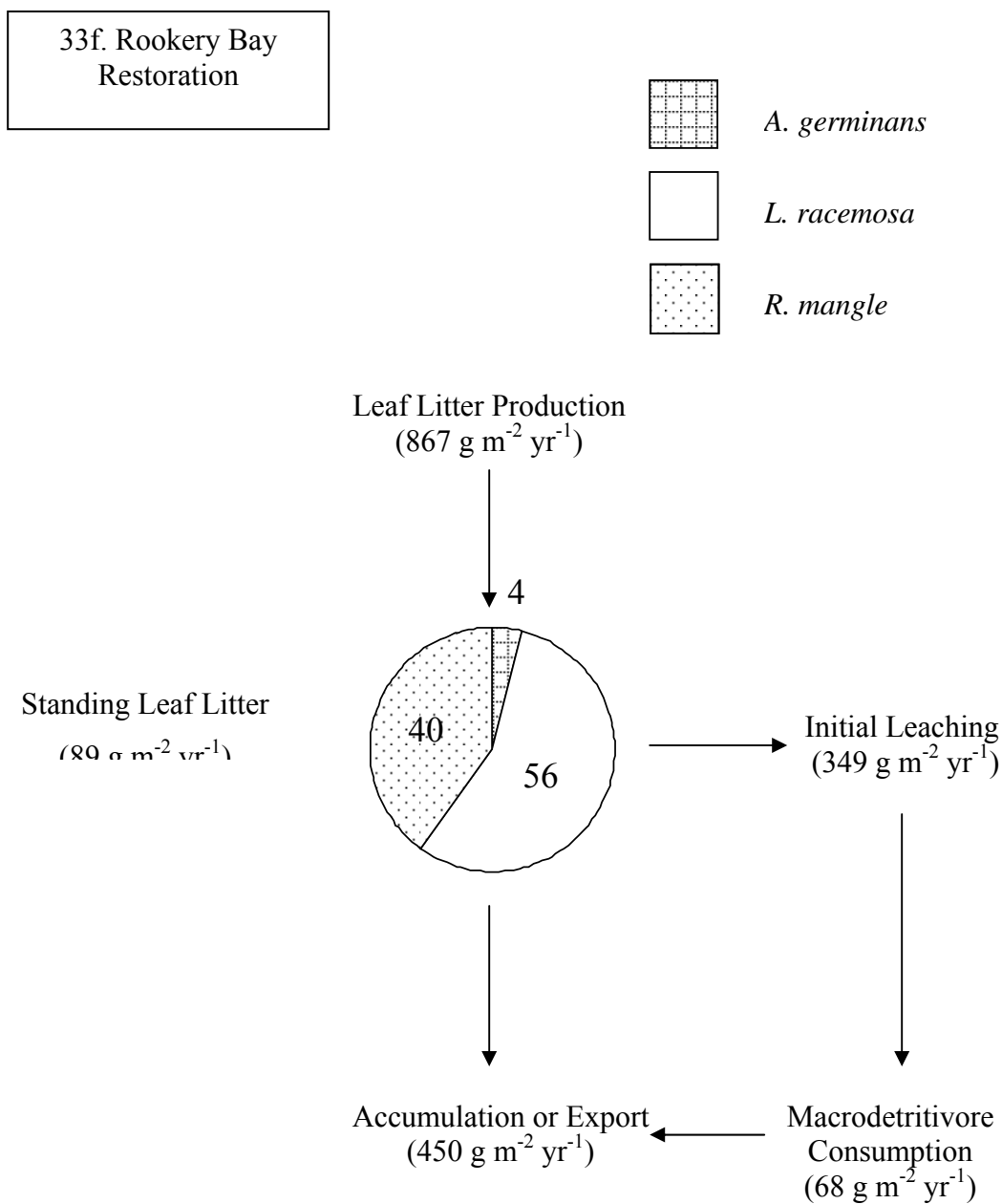


Figure 32 (continued).

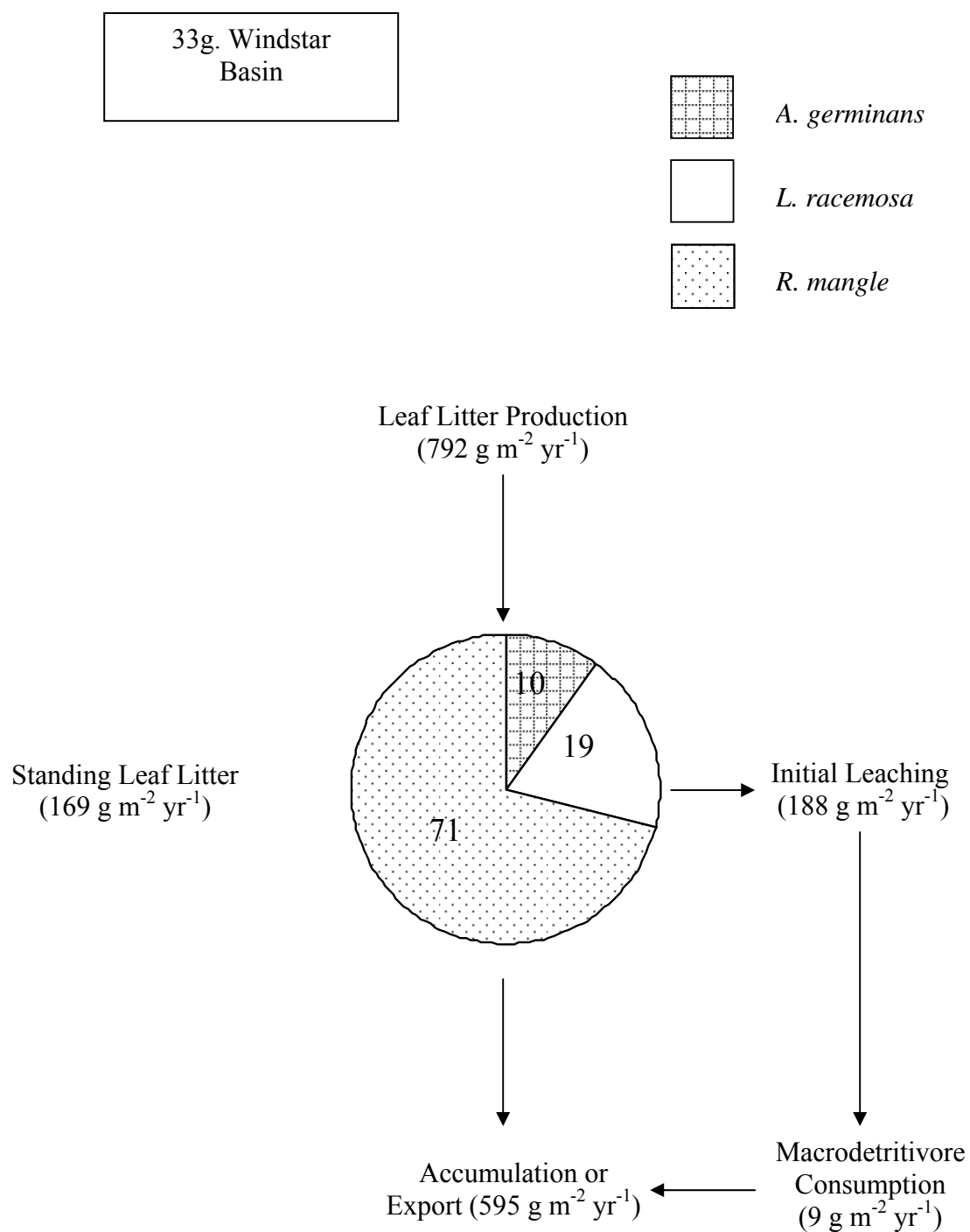


Figure 32 (continued).

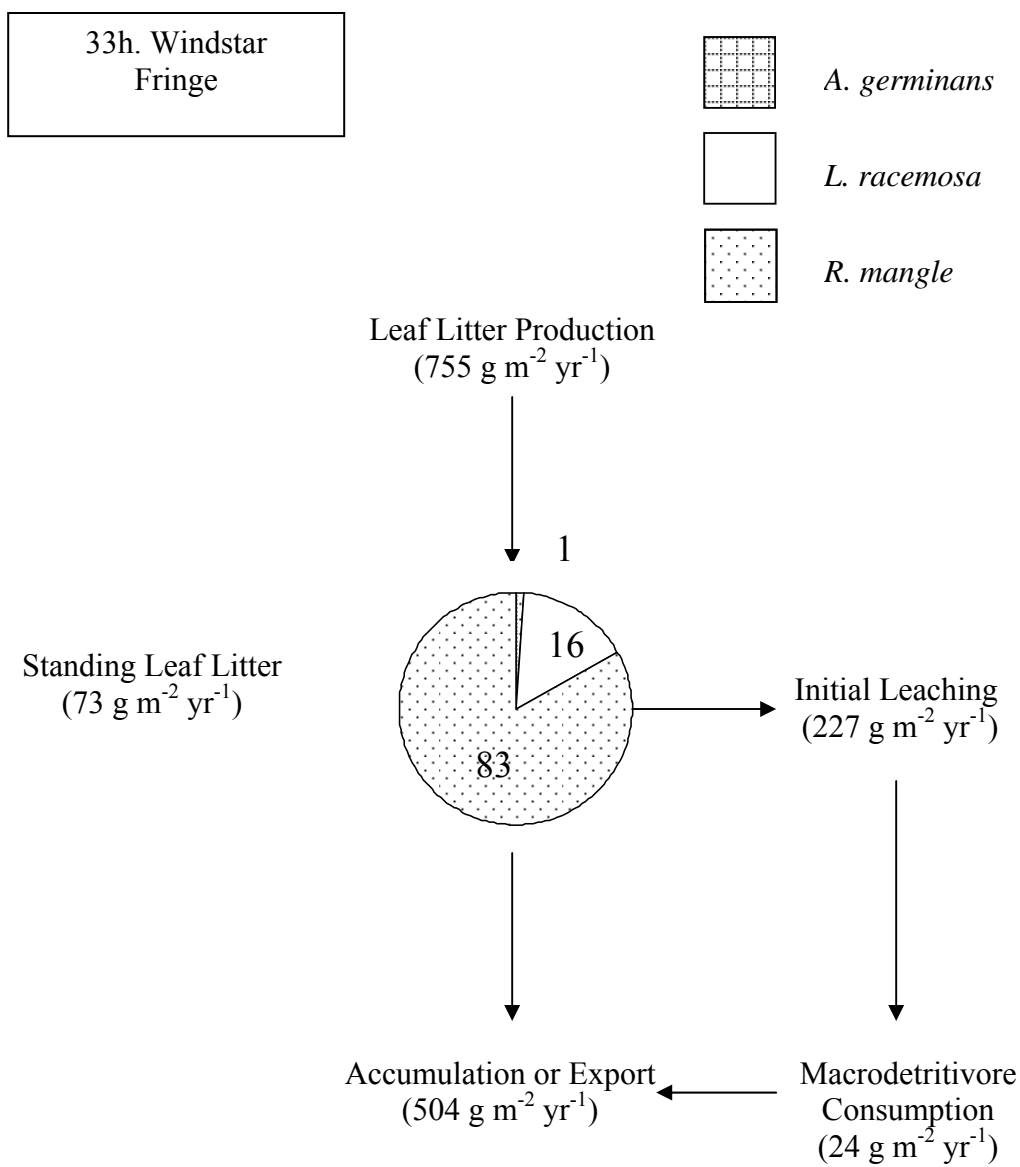


Figure 32 (continued).

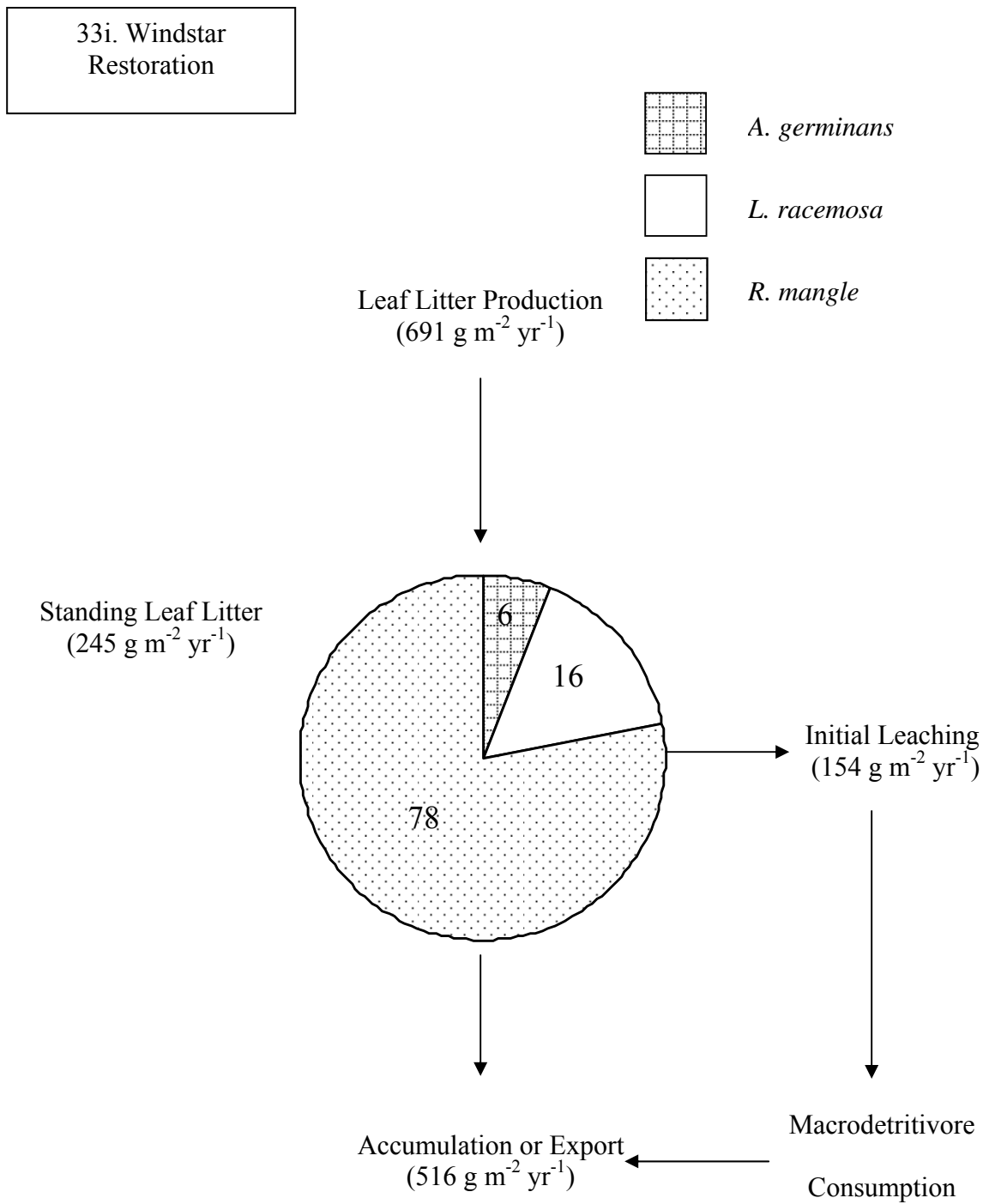


Figure 32 (continued).

Table 24. A summary of mangrove macrodetritivore studies in different geographic regions.

Macrodetritivore	Preferred leaves	Non-preferred Leaves	Study Type	Removal rates	Tidal flux and influence	Location	Citation
<i>Melampus coffeus</i> (gastropod)	<i>A. germinans</i>	<i>L. racemosa</i> <i>R. mangle</i>	Tethering	24-117 g m ⁻² yr ⁻¹	1.2 m; lower intertidal	Naples, Florida, USA	This study
<i>Melampus coffeus</i> (gastropod)	<i>A. germinans</i>	<i>L. racemosa</i> <i>R. mangle</i>	Tethering	9-68 g m ⁻² yr ⁻¹	1.2 m; upper intertidal	Naples, Florida, USA	This study
<i>Melampus coffeus</i> (gastropod)	<i>A. germinans</i>	<i>L. racemosa</i> <i>R. mangle</i>	Tethering	3-62 g m ⁻² yr ⁻¹	1.0 m; upper intertidal	Ft. Pierce, Florida, USA	This study
Grapsid crustaceans	<i>R. mangle</i>	<i>L. racemosa</i> , <i>A. germinans</i>	Tethering	200 g m ⁻² yr ⁻¹	1.0 m; lower intertidal	Ft. Pierce, Florida, USA	This study
<i>Melampus coffeus</i> (gastropod) (2000)	<i>A. germinans</i> ,	<i>R. mangle</i> <i>L. racemosa</i>	Tethering	7-204 g m ⁻² yr ⁻¹	1.2 m; upper intertidal	Naples, Florida, USA	McKee and Faulkner
<i>M. coffeus</i> (gastropod)	<i>R. mangle</i>	n/a	Tethering	2 of 100 leaves	1.2 m; various	Naples, Florida, USA	McIvor and Smith (1995)
<i>M. coffeus</i> (gastropod)	<i>A. germinans</i> , <i>R. mangle</i>	<i>L. racemosa</i>	Tethering	0-84% affected	<1.0 m; upper intertidal	St. Petersburg, Florida, USA	Proffitt <i>et al.</i> (1993)
<i>Ucides cordatus</i> , and <i>Goniopsis cruentata</i> (crustaceans)	<i>A. germinans</i> , <i>L. racemosa</i>	<i>R. mangle</i>	Tethering	1.96% day ⁻¹	<0.5 m; lower intertidal	Twin Cays, Belize	Middleton McKee 2001
<i>Ucides cordatus</i> , and <i>Goniopsis cruentata</i> (crustaceans)	<i>A. germinans</i> , <i>L. racemosa</i>	<i>R. mangle</i>	Tethering	0.02% day ⁻¹	<0.5 m; upper intertidal	Twin Cays, Belize	Middleton McKee 2001
<i>Ucides occidentalis</i> crustaceans	<i>Rhizophora</i> spp.	n/a	Placement on forest floor	up to 2 g m ⁻² d ⁻¹	>2 m; lower intertidal	Guyas River estuary, Ecuador	Twilley <i>et al.</i> 1997

Table 24 (continued).

Macrodetritivore	Preferred leaves	Non-preferred Leaves	Study Type	Removal rates	Tidal flux and influence	Location	Citation
<i>Terebralia palustris</i> (gastropod)	<i>Cerriops tagal</i>	n/a	Tethering	43 g m ⁻² yr ⁻¹	>2.5 m; upper intertidal	Gazi Bay, Kenya, East Africa	Slim <i>et al.</i> (1997)
<i>Sesarma guttatum</i> (crustacean)	<i>R. mucronata</i>	n/a	Tethering	170 g m ⁻² yr ⁻¹	>2.5 m; lower intertidal	Gazi Bay, Kenya East Africa	Slim <i>et al.</i> (1997)
<i>Sesarma</i> spp. (crustaceans)	<i>C. tagal</i> , <i>Brughiera exaristata</i>	n/a	Tethering	580-1022 g m ⁻² yr ⁻¹	>2 m; upper intertidal	Queensland, NE Australia	Robertson and Daniel (1989b)
<i>Sesarma</i> spp. (crustaceans)	<i>A. marina</i>	n/a	Tethering	173 g m ⁻² yr ⁻¹	>2 m; middle intertidal	Queensland, NE Australia	Robertson and Daniel (1989b)
<i>Sesarma messa</i> (crustacean)	<i>R. stylosa</i>	n/a	Tethering	154 g m ⁻² yr ⁻¹	> 2 m; lower intertidal	Queensland, NE Australia	Robertson (1986)
<i>Sesarma erythrodactyla</i> (crustacean)	<i>A. marina</i>	<i>B. gymnorhiza</i> , <i>R. stylosa</i>	Captive	0.2-24.7 mg dry wt ind ⁻¹ 4 days ⁻¹	>2 m	Queensland, Australia	Camilleri (1989)
<i>Sesarma</i> and <i>meinerti</i> (crustacean)	<i>A. marina</i>	n/a	Captive	285 g m ⁻² yr ⁻¹	> 2 m	Mganzana estuary, Transkei, South Africa	Emmerson McGwynne (1992)
<i>Neosarmatium smithi</i> (crustacean)	Decayed <i>Cerriops tagal</i>	Fresh, senescent <i>Cerriops tagal</i>	Captive	0.004-0.062 g ww ⁻¹ leaf g ⁻¹ crab ⁻¹ 24 h ⁻¹	> 2 m	North Queensland, Australia	Giddins <i>et al.</i> (1986)
<i>Chiromanthes bidens</i> and <i>C. maipoensis</i> (crustaceans)	Brown <i>Kandelia candel</i>	n/a	Captive	0.04 g dry wt g crab wt ⁻¹ day ⁻¹		Hong Kong, Japan	Lee (1989b)

Ft. Pierce Fringe site also transported leaves into burrows. This leaf storage presumably results in the leaching of tannins or other chemicals that may inhibit digestion of the leaf material (Giddens *et al.* 1986). Burial of leaves decreases the amount of organic matter available for export to nearby systems (Slim *et al.* 1997), but increases the amount available to organisms that can access the burrows (Giddens *et al.* 1986). This activity increases in situ nutrient cycling although some nutrient transport can occur through movement of fecal matter. Emmerson and McGwynne (1992) observed leaves brought into artificial burrows during several feeding experiments although most leaves were consumed less than 24 hours after removal. Similarly, in an Australian mangrove forest, 37.8 to 53.3 % of leaves were pulled down burrows in a 6 hour period, but most leaves retrieved from burrows only had petioles remaining and were obviously grazed (Robertson 1986).

Depending upon location or zonation, different macrodetritivore species or groups of species will impact litter degradation (Robertson and Alongi 1988, Lee 1989b, Slim *et al.* 1997). For example, crustacean consumption of leaf litter was dominant in the Ft. Pierce fringe site while the gastropod *M. coffeus* accounted for most of the macrodetritivore consumption of leaf litter in the nearby basin forest. The results from the Ft. Pierce basin and fringe sites mirrored results seen by Slim *et al.* (1997), who found that crustaceans were more active in an area with frequent tidal inundation and gastropods played a more prominent role in a less tidally active environment. In contrast, leaf litter turnover in lower and upper tidal areas of a Hong Kong shrimp pond was most affected by gastropods and crustaceans, respectively (Lee 1989b). Lee (1989b) partly attributed the zonation of macrodetritivores to a greater need of moisture by gastropods.

The Pacific Rim is considered to be the center of mangrove origin, as evidenced by the higher number of mangrove plant species in that region compared to other parts of the

world, although concern exists regarding the generality of this evolutionary pathway (Duke 1992). The Pacific Rim region also appears to have greater macrodetritivore activity (Table 23) than the New World, which could be partly due to a longer or different evolutionary history of the mangrove ecosystem there as compared to the Neotropics. However, environmental factors could also be contributing to the presence of very active macrodetritivores in these forests. Additionally, one of the important differences is the macrodetritivore species present, especially whether crustaceans or gastropods dominate the location.

Much work attempts to understand differences and similarities between systems varying geographically (e.g., New World v. Old World) or situated in different energy areas of an ecosystem (e.g., basin v. fringe). This work indicates that the generally accepted paradigm of geographic differences in macrodetritivore roles in initial litter processing and potential effect on ecosystem carbon and nutrient dynamics needs revision. As seen elsewhere (Lee 1989b, McKee and Faulkner 2000), macrodetritivore impacts on leaf litter degradation occurred in several different mangrove forest types and under different environmental conditions within this study. In addition, the scale of the impact that macrodetritivores had varied among forest types, site histories, locations, and macrodetritivore characteristics.

Robertson and Daniel (1989b) stated that, contrary to effects of macrodetritivores in Australia, Caribbean macrodetritivore influence decreases with distance from low tide level. However, the reference they use as an authority for the Caribbean (Twilley *et al.* 1986), only mentions that higher grazing of mangrove leaves by invertebrates may occur in moister areas and did not actually measure detritivore impacts. Middleton and McKee (2001) found that crustacean consumption of leaf litter was greatest at lower intertidal zones on a Belizean

island. During the current study, macrodetritivore activity varied inconsistently with tidal position. At Windstar, most macrodetritivore activity occurred in the restoration area (an upper tidal site). Rookery Bay macrodetritivore activity was similar in interior and shoreline sites. Only at Ft. Pierce did the highest macrodetritivore (crustacean) activity occur at the lowest tide level (fringe site) while less macrodetritivore (*M. coffeus*) consumption occurred in the higher tidal area (basin site). Within any tidal area, rates of leaf consumption are controlled by the types and numbers of leaf consumers. Variations in invertebrate populations are often attributed to seasonal or short-term abiotic environmental characteristics (Heath and King 1964, Lee 1989b, Pelegri and Twilley 1998).

Much of the previous research involving macrodetritivore effects on leaf litter dynamics has focused on short-term (1 day or less) processing (Lee 1989b, McIvor and Smith 1995). Decomposition studies often examine leaf mass loss over a long time period and in litter bags that exclude macrodetritivores, while much of the macrodetritivore activity loss occurs within the first month after leaf fall due to direct consumption (Lee 1989a, Robertson and Daniel 1989b, McKee and Faulkner 2000). As demonstrated within this study, organisms with extremely obvious or rapid removal techniques (*e.g.*, crustaceans pulling leaves into burrows almost immediately after leaf abscission) will not always be those that significantly impact degradation and cycling (McKee and Faulkner 2000). During this study many of the leaves were completely consumed or removed from the forest floor (*i.e.*, buried by crustaceans) during the two to three week period that the leaves were tethered.

Previous studies demonstrated that seasonal patterns of macrodetritivore consumption of leaf litter do occur. McKee and Faulkner (2000) observed a variation in macrodetritivore activity over time, although seasonal differences were not reported.

Mangrove leaf removal by sesarmid crabs followed the seasonality of litter fall in Australia (Robertson 1986, Robertson and Daniel 1989b). Twilley *et al.* (1997) suggested that leaf removal in a mangrove forest in Ecuador would be greater during the rainy season due to higher crustacean activity at that time. During this study, seasonal differences were also apparent, with warmer seasons (i.e., Summer and Spring) having greater *M. coffeus* densities (Table 20) and macrodetritivore consumption rates (Table 21) than cooler seasons (i.e., Fall and Winter). The warmer seasons (Spring 1999 and Summer 1999) also showed a greater degradation rate compared to cooler seasons (Fall 1999 and Winter 2000).

Several inter-related processes affect initial leaf litter consumption and turnover in mangrove forests. Previous discussions regarding macrodetritivore species composition are extremely relevant. Different species and different populations of macrodetritivores consume leaf litter at different rates. Additionally, different age- or size-classes of an organism often have different feeding habits. Variations in hydrology (caused by differences in tides and elevations) can result in differential leaf export (and movement of leaves between forests) and leaching rates as well as changing nutritional content of leaf litter. Forest productivity, measured as leaf litter fall, is known to vary among forest types and several environmental factors, including salinity and soil redox potential. The type of available litter (leaves or wood and nutritional content of both) affects both the ability and willingness of consumers to eat as well as the effects of physical processes that influence breakdown.

Hydrodynamically, the sites can be placed into one of two groups. Sites with constricted hydrodynamics include Ft. Pierce basin, Ft. Pierce dwarf, Ft. Pierce fringe, and Windstar restoration. Open sites include Rookery Bay basin, Rookery Bay fringe, Rookery Bay restoration, Windstar basin, and Windstar fringe. While this information must be

interpreted with caution, since three of the five open sites were at Rookery Bay and none occurred in Ft. Pierce, several differences with regards to litter cycling can be noted between the two sets of sites. With the exception of the Windstar basin site, the open sites usually had greater leaching rates than the constricted sites (Table 23). Due to their relatively high leaching rates, the open sites usually had a lower percentage of leaf litter available for export or accumulation compared to the restricted sites. Due to their higher leaching and consumption rates, the Rookery Bay sites had less available for export or accumulation compared to the Naples sites (Table 23). Constricted sites tended to have a greater percentage of standing litter compared to litter fall.

In mangrove forests worldwide, crustaceans generally have greater leaf consumption rates than gastropods (Table 24). In studies comparing nearby systems with both types of macrodetritivores (Slim *et al.* 1997, current study), crustaceans consumed more of the leaf litter than did gastropods (Table 24). However, in several instances during this study, populations of *M. coffeus* skeletonized individual leaves (Figure 27) within a 24-hour period during the tethering trials. The speed of consumption of individual mangrove leaves by gastropods seen in this study has not been reported for the New World (Proffitt *et al.* 1993, McIvor and Smith 1995, McKee and Faulkner 2000), although higher rates have occurred (Table 24).

In four of the five sites with the highest leaf attack rates, macrodetritivores, primarily *M. coffeus*, attacked *A. germinans* preferentially (Figure 29). In the other area with a high attack rate (the Ft. Pierce Fringe site), *R. mangle* was attacked most frequently. As seen in Proffitt *et al.* (1993), feeding preferences in the tethering (Figure 29) and laboratory trials (Figure 31) differed. *Rhizophora mangle* usually had the greatest amount of litter fall but was not preferentially consumed by macrodetritivores except at the Ft. Pierce Fringe site

(Figure 29). The *M. coffeus* were at their greatest densities in the Naples restoration forests, areas with a dominant *L. racemosa* canopy.

Several factors can be involved in leaf choice by macrodetritivores, including nutrient and tannin content, leaf physiology, and environmental conditions (Horner *et al.* 1988, Farnsworth and Ellison 1991, McKee and Faulkner 2000). In this study, initial nutrient content (expressed as the C:N ratio) of *A. germinans* and *L. racemosa* was more palatable than *R. mangle* (Table 22). Tannin content of *Avicennia* spp. is lower than that of *Rhizophora* spp., also increasing the *Avicennia* spp. leaves palatability relative to *Rhizophora* (Handley 1954, Heath and King 1964, Neilsen *et al.* 1986). *Laguncularia racemosa* leaves were a much greater component in the litter fall as compared to standing litter, indicating that some preferential consumption may have occurred. In both of the restoration sites, turnover rates for *L. racemosa* leaves were greater than for the other two species.

Leaves that have been on the forest floor for several days or weeks are assumed to be more palatable to macrodetritivores compared to newly abscised leaves due to lower tannin concentrations from leaching and lower C:N ratios (Heath and King 1964, Camilleri 1989, Farnsworth and Ellison 1991, Wafar *et al.* 1997). When presented with fresh leaves, *M. coffeus* in captivity will often wait several days before consumption (Proffitt *et al.* 1993, this study). Similarly, in areas with infrequent inundation, macrodetritivores have more time for consumption of leaf litter compared to areas with frequent tidal inundation (Lee 1989b, Slim *et al.* 1997, this study's comparison of the Ft. Pierce basin and fringe sites, respectively). A smaller tidal amplitude may also allow for greater leaf consumption by detritivores because less material is physically removed on a daily basis. This situation could diminish the need for burial of leaves by macrodetritivores to leach tannins (Robertson and Daniel 1989b) or

other inhibitory compounds because the leaves would be leached *in situ*. Leaves on the forest floor also tend to become more nutritious over time (this study, Lee 1989b, Conner and Day 1991), thereby leading to delayed feeding by detritivores (Wafar 1997).

Consequently, short-term observations of macrodetritivore-leaf interactions over one tidal cycle or a 24-hour period (*e.g.*, McIvor and Smith 1995, Slim *et al.* 1997) may not be sufficient to fully evaluate macrodetritivore impacts in areas with infrequent tidal inundations.

Previous research showed preference by macrodetritivores for both decayed leaves (Giddens 1986, Lee 1989b, Proffitt *et al.* 1993) and newly abscised leaves (Mook 1986). Crustaceans in the Indo-Pacific (Robertson 1986, Robertson and Daniel 1989) and New World (Twilley *et al.* 1997, Middleton and McKee 2001, this study) both consume and bury new leaves shortly after abscission. If macrodetritivores preferentially consume older leaves, then the percentage of leaves attacked should increase over time. During this study, the increases in percent attack rates were often different (both less and greater) than expected from the initial attack rate. Therefore, there was not a strong indication that macrodetritivores were preferentially consuming older leaf material, even though the C:N ratio decreased during the study period (Figure 30). The decrease in the C:N ratio did not come close to the range of 17-20 usually described as of high nutritional value (Boyd and Goodyear 1971, Wafar *et al.* 1997). Mook (1986) showed that the caloric absorption of fresh *R. mangle* leaves by *M. coffeus* was more efficient than for decayed leaves. Although not studied here, macrodetritivores consuming newly abscised leaves could be responding to the visual stimulus of the bright colors of newly abscised leaves contrasting with the brown forest floor.

In situ leaf litter consumption by macrodetritivores decreases the amount of nutrients exported to nearby systems. This has important implications for nutrient cycling (Robertson and Daniel 1989) and maintenance of mangrove forests in the face of continuing sea-level rise (Cahoon and Lynch 1997, Middleton and McKee 2002). Additionally, Total Maximum Daily Loads (TMDL's) as required in the Clean Water Act of 1972 have recently become very important management and regulatory tools due to consent decrees between the U.S. Federal Government and several environmental non-governmental organizations. As the name implies, the TMDL process attempts to understand the maximum assimilative capacity of a receiving water body (*e.g.*, estuary or tidal stream) for a wide suite of pollutants. This information is then (ideally) used to regulate point and non-point discharges by surrounding developments and to encourage removal of pollutants. Knowledge of correct inputs of nutrients from natural systems (and resulting ambient conditions for the water bodies) is important in the TMDL goal-setting process. If natural inputs are over-estimated by ignoring macrodetritivore cycling of leaf litter, incorrect estimates of background loadings could be used to set allowable pollution levels too high.

Comparison of Restored and Natural Mangrove Forests

Variations in intertidal crustacean populations and changes in community structure over time have been suggested as two means to assess managed and restored mangrove forests (Ashton *et al.* 2003). Other assessments of soil and decomposition information (McKee and Faulkner 2000) and juvenile fish populations (Serviss and Sauers 2003) show that mangrove restoration projects in Florida provide ecosystem services similar to those of mature forests. Other alterations in the system, such as nearby dredging projects and hydrological alterations, may not necessarily impact the local mangrove forest structure but could change the macrodetritivore community. McKee and Faulkner (2000) showed that the

soils at these restoration sites differed from the nearby basin sites in bulk density and organic matter content, both of which can affect the composition of macrodetritivore communities (Plaziat 1984, Frusher *et al.* 1994). However, managers and restoration scientists continue to suggest and demonstrate that better assessment information needs to be gathered (Stevenson *et al.* 1999).

Restored areas should ideally begin to mimic nearby natural areas over time. The two mangrove restoration sites examined during this study (at Windstar and Rookery Bay) appear to have similarities and differences with nearby basin forests, the expected climax forest for the relative intertidal locations of the restoration projects. Environmental factors, including porewater salinity, litter fall, and standing litter were similar between each restored forest and the nearby basin forest (Table 39), although forest density was greater (with much smaller trees) within the restoration sites. Additionally, the mature basin forests were dominated by *R. mangle*, while the restored forests had a large percentage of *L. racemosa*, recognized as an early successional species. Greater numbers of *M. coffeus* occurred within the Naples restoration sites (Table 20), and the consumption rates of leaf litter were higher (but not significantly different) from those in the nearby reference (basin) forests (Table 21). Other gastropod studies have reported lower numbers in restored areas compared to nearby reference sites (Peck *et al.* 1994, Armitage and Fong 2004), but these sites had been restored within five years, while the current study examined sites 8 and 17 years post-restoration. The consumption rates within the restoration sites also more closely mimicked the nearby reference forests than the nearby fringe forests or each other. Standing leaf litter was highest in the Windstar restoration site, probably because of a constricted outlet to Naples Bay. However, due to the similarities in litter fall, consumption, and leaching rates between the sets of natural and restored forests, the amount of leaf litter

available for export or accumulation in the Naples basin and restoration sites was similar (Figure 32).

Conclusions

Macrodetritivores now have been shown to have a significant impact on mangrove leaf litter cycling within most biogeographic regions. This study demonstrated that, by removing from 3-200 g leaf biomass $\text{m}^{-2} \text{yr}^{-1}$ in several different types of mangrove forests, macrodetritivores do affect leaf litter cycling within Neotropical mangrove forests. Leaf macrodetritivory has now been shown in several New World forests, (McKee and Feller 1992, Proffitt *et al.* 1993, Twilley *et al.* 1997, McKee and Faulkner 2000, Middleton and McKee 2002, and the current research). The information comes from both North and South America and both coasts of Florida, demonstrating that macrodetritivores are important initial leaf processors and consumers in many of these systems. However, their impact varies widely due to forest type, location, and macrodetritivore community composition. Macrodetritivore communities varied widely in this study, with the Ft. Pierce fringe site dominated by grapsid crustaceans and other sites primarily populated by *M. coffeus* (or few or no macrodetritivores). The crustaceans consumed leaf litter at a much higher rate than within any of the areas with *M. coffeus*. Areas in relatively close proximity (Windstar and Rookery Bay) showed widely differing leaf litter cycle processes, with variation between the areas in litter fall, leaching, leaf consumption by macrodetritivores, and leaf litter available for accumulation or export after approximately two weeks. This variation was as great as that seen within the two areas among their respective forests types (basin, fringe, and restoration) and is probably a result of hydrologic differences, with Windstar situated on Naples Bay and Rookery Bay situated on Henderson Creek (creating a lower salinity regime for the Rookery Bay sites). The Ft. Pierce sites were completely different from either the

Windstar or Rookery Bay sites with regards to litter cycling, having both the highest (Ft. Pierce fringe) and lowest (Ft. Pierce dwarf) macrodetritivore consumption rates. Ft. Pierce fringe was the only site where the leaf consumption rate was greater than the leaching rate. Areas with similar litterfall and leaching rates (Fort Pierce fringe and the Windstar sites) had very different consumption rates (high at the Fort Pierce fringe site and low at the Windstar sites), resulting in divergent litter cycling pathways. Seasonal differences occurred, with macrodetritivore activity being greatest during warmer periods. The two restoration projects examined during this study appear to have similar functionality with regards to nearby natural forests and show the same type of variation due to hydrologic factors seen in the natural mangrove forests.

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VITA

What a wonderfully strange trip it has been. Gary Eugene Raulerson has reached that tumultuous point in his life, where, after approximately 36 years, he will no longer be a student, much to the delight (and relief) of his family. While growing up in St. Petersburg, Florida, his family did outdoor activities out the wazoo (a lot of camping and fishing, canoeing, and tubing down the Ichetucknee) and he became an Eagle Scout (explaining a lot of his interest in the natural environment and his concern about its preservation). After graduation from Lakewood High School, he attended King College, the University of North Carolina at Chapel Hill, the University of Florida, the University of Kentucky, and last (but not least), Louisiana State University and Agricultural and Mechanical College, earning several degrees along the way (five out of six is not bad). Along the way he also accumulated employment as the Senior Environmental Scientist for the Sarasota Bay National Estuary Program, gained a bunch of pets, and got married to a wonderful woman who continues to put up with him in spite of everything else.