

A MULTI-DISCIPLINARY EVALUATION OF THE INVASION AND MANAGEMENT OF
MELALEUCA QUINQUENERVIA

By

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To the Boys

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Abstract of Dissertation Presented to the Graduate School
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A MULTI-DISCIPLINARY EVALUATION OF THE INVASION AND MANAGEMENT OF
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Ecosystem invasion by exotic plant species poses a significant threat to community biodiversity, function, and stability in the Florida Everglades. One of the most problematic invasive species in this ecosystem is *Melaleuca quinquenervia* (Cav.) Blake. The goal of my dissertation was to use a multi-scale, interdisciplinary approach to evaluate the ecosystem-level consequences of the invasion and management of *M. quinquenervia*. The results presented include above and belowground storages of nutrients in invaded and non-invaded systems, alterations of soil microbial biomass and function, evaluations of biological and chemical control methods, and plant community response to a native disturbance regime in the context of management.

Overall, both the invasion and management of *M. quinquenervia* altered basic ecosystem functions of nutrient storage and cycling, plant community diversity, and community response to native disturbance. We found that in the absence of top-down control from herbivory, *M. quinquenervia* trees were able to create a positive feedback loop to growth whereby increased quality and quantity of above- and below-ground biomass drove higher levels of storage and availability of below-ground resources. In addition, analysis of large-scale research plots in native, invaded, and managed sub-tropical wetland sites revealed that the use of herbicides to

control *M. quinquenervia* invasion may damage long-term ecosystem structure and function. We found that after a seasonal fire plots that had been chemically treated to control *M. quinquenervia* populations had the lowest storages of critical plant nutrients and the fewest number of mature native trees.

The results of this study will benefit local efforts to manage invasive species. Currently there is a need to develop a better understanding of the ecological consequences of exotic species invasion and methods for countering them. This issue is vital to the restoration of the Everglades because efforts are underway to restore hydrologic systems in Florida's natural areas without a good understanding of ecosystem-level effects of exotic plants, which may ultimately hinder or even prevent restoration. Elucidation of the extent, duration, and impact of the changes caused by exotics will help in developing more effective restoration and management techniques.

CHAPTER 1 INTRODUCTION

Ecosystem Consequences and the Management of Plant Invasions

Ecosystem invasion by exotic plant species poses a significant threat to community diversity, function, and stability (Kohli et al. 2004, Yurkonis et al. 2005). Exotic plants often thrive in new habitats where they are free of top-down regulation from herbivory which allows them to out-compete native plant species and dominate ecosystems (D'Antonio and Meyerson 2002). Although it is clear that exotic species invasion can alter the basic structure of native plant communities, the resulting consequences for ecosystem function are less predictable.

Declines in native species diversity and abundance may reduce or eliminate an ecosystem's ability to provide ecological goods and services, such as waste processing and carbon sequestration (Fenn et al. 2003). However, studies have found both positive and negative changes in the rates of nutrient storage and cycling of invaded ecosystems (Ehrenfeld 2003). These changes may encompass functional changes in plant structure and growth rate which can alter above- and belowground nutrient pool sizes (Ehrenfeld 2003). For example, grassland invasion by woody plants has been shown to increase the storage of carbon in standing biomass (Jackson et al. 2002). In addition, exotic plants may differ from native species in litter nutrient concentration and relative decomposability or litter quality (Ehrenfeld 2003). A sample of 30 invasive species from Hawaii was found to have higher foliar nutrient levels as compared to native plants, potentially altering the rate of ecosystem nutrient fluxes (Baruch and Goldstein 1999).

Federal, state, and local governments have created comprehensive weed control programs to reduce the deleterious effects of these exotic plant invasions. The most common method of controlling exotic plants is by using herbicides. Applications must be made in perpetuity to

maintain satisfactory control and several programs have touted the “maintenance control” concept whereby annual costs are reduced because populations are treated regularly and thereby kept at relatively low levels of density and abundance (Ramey and Hassell 2005). However, herbicides can injure adjacent native vegetation and, despite the “maintenance control” concept, require large investments of resources. Mechanical control, or the physical removal of exotic populations, is costly and time consuming thereby limiting its effectiveness for large scale efforts. This approach can also have significant negative collateral effects on local flora and fauna.

Classical biological control attempts to reunite weeds with their coevolved natural enemies, most of which are insects (Center et al. 2002). However although successful programs are self-sustaining, they can take a decade to implement and the relatively slow action of the biological control agents is incompatible with current management practices using herbicides (Center et al. 1999). While the goal of these all these approaches is to reduce exotic populations and restore ecosystem integrity, little work has been done to monitor and evaluate their impact on ecosystem function.

***Melaleuca quinquenervia*: A Case Study of Invasion and Management in the Florida Everglades**

Melaleuca quinquenervia (Cav.) Blake, otherwise known as the paper-bark tree, cajeput, punk tree, or white bottlebrush tree is a member of the Myrtaceae family, sub family Leptospermoidae. This tall evergreen tree historically occupies tropical wetland sites throughout its native range along the eastern coast of Australia (Kaufman and Smouse 2001). It was introduced into South Florida in 1886 (Dray et al. 2006), originally for sale as an ornamental, but later was used for erosion control, as a forestry crop, and as an agricultural windrow plant (Meskimen 1962, Stocker and Sanders Sr. 1981, Bodel et al. 1994).

The exotic tree colonized and thrived in most natural areas of South Florida, including bayhead tree islands, sawgrass prairies, pine flatwoods, pastures, and cypress forests (Bodel et al. 1994). *M. quinquenervia* has several morphological adaptations that make it well suited to the dynamic environmental conditions found in South Florida including its tolerance to variable water pH, salinity, and depth (Kaufman and Smouse 2001). Dense stands of *M. quinquenervia* are found in well drained, seasonally saturated, and permanently flooded sites (Bodel et al. 1994). Plant survival is enhanced by large numbers of aerenchymenous surface roots produced shortly after flooding (Serbesoff-King 2003). Trees can produce sinker roots that extend down to the water table during dry periods (Serbesoff-King 2003). *M. quinquenervia* is also a competitive rooter and it aggressively colonizes areas dominated by the roots of native plants (Lopez-Zamora et al. 2004).

Once established, *M. quinquenervia* trees have a high growth rate and reach reproductive maturity at three years after which they may flower two to five times a year (Bodel et al. 1994). A single *M. quinquenervia* tree can hold an estimated 5.6 million viable seeds in its canopy which, once released, may remain viable in the soil for at least three years (Van et al. 1998, Rayamajhi et al. 2002). Seeds are held in capsules that open in response to desiccation, frost, or fire (Serbesoff-King 2003). The high concentrations of essential oils found in mature *M. quinquenervia* trees fuel canopy fires that can kill native vegetation. These perturbations are followed by massive releases of *M. quinquenervia* seed and may lead to the creation of *M. quinquenervia* monocultures (Serbesoff-King 2003).

By the early 1980s it became clear that *M. quinquenervia* was significantly altering the plant communities of the Florida Everglades. In 1980, a survey completed by the U.S. Forestry Service revealed that 161, 874 hectares of land was covered by “pure” *M. quinquenervia* stands

(Bodle et al. 1994). LaRoche and Ferriter (1992) estimated that once *M. quinquenervia* populations reached a critical ecosystem concentration of two to five percent, ninety-five percent infestation occurred within 25 years. Native plant communities are altered significantly following *M. quinquenervia* invasion (Mazzotti et al. 1997). DiStefano and Fisher (1983) found that the relative density, frequency, and dominance of several native plant species were diminished significantly in sites invaded by *M. quinquenervia* as compared to neighboring non-invaded sites. This difference was explained in part by potential allelopathic properties of *M. quinquenervia* leaf extracts that reduced seed germination and seedling growth of native plant species. In addition, Mazzotti et al. (1981) found decreased diversity and abundance of small mammals in *M. quinquenervia* stands as compared to native plant communities.

Myers (1984) identified the *Pinus elliottii*-*Taxodium distichum* ecotone as one of South Florida's most susceptible habitats for *M. quinquenervia* invasion. This is the transition zone between upland *P. elliottii*-dominated sites and depressional *T. distichum*-dominated swamps where neither species can grow to its full potential (Myers 1983). Greenhouse and field research in this ecotone found high survival and growth rates for *M. quinquenervia* seedlings, indicating the suitability of this area for *M. quinquenervia* invasion (Myers 1984). Ewel (1986) agreed with Myers' assessment and stated that ecosystem alteration after such introductions was inevitable and that understanding the interactions between native and introduced species was key in developing effective management strategies.

Perhaps the most successful integrated pest management project in South Florida to date has been the effort to control *M. quinquenervia* in the Everglades. Inter-agency cooperation has led to the integration of chemical, mechanical, and biological control methods to reduce the impact of *M. quinquenervia* (Ferriter et al. 2005). The South Florida Water Management District

(SFWMD) has sustained a multi-year campaign to chemically and mechanically control *M. quinquenervia* on public lands. In 2003 alone the SFWMD treated 1,795 hectares of *M. quinquenervia* with ground application and 4,118 hectares using aerial applications of herbicides (Ferriter et al. 2005). In addition, the SFWMD partially funded a biological control project headed by the United States Department of Agriculture, Agricultural Research Service (ARS) (Ferriter et al. 2005). This project, begun in 1986 at the ARS Invasive Plant Research Lab in Fort Lauderdale, is responsible for the release of four biological control agents to reduce or eliminate the capacity of *M. quinquenervia* to invade (Ferriter et al. 2005). Two of the biological agents, *Oxyops vitiosa* Pascoe (Coleoptera: Curculionidae) and *Boreioglycaspis melaleucae* Moore (Hemiptera: Psyllidae), have successfully established and are suppressing *M. quinquenervia* reproduction, growth, and recruitment on a landscape scale (Tipping et al. 2009).

Although there have been significant reductions in the rates of growth, reproduction, and spread of *M. quinquenervia* no work has been done investigating the ecosystem impacts of different management strategies (Tipping et al. 2008). Invasive plant management programs are often evaluated based on the quantity of plant biomass removed or reduction in rates of exotic population spread. However, other factors need to be considered in program evaluation including the impact on non-target vegetation, recovery of native plant communities, and alteration of ecosystem function (Denslow and D'Antonio 2005). My Ph.D. dissertation investigated the implications of *M. quinquenervia* invasion on the decomposition of organic matter, above and belowground storages of nutrients, soil microbial community biomass and function, and plant community response to a native disturbance. In addition, this work explored the consequences and benefits provided by current management strategies. The key processes measured and presented in the following chapters are identified in Figure 1-1.

Objective 1. An Investigation of Ecosystem-Alteration after Management of *Melaleuca quinquenervia*.

The first objective of my Ph.D. dissertation was to investigate the impact of the *M. quinquenervia* biological control agents on ecosystem processes. My previous research examined the potential impact of *M. quinquenervia* insect biological control agents on ecosystem processes (Martin et al. 2009). In 2005, litterfall was collected from an area dominated by mature *M. quinquenervia* trees and saplings that had been under attack by *O. vitiosa* since 1998 and *B. melaleuca* since 2002. In these plots litterfall was approximately 60 g dry weight m⁻² year⁻¹. Although not quantified, the *M. quinquenervia* leaves collected during litterfall sampling had noticeable insect feeding damage. Post biological control litterfall values were significantly lower than rates reported in other studies. Van et al. (2002) reported pre-biological control litter production of 750 to 930 g dry weight m⁻² year⁻¹. The nutrient poor, sandy surface soils of many of Florida's forests do not have a large capacity to store nutrients vital for ecosystem maintenance. Reductions in litterfall after invasion and subsequent biological management of *M. quinquenervia* may result in changes to soil nutrient storage and availability which in turn could have significant consequences for community and ecosystem restoration.

The work presented in Chapter 2 tested two main hypotheses: 1) herbivory from the biological control agents will lower *M. quinquenervia* litter quality and rates of litter production and 2) herbivore-induced changes in litter quality will lower soil nutrient storage and availability before and after a seasonal fire.

Objective 2. Assessing the Impact of a Seasonal Fire on Native, Invaded, and Managed Plots.

Many ecosystems depend on regular disturbances, such as seasonal fires, to maintain community structure and function. This is especially true in Florida where many native plant communities depend on seasonal fires (Wade et al. 1980). Fires influence ecosystem function by

opening canopies and triggering the seed release and germination of plant species (Neary et al. 1999). Fire-adapted species also rely on temporary pulses of soluble nutrients and reductions in plant competition (Neary et al. 1999). However, many of Florida natural areas have been invaded by exotic plants, including the fire-adapted *M. quinquenervia*, which have altered native fire patterns (Wade et al. 1980). While knowledge of the consequences of fire on aboveground processes is vital, belowground alterations may be of equal importance to understanding ecosystem function. Little work has been done to evaluate the effects of fire on nutrient storage and availability in Florida's invaded and managed ecosystems. Therefore, the second objective of my Ph.D. dissertation was to elucidate the changes in nutrient storages and availability in native, invaded, and managed sites after a seasonal fire.

The work presented in Chapter 3 tested two main hypotheses were tested: 1) *M. quinquenervia* invasion and treatment with an herbicide will reduce the quantity and availability of nutrients before and after a seasonal fire compared to a non-invaded site and 2) *M. quinquenervia* invasion and treatment with biological control agents will not alter the quantity and availability of nutrients before and after a seasonal fire compared to a non-invaded site.

Objective 3. An Analysis of Native and Non-native Litter Quality.

The third objective of my Ph.D. dissertation was to investigate differences in rates of organic matter turnover and nutrient release from *M. quinquenervia* litter and the litter two native tree species. Organic matter decomposition and the subsequent release of plant available nutrients is a vital ecosystem process that is controlled by biotic and abiotic factors such as environmental conditions (temperature, pH, and available moisture) and the chemical composition of plant litter. For example, the ratio of soluble fibers (e.g. sugars and carbohydrates) to resistant materials (e.g. lignin) in organic matter can affect the rate of decomposition and subsequent release of plant available nutrients. The alteration of organic

inputs after a disturbance, such as exotic plant invasions, can alter basic ecosystem structure and function (Ehrenfeld 2003, Mack and D'Antonio 2003). Baruch and Goldstein (1999) and Ehrenfeld (2003) found that the litter of exotic plants may differ from native species in chemical composition, which could alter the rate of ecosystem nutrient fluxes.

The work presented in Chapter 4 tested two main hypotheses were tested: 1) *M. quinquenervia* will have the slowest rate of decomposition and 2) *M. quinquenervia* litter will release least amount of carbon, nitrogen, and phosphorus compared to *T. distichum* and *P. elliotii* litter.

Objective 4. Recovery of Plant Community Structure after a Seasonal Fire

The fourth objective of my Ph.D. dissertation was to investigate the impact of the *M. quinquenervia* invasion and management on plant community structure in invaded and managed forest plots. It is often assumed that control methods reduce the competitive advantage of invasive plants and allow native plant communities to restore pre-invasion conditions. Approaches to restoring communities after the management of exotics can run the gamut from passive to active. The most passive approach relies on native plant communities recovering on their own, while more active methods involve directed efforts like replanting natives. Selecting the best approach depends on several factors including cost and the impact of the management itself on the native plant community. Mechanical, chemical, and biological control programs have contained the spread and eliminated the invasive potential of existing *M. quinquenervia* populations (Ferriter et al. 2005, Tipping et al. 2008, Tipping et al. 2009). However, live non-invasive *M. quinquenervia* trees remain part of vegetative landscape and are targets for future management. Treatment of remnant *M. quinquenervia* populations with chemical or mechanical methods may cause significant collateral damage to native plant communities and may

negatively influence ecosystem function. Further work is needed to determine if communities would actually benefit from the removal of this exotic, but now less invasive plant.

The work presented in Chapter 5 will test two main hypotheses: after a seasonal fire 1) plant community structure will not be different in an invaded and biologically controlled site but will be different in an invaded and chemically controlled site compared to the non-invaded site and 2) the re-invasion of *M. quinquenervia* will be most severe in the chemically controlled site compared to the biologically controlled and non-invaded sites.

Figure

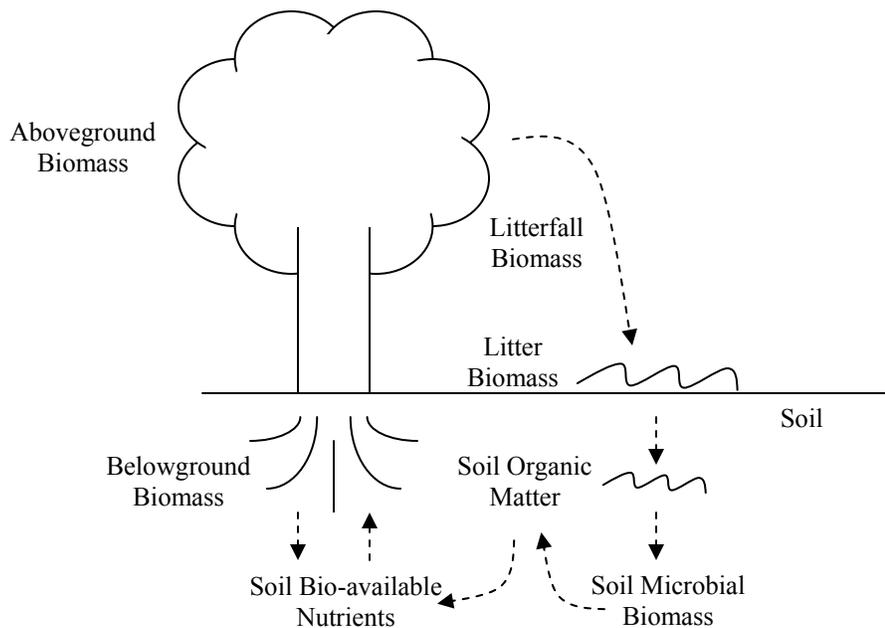


Figure 1-1. Conceptual model of a forest ecosystem indicating the potential processes and components that may be altered by *Melaleuca quinquenervia* invasion and management.

CHAPTER 2 HERBIVORY INTERRUPTS INVADER SUCCESS BY DECREASING PLANT GROWTH AND ALTERING NUTRIENT DYNAMICS

Introduction

Invasive plants can thrive in new habitats where they out-compete native plants and dominate communities and whole ecosystems (Mack and D'Antonio 1998, Mack et al. 2000, Mitchell and Power 2003). The reasons for their success are debated and have led to the creation of hypotheses that roughly break down into either top-down or bottom-up centric explanations of invasion or some combination of both (Shea and Chesson 2002, Blumenthal 2006). The enemy release hypothesis attributes their success to reductions in top-down forces where natural enemies are left behind when plants invade into a new area (Keane and Crawley 2002). Conversely, the resource hypothesis suggests that invasion is facilitated by more bottom-up forces such as resource availability (Davis et al. 2000).

The enemy release hypothesis forms the cornerstone for the practice of classical biological control of weeds whereby coevolved, host specific insect herbivores from the plant's native range are reunited with the plant in its extant range, thereby restoring some level of top-down regulation via herbivory (Mack et al. 2000). This practice has led to the successful control of many exotic species including the floating aquatic plant *Salvinia molesta* Mitchell (Room et al. 1981). However, bottom-up forces may affect top-down controls when the presence of excessive resources like eutrophication allows plants to compensate for herbivory (Heard and Winterton 2000). Blumenthal (2006) suggested that both resource availability and enemy release act in concert to facilitate invasion. He also predicted that fast-growing, presumably high resource plant species like *Melaleuca quinquenervia* (Cav.) Blake would benefit more from enemy release.

Melaleuca quinquenervia, otherwise known as the paper-bark tree, cajeput, punk tree, or white bottlebrush tree is a member of the Myrtaceae family, sub-family Leptospermoidae. This evergreen tree historically occupies tropical wetland sites throughout its native range along the eastern coast of Australia (Kaufman and Smouse 2001). It was introduced into South Florida in 1886 (Dray et al. 2006), originally for sale as an ornamental, but later was used for erosion control, as a forestry crop, and as an agricultural windrow plant (Meskimen 1962, Stocker and Sanders Sr. 1981, Bodel et al. 1994). Once established, *M. quinquenervia* trees have a high growth rate and reach reproductive maturity in three years after which they may flower two to five times a year (Bodel et al. 1994). A single *M. quinquenervia* tree can hold an estimated 5.6 million viable seeds in its canopy which, once released, may remain viable in the soil for at least three years (Van et al. 1998, Rayamajhi et al. 2002). The high concentrations of essential oils found in mature *M. quinquenervia* trees fuel canopy fires that can kill native vegetation. These perturbations are followed by massive releases of *M. quinquenervia* seed and may lead to the creation of *M. quinquenervia* monocultures (Serbesoff-King 2003).

Although there are over 450 known herbivores that provide top-down regulation of *M. quinquenervia* in its native range, there are no known native specialist herbivores that feed on the plant in its introduced range (Burrows and Balciunas 1999, Costello et al. 2003). However, currently the growth and reproductive capacity of *M. quinquenervia* are being suppressed by two intentionally introduced, specialized insect herbivores, *Oxyops vitiosa* Pascoe (Coleoptera: Curculionidae) and *Boreioglycaspis melaleucae* Moore (Hemiptera: Psyllidae) (Tipping et al. 2008). *Oxyops vitiosa* larvae and adults feed on buds and newly flushing leaves (Balciunas et al. 1994). The feeding activity of the larvae is the most damaging to the plant and causes long, window-like scars on leaves (Purcell and Balciunas 1994). Larvae are covered in a thick viscous

coating consisting of essential oils sequestered from *M. quinquenervia* which provides a potent anti-predator defense (Wheeler et al. 2002). *Boreioglycaspis melaleucae* feed on plant phloem and third through fifth instar nymphs secrete a waxy flocculence (Purcell et al. 1997, Wineriter et al. 2003). Both species are established throughout the State of Florida and are suppressing *M. quinquenervia* on a landscape level (Center et al. 2006, Tipping et al. 2008).

Many of Florida's natural areas that have been invaded by *M. quinquenervia* depend on regular disturbances like fires to maintain community structure and function. Native plant communities in these areas depend on seasonal fires to open canopies and trigger the seed release and germination of plant species, provide temporary pulses of soluble nutrients, and reduce plant competition (Wade et al. 1980, Neary et al. 1999). The invasion of *M. quinquenervia* and other exotic plants have altered native fire patterns which may have long-term consequences for ecosystem function (Wade et al. 1980). While understanding the consequences of fire on aboveground processes is vital, understanding belowground alterations to ecosystem functions is no less important particularly after the invasion and management of exotic plants.

This work was part of a larger study that examined how the absence of top-down controls affects *M. quinquenervia* growth, survival, and inter-specific competition in a resource-limited ecosystem (Tipping et al. 2009). To date, the study has found increases in plant density, height, and survival in herbivore-free plots (Tipping et al. 2009). The major objective of this work was to elucidate the mechanisms by which *M. quinquenervia* can dominate a resource limited ecosystems when freed from the top-down control of herbivory. In particular, we were interested in the consequences for above- and below-ground nutrient transfer, storage, and availability before and after a seasonal fire. Two main hypotheses were tested: 1) herbivory from the biological control agents will lower *M. quinquenervia* litter quality and rates of litter production

and 2) herbivore-induced changes in litter quality will lower soil nutrient storage and availability both before and after a seasonal fire.

Materials and Methods

Site Description

The study site was located in the Belle Meade Tract of the Picayune Strand State Forest in Collier County, Florida (Figure 2-1). This area consists of nearly level, poorly drained, low fertility soils which are loamy, siliceous, hyperthermic Arenic Glossoqualfs. The soil series is Pineda-Boca-Hallandale which is characterized by moderately to poorly drained sands over-lying limestone bedrock at a depth of approximately 1.4 m (USDA 1998). The water table fluctuates annually between greater than 15 cm below the soil surface to approximately 25 cm above. The area has a distinct wet season from approximately July to December and a dry season from January to June. Average annual rainfall in this region is approximately 1.36 m (SERC 2007). Vegetation in this area was a mixed *Pinus elliottii* Englem-*Taxodium distichum* (L.) L.C. Rich var. *nutans* (Ait.) Sweet forest with a hardwood under-story and a few mature *M. quinquenervia* trees. Over the past several decades, many areas in this landscape have been invaded more extensively by *M. quinquenervia* and are now characterized by sparse populations of mature trees with dense understories of seedlings and saplings that can exceed 100 plants per square meter.

Plot Description

This work was part of a larger study that examined how the absence of top-down controls affects *M. quinquenervia* growth, survival, and inter-specific competition. The experimental design is presented here briefly and in full in Tipping et al. 2009. In order to assess the establishment and spread of *B. melaleuca* four permanent transects were established in March 2002 radiating out in cardinal directions from a central location. Pairs of 9 m² plots, separated

by at least 10 m, were demarcated at the central location and at 30, 60, and 100 m intervals in each direction (n = 26). However, because the insect quickly spread beyond the limits of the transects, the plots were used to assess the impact of the introduced agents (Center et al. 2006).

Two treatments were assigned randomly to each pair of 9 m² plots #1) sapling or pre-reproductive *M. quinquenervia* with herbivory (hereafter referred to as the “herbivory plots”) and area #2) sapling *M. quinquenervia* with no herbivory (hereafter referred to as the “non-herbivory plots”). In both areas saplings average about 2 m in height and had not yet flowered and produced seeds. Plants in the herbivory plots have been under attack by *O. vitiosa* since 1998 and *B. melaleuca* since 2002, while those in the non-herbivory plots have been protected from herbivory by the biological control agents since 2002 by monthly foliar applications of acephate (OS—dimethyl acetylphosphor-amidothiote). A concentration of 0.367% (v/v) acephate was applied to all plant foliage until runoff every 4–6 weeks during 2003 through 2007 using a hand pressurized backpack sprayer.

In early May of 2007 the Great Basal fire burned approximately 8, 000 hectares in southwest Florida and all of the established experimental plots. As the fire was not planned no direct measurements of the fire intensity were taken. However, all of the plots were equally affected as well as the entire surrounding landscape. The above- and belowground samples were taken 24 to 48 hours after the fire.

Litter and Soil Sampling

On September 3, 2006, two 0.25 m² litter-traps were deployed in the twenty-six 9 m² plots. Litterfall was collected every month until the fire in May 2007, air dried to a constant weight, separated into component parts, and reported on a dry weight basis. On March 27, 2007 and May 15, 2007, the litterpool was sampled in every 9 m² plot (n=13 in each treatment) by placing two 0.1 m² frames on the surface of the soil and collecting all of the organic material therein.

Litterpool samples were separated into undecomposed Oi, moderately decomposed Oe, humified Oa, and woody biomass layers. Litterpool samples were air dried to a constant weight and reported on a dry weight basis. Fire intensity was estimated by calculating the percentage of the total litterpool that was lost after the May 2007 fire.

On March 27, 2007 and May 15, 2007, a belowground biomass was estimated by taking a 5 cm diameter soil core from a randomly selected location within each plot. Each belowground biomass core was separated at two depths, 0–5 cm and 5–15 cm, and sieved to separate fine roots which were then rinsed, air dried to a constant weight, and weighed. A second 5 cm diameter soil core was taken as above and also separated into 0-5 cm and 5-15 cm depths. These soil samples were returned to the laboratory, sieved to remove roots and large plant debris, homogenized, and kept at 4°C for a maximum of 10 days before microbial analysis.

Litter Quality Analysis

Litter quality was measured with a sequential extraction using an Ankom A200 Fiber Analyzer (Rowland and Roberts 1994). 0.5 g of coarsely ground litter material was weighed and sealed into Ankom filter bags. The bags were extracted with a neutral detergent to remove soluble cellular contents (sugars, carbohydrates, lipids, etc.) followed by an acid detergent to removal hemi-cellulose. The residual (hemi-cellulose, lignin, and ash) was combusted at 550°C for 4 hours to determine ash content. The resistant pool is composed of the hemi-cellulose and lignin components. Litter quality was calculated on a dry mass basis.

Soil Characteristics

Percent moisture and bulk density of soils were determined by drying 20 to 30 g sub-samples of field-moist, sieved, and homogenized soil at 70°C for three days. Bulk density and percent moisture were determined on a wet soil weight basis and pH was measured on a 2:1 water: soil slurry with an Accumet Research, AR50 dual channel pH/ion/conductivity meter.

Soil organic matter was measured by loss on ignition from 0.2 to 0.5 g samples of dried and ground soils, which were first measured into 50 mL beakers (Luczak et al. 1997). The beakers were placed in a muffle furnace and brought to 250°C for 30 minutes. The furnace temperature was then increased to 550°C for 4 hours. Organic matter content was calculated as the mass loss on ignition on a dry weight basis.

Nutrient Analyses

Dried and ground soil and plant material were analyzed for percent carbon and nitrogen on a Thermo-Electron, 1112 Series elemental analyzer. Total phosphorus was determined by a two-phase acid extraction after loss on ignition (Andersen 1976). The ash remaining in the 50 mL beaker was moistened with 2 to 3 mL distilled de-ionized water and then extracted with 20 mL of 6 N hydrochloric acid (HCl). All of the water was removed and the hot plate was placed on high for 30 minutes to completely dry the samples. After cooling, 2.25 mL of 6N HCl was added to each beaker and the beakers placed on a hot plate until almost boiling. Extracts were then filtered through a #41 Whatman filter into 50 mL volumetric flasks that were then brought to volume with distilled de-ionized water. Total phosphorus was measured with an automated ascorbic acid method on a Bran and Luebbe Auto Analyzer 3, Digital Colorimeter (Method 365.4; USEPA 1993).

Microbial Biomass

Microbial biomass carbon (MBC) was measured by a modified chloroform-fumigation extraction method (Vance et al. 1987). Two replicates of 1 g field-moist soil samples were weighed into 50 mL centrifuge tubes. One of the duplicates was immediately extracted with 25 mL of 0.5 M potassium sulfate (K_2SO_4), shaken for 1 hour, and then filtered through a Whatman #41 filter. The second replicate of soil underwent chloroform fumigation where 0.5 mL of chloroform was added to each tube and the tubes were placed in a dessicator with a beaker

containing 30 mL of chloroform and boiling chips. The dessicator was vacuum-sealed for 24 hours then alternatively filled with air and evacuated ten times to remove all residual chloroform. The tubes were then extracted as described above and all extracts were stored at 4°C until analysis for MBC. This was calculated as the difference between the total carbon in the fumigated and un-fumigated soil extracts as measured on a Shimadzu TOC 5050C, total organic carbon analyzer.

Nutrient Availability

Potentially mineralizable nitrogen (PMN) was measured with a modified incubation-extraction method that calculates a mineralization potential based on the net production of ammonium during a 10 day anaerobic incubation (White and Reddy 2000). In order to determine the initial amount of ammonium in the soil, a set of 1 g field-moist soil samples were weighed into 50 mL centrifuge tubes. The tubes received 25 mL of 0.5M K₂SO₄, shaken on a longitudinal shaker for one hour, and extracts were filtered through a #41 Whatman filter. An additional set of 1 g field-moist soil samples were weighed into 50 mL serum bottles with 5 mL of deionized water. These bottles were sealed with butyl rubber stoppers and aluminum crimps and their head-space was purged with oxygen (O₂)-free nitrogen (N₂) gas for 2-5 minutes. Bottles were incubated in the dark at 35°C for 10 days then extracted as described above with 25 mL of 0.5 M K₂SO₄ to determine final ammonium concentration. Total ammonium was determined with an automated colorimetric method on a Bran and Luebbe Auto Analyzer 3, Digital Colorimeter (Method 353.2; USEPA 1993). Specifically mineralizable nitrogen (SMN) was determined by dividing PMN by the concentration on nitrogen in the soil (SMN = PMN * TN⁻¹).

Potentially mineralizable phosphorus (PMP) was measured with a modified incubation-extraction method under aerobic conditions (Grierson et al. 1999). Soils were incubated at a

temperature of 35°C for a period of 10 days in capped 125 mL polyethylene bottles that contained 5 g of soil held under optimal percent moisture conditions (4-7%). Soils were aerated every three days and moisture content was adjusted if necessary. On day 10, soil sub-samples were collected from each incubation bottle and analyzed for available phosphorus. Soil samples were extracted with 0.1 M potassium chloride (KCl) at a ratio of 10:1, shaken for one hour, and then filtered with 0.45 µm membrane filters. Available phosphorus was measured with an ascorbic acid method on a Shimadzu Spectrophotometer UV-160 (Method 365.4; USEPA 1993). Specifically mineralizable phosphorus (SMP) was determined by dividing PMP by the concentration on phosphorus in the soil ($SMP = PMP * TP^{-1}$).

Statistical Analyses

Values of measured soil and vegetation characteristics, as well as microbial population size and activity, were calculated as a mean for each plot. ANOVA tests were used to detect any differences between the measured parameters. Differences are reported as significant for tests with p values ≤ 0.05 . Data that varied from normal distributions were transformed with square root(x), arcsin(x), or log(x+1) functions. The datasets that were transformed with the square root(x) function were: pre- and post-fire litterpool biomass and moisture, pre- and post-fire litter carbon, nitrogen, and phosphorus storage, pre- and post fire soil organic matter (0-5 cm), pre- and post fire soil nitrogen concentration (0-5 and 5-15 cm), pre and post fire nitrogen availability (0-5 cm), and pre- and post-fire microbial biomass carbon (0-5 and 5-15 cm). The fire intensity dataset was transformed with the square arcsin(x) function. The datasets that were transformed with the square log(x+1) function were: pre-and post fire carbon concentration (0-5 cm), pre- and post-fire phosphorus concentration (0-5 and 5-15 cm), pre- and post-fire soil carbon storage (0-5 and 5-15 cm), and pre- and post-fire phosphorus storage (5-15 cm). All statistical analyses were performed using JMP 7.0.1 software (SAS Institute, North Carolina, USA).

Results

Full model results for the main effects and interactions are reported in Tables A-1 through A-10. Based on the magnitude of the results the main effects of treatment, site, and depth were the most important determinants of the measured response variables. There were no consistent transect effects for any of the measured variables.

Both the total litterfall biomass and *M. quinquenervia* litterfall biomass were greater in the non-herbivory plot compared to the herbivory plot (Table 2-1, Figure 2-1). Higher concentrations of carbon, nitrogen, and phosphorus were found in the *M. quinquenervia* leaf litterfall in the herbivory plots (Table 2-2). There were no differences in the moisture, total biomass, and % biomass loss of the litter between the treatment areas (Table 2-3). Both treatment areas had lower levels of litter moisture after the fire (96.5 and 94.7% less for the herbivory and non-herbivory plots, respectively) (Table 2-3). Pre- and post-fire values for litter carbon, nitrogen, and phosphorus storage were not different between treatment areas (Figure 2-5, 2-6, and 2-7). Pre- and post-fire values for soil moisture, bulk density, and organic matter are reported in Table 2-4.

Unlike litterfall, there were no differences on the pre- or post-fire concentrations of the carbon or nitrogen in the litter between treatment areas (Table 2-5). The litter in the non-herbivory plots had the highest concentration of phosphorus both before and after the fire (Table 2-5). The soil in the non-herbivory plots had higher concentrations of carbon, nitrogen, and phosphorus at the 0-5 and 5-15 cm depths before and after the fire with one exception, namely post-fire phosphorus at 5-15 cm. (Table 2-5).

The storage of carbon in the 0-5 cm soil depth was higher after the fire in both treatment areas (1.4 and 2.3 times in the herbivory and non-herbivory plots, respectively) (Figure 2-5). The storage of carbon in the 5-15 cm soil depth was also higher after the fire in both treatment

areas (2.2 and 2.1 times in the herbivory and non-herbivory plots, respectively) (Figure 2-5). Nitrogen storage in the 0-5 cm soil depth was higher after the fire in both treatment areas (1.3 and 1.9 times in the herbivory and non-herbivory plots, respectively) (Figure 2-6). The same was true for nitrogen storage in the 5-15 cm soil depth which was also higher after the fire in both treatment areas (1.3 and 1.4 times in the herbivory and non-herbivory plots, respectively) (Figure 2-6). Phosphorus storage in the 0-5 cm soil depth was higher after the fire in both treatment areas (1.4 and 1.8 times in the herbivory and non-herbivory plots, respectively) (Figure 2-7). Similarly, phosphorus storage in the 5-15 cm soil depth was higher after the fire in both treatment areas (1.8 and 1.4 times in the herbivory and non-herbivory plots, respectively) (Figure 2-7).

Although nitrogen availability increased within both treatment areas after the fire, there were no differences between treatments (Table 2-7). Phosphorus availability did not change within treatment plots post-fire and there were no differences between treatments (Table 2-7). Microbial biomass carbon (MBC) was not different in the 0-5 cm soil depth between treatment areas, both before and after the fire, despite the fact that MBC was lower in the 0-5 cm soil depth in the herbivory plots before the fire (Table 2-8). Overall, post-fire MBC was lower within individual treatment areas at both soil depths (Table 2-8).

The data collected on the storages of carbon, nitrogen, and phosphorus were combined to give a broader ecosystem picture (Figures 2-5, 2-6, and 2-7). Before the fire, there was no difference in the total carbon storage between the two treatments ($p = 0.48$, Figure 2-5). However, after the fire, the non-herbivory plots stored more carbon than the herbivory plots ($p = 0.0343$, Figure 2-5). The total storage of nitrogen did not differ between treatments before or after the fire ($p = 0.41$ and 0.30 , Figure 2-6). However, nitrogen storage increased in both

treatment plots after the fire ($p = 0.22$ and 0.0008 , Figure 2-6). The total storage of phosphorus did not differ between the herbivory and non-herbivory plots. Although post-fire phosphorus storage increased at both depths within treatments ($p = 0.02$ and 0.003 for herbivory and non-herbivory, respectively), there were no differences between treatments either before or after the fire (Figure 2-7). Mean (\pm SE) root biomass was greater in the 0-5 cm soil depth in the non-herbivory plots ($254.43 \pm 89.5 \text{ g m}^{-2}$) compared to the herbivory plots ($70.55 \pm 15.07 \text{ g m}^{-2}$). The same was true in the 5-15 cm soil depth where mean root biomass was $240.37 \pm 45.00 \text{ g m}^{-2}$ in the non-herbivory plots and $47.01 \pm 14.06 \text{ g m}^{-2}$ in the herbivory plots.

Discussion

Herbivory and Nutrient Dynamics

Fast-growing, high resource adapted plants may disproportionately benefit from the lack of the top-down regulation of herbivory when introduced into new habitats (Fine et al. 2004, Blumenthal 2006). One such species, the Australian tree *M. quinquenervia*, has successfully colonized and invaded natural areas within Florida regardless of resource conditions. However, there is a dearth of studies on how these species maintain higher growth and reproduction rates in low resource environments. The results of this study elucidated how *M. quinquenervia* altered above- and belowground nutrient dynamics in a low resource environment in a way which may act to promote and maintain site dominance in the absence of herbivory.

As hypothesized, both the total litterfall and *M. quinquenervia* leaf biomass in the litterfall was greater in the non-herbivory plots (Table 2-1, Figure 2-1). The feeding activity of *O. vitiosa* larvae caused a significant amount of damage to the leaf material in the herbivory plots. A 2003 study showed that a single large *O. vitiosa* larvae can remove over 200 mg of fresh leaf biomass before it pupates (Wheeler 2003). Tipping et al. (2008) found that the insect exclusion treatment removed 98% of the larvae in the non-herbivory plots, resulting in 42 times fewer large larvae on

the *M. quinquenervia* trees. Plant density in the herbivore plots declined steadily over the previous five years as a direct result of herbivory by *O. vitiosa* (Tipping et al. 2009). These lower plant densities, coupled with continuing defoliation by herbivores, likely reduced the standing biomass that could contribute to litterfall in this study.

The *M. quinquenervia* leaf litterfall in the non-herbivory plots had lower tissue carbon and nitrogen concentrations compared to the herbivory plots (Table 2-2). Several studies have shown that herbivory can increase the quality of litterfall in forest ecosystems (Chapman et al. 2003, Chapman et al. 2006). Franks et al. (2006) found that high densities of *B. melaleuca* caused *M. quinquenervia* seedlings to drop leaves prematurely which could interrupt the natural cycle of nutrient resorption during senescence and result in higher quality leaf litter. Overall, there was no difference in the concentration of phosphorus in the leaf litterfall which resulted in relatively phosphorus-rich tissues in the non-herbivory plots (Table 2-2). However, the greater volume of litterfall in the non-herbivory plots offset its lower overall nutrient concentration, resulting in the transfer of 9 times more carbon, 10 times more nitrogen, and 17 times more phosphorus to the soil than in the herbivory plots during the six month sampling period (Table 2-1)

Despite the 5 fold difference in litterfall between treatments, the total litter biomass on the soil surface was not different (Table 2-3). The carbon and nitrogen concentrations of the litter were the same between treatments, while the concentration of phosphorus was greater in the non-herbivory plots (Table 2-5). This is most likely due to the relative composition of the litter between the plots where 78% of the litter in the herbivory plots consisted of relatively low-nutrient wood and humified organic material compared to only 49% in the non-herbivory plots ($p = 0.002$) (Figure 2-4). Although the variability of the litter composition complicated individual

treatment comparisons, there was clear trend of higher storages of carbon, nitrogen, and phosphorus in the herbivory plots (Figures 2-5, 2-6, and 2-7).

The high rate of litterfall and low litter biomass indicates that the organic matter in the non-herbivory plots is decomposing at a relatively rapid rate. In order to estimate turnover or residence time of the litter, it was assumed that the ecosystem was in a steady state (Chapin et al. 2002). Projecting the measured litterfall rates over a year-long period, the turnover time of the litter in the herbivory and non-herbivory plots was estimated at 4.4 and 1.6 years, respectively ($p = 0.002$). In addition, the turnover time of the litter in both treatment areas was positively correlated with resistant:P ratios of the *M. quinquenervia* leaf litterfall (Figure 2-3). Several studies have found that the ratio of soluble fibers (e.g. sugars and carbohydrates) to resistant materials (e.g. lignin) in organic matter can affect the rate of decomposition and subsequent release of plant available nutrients (Baruch and Goldstein 1999, Ehrenfeld 2003). The leaves in the non-herbivory plots contained less resistant materials and more phosphorus thereby increasing the rate of litter turnover (Table 2-2). The faster turnover of the litter in the absence of herbivory should result in significantly more nitrogen and phosphorus being mineralized and made available for plant growth.

Although the absence of herbivory significantly increased the organic matter and nutrient additions to the soil, there were no differences in nitrogen storage or availability between treatments in the 0-5 or 5-15 cm soil depths (Table 2-7). In contrast, while the storage of phosphorus was higher at 0-5 cm in the non-herbivory plots, phosphorus availability was greatest in the herbivory plots at both soil depths (Table 2-7). This result was contrary to our hypothesis that storage and availability of nutrients would be higher in non-herbivory plots. Several studies have shown that herbivory can alter the soil nutrient availability through the addition of high

quality materials (Franzluebbers 1999, Chapman et al. 2003, Ehrenfeld 2003). Chapman et al. (2006) found that herbivory by scale insects increased litter quality and nutrient cycling rates in a forested ecosystem. In contrast, we found that herbivory decreased the quantity and quality of nutrient inputs to the soil. The observed decrease in phosphorus availability in this study may indicate higher levels of microbial and plant uptake in the non-herbivory plots.

Alterations in soil microbial communities can have significant impacts on ecosystem functions like nutrient storage and cycling (Kourtev et al. 2003). Wardle et al. (2004) detailed how plant community structure drives changes in soil microbial community size and composition via a series of aboveground-belowground feedback loops. Several studies have shown that through the addition of high quality materials (e.g. frass and pre-senescent leaf litterfall), herbivory can increase levels of soil microbial biomass (Bardgett and Wardle 2003, Chapman et al. 2003). In contrast, we found that the absence of herbivory increased the addition of high quality leaf litter to the soil surface which supported higher levels of soil microbial biomass (Table 2-8). This may lead to a more rapid turnover of soil resources thereby increasing nutrient availability and potential for plant growth.

A potential mechanism whereby *M. quinquenervia* out-competes native species is through a highly competitive root system. Lopez-Zamora et al. (2004) found that *M. quinquenervia* plants developed higher root densities than native grass competitors and maintained these densities throughout the soil profile, independent of moisture content. Similarly, Martin et al. (2009) found that the ratio of aboveground to belowground biomass was higher in a *M. quinquenervia* invaded forest compared to a native forest. In this study there were 4.2 times more root biomass in the non-herbivory plots ($p = 0.001$). This may be a function of plant density with 29.2 saplings growing in the herbivory plots and 70.8 saplings growing in the non-

herbivory plots (Tipping, unpublished data). However, trees in the non-herbivory plots still produced 1.73 times more root biomass per plant after adjusting for density ($p = 0.004$). This relatively higher root biomass per tree may result in greater capture of nutrient resources.

Herbivory and Fire Interactions

Many of Florida's low resource forests depend on disturbances such as fire to maintain ecosystem structure and function (Wade et al. 1980, Neary et al. 1999). In the past *M. quinquenervia* has been able to benefit from native fire regimes and dominate systems (Serbesoff-King 2003). To date, no work has been done evaluating the combined effects of herbivory and fire on ecosystem function in *M. quinquenervia* dominated forests. The results of this study show that the herbivore exclusion treatment altered both the above and belowground ecosystem response to a fire.

Not surprisingly, both the herbivory and non-herbivory plots lost a significant amount of litter biomass after the fire, specifically 73 and 79%, respectively (Table 2-3). While both treatment areas experienced reductions in carbon and nitrogen storage in the litter, the non-herbivory plots lost the largest percentage of the litter carbon (74%, $p = 0.42$) and nitrogen (50%, $p = 0.4$). Other studies have reported similar losses of aboveground nitrogen after fires (Kauffman et al. 1993, Hughes et al. 2000, Wan et al. 2001, Wanthongchai et al. 2008). Nutrient losses from aboveground litter after fire can be caused by volatilization and particulate transport, transformation of organic to inorganic forms, and transport by wind and water (Certini 2005). In contrast, litter storage of phosphorus increased after the fire, a finding contrary to other reported studies (Kauffman et al. 1993, Hughes et al. 2000, Wanthongchai et al. 2008). It is possible that the intensity of the fire in our experimental plots volatilized carbon and nitrogen, while depositing phosphorus rich ash onto the soil surface. Unfortunately, as this fire was not planned, there were no intensity measurements taken during the burn.

Carbon, nitrogen, and phosphorus storage increased after the fire in both treatments at both soil depths (Figures 2-5, 2-6, and 2-7). However, soils in the non-herbivory plots stored more nutrients with the greatest increases in carbon (64%, $p = 0.44$), nitrogen (55%, $p = 0.35$), and phosphorus (83%, $p = 0.11$) storages occurring at 0-5 cm. The observed differences are likely the result of the incorporation of nutrient rich ash produced from the combustion of the larger litter pool into the surface soils of the non-herbivory plots. In addition, the non-herbivory plots had a larger per plant root biomass. The trees killed by the fire may have released nutrients from the root biomass into the soil (Certini 2005).

As expected, both plots experienced an increase in nitrogen availability post-fire, a finding supported by many studies (Giardina and Rhoades 2001, Carter and Foster 2004, Wanthongchai et al. 2008) (Table 2-7). However, while there was no difference in the availability of phosphorus in the herbivory plots, the availability of phosphorus increased in the non-herbivory plots after the fire in both soil depths (Table 2-7). As discussed above, this is most likely the result of the combustion of the larger, relatively phosphorus rich litter pool. Changes in the storage and availability of nutrients may have unpredictable future effects on ecosystem structure and function. Ross et al. (1997) found that the higher nitrogen and phosphorus availability after a fire increased the foliar nutrient content of the re-colonizing plant communities. The increases found in nutrient availability post-fire may accelerate *M. quinquenervia* growth and reproduction thereby increasing the severity of the problem.

Synthesis and Conclusion

This study identified an indirect mechanism whereby *M. quinquenervia* out-competes native plants and maintains a dominant position in low-resource ecosystems. When freed from the top-down regulation of herbivory, *M. quinquenervia* creates a positive feedback loop to growth and reproduction (Figure 2-8). Initially, high above- and below-ground biomass

production allows *M. quinquenervia* to out-compete native plants for nutrient and light resources. Higher rates of nutrient uptake produce greater amounts of high quality standing biomass, which eventually falls to the soil at a much higher volume. This high quality litter maintains a larger population of soil microbial biomass that processes litter and soil nutrients at a faster rate. The resultant mineralized nutrients are quickly taken up by the extensive *M. quinquenervia* root biomass, further increasing the production of vegetative and reproductive biomass.

The no herbivory advantages formerly experienced by *M. quinquenervia* have now been removed with the introduction and establishment of two specialized herbivores. As a result, all ages of *M. quinquenervia* are now under continuous attack by insect herbivores, from the most recently recruited seedlings to the tallest and fully mature trees. This relentless herbivory slows the rate of above-ground biomass production and reduces the size of the root zone (Figure 2-8). In addition, herbivores remove a significant amount of standing biomass, thereby preventing it from falling to the forest floor. The remaining litterfall has higher concentrations of resistant materials such as lignin which, in turn, increases its turnover time. Concomitantly smaller pools of soil microbial biomass are supported, which further reduces the rate of nutrient turnover. This is clear evidence of how herbivory not only controls populations of *M. quinquenervia* directly by reducing plant growth and reproduction, but also indirectly by interrupting its positive feedback growth cycle which would otherwise maintain its dominance in the ecosystem.

We predict that *M. quinquenervia* populations exposed to herbivory will be less invasive after native disturbances such as fire. A post-fire census of the experimental plots revealed that 73% of the trees were killed in the herbivory plots compared to only 41% of the trees in the non-herbivory plots (Tipping, unpublished data). Surviving trees in the herbivory plots may have been weakened by herbivory perhaps resulting in less root biomass which should reduce their

ability to efficiently scavenge the pulse of available nutrients produced immediately after the fire. Native plants should benefit from the reduced competition for light, space, and nutrients. In contrast, without herbivory, populations of *M. quinquenervia* will likely benefit disproportionately from the increases in storage and availability of nutrients, compared to native plants. Although some plant mortality would be expected from fires, over the longer term populations may actually benefit from reduced intra-specific competition. Thus *M. quinquenervia* would continue to invade and dominate high and low resource plant communities.

Tables and Figures

Table 2-1. Mean (\pm S.E.) of *Melaleuca quinquenervia* litterfall biomass and nutrient transfer measured in the herbivory and non-herbivory plots.

Variable	Herbivory	Non-herbivory	<i>P</i>
	-----g m ⁻² 6 months ⁻¹ -----		
<i>M. quinquenervia</i> biomass	11.0 \pm 3.79	104 \pm 5.35	<0.0001
Carbon	5.11 \pm 1.57	47.6 \pm 2.31	<0.0001
Nitrogen	0.09 \pm 0.03	0.91 \pm 0.05	<0.0001
	-----mg m ⁻² 6 months ⁻¹ -----		
Phosphorus	1.33 \pm 0.39	22.9 \pm 1.85	<0.0001

Table 2-2. Mean (\pm S.E.) of *Melaleuca quinquenervia* litterfall nutrient concentration and quality measured in the herbivory and non-herbivory plots.

Variable	Herbivory	Non-herbivory	<i>P</i>
	-----mg g ⁻¹ -----		
Carbon	511 \pm 17.0	458 \pm 9.99	0.016
Nitrogen	11.7 \pm 0.86	8.75 \pm 0.22	0.007
	-----mg kg ⁻¹ -----		
Phosphorus	225 \pm 23.5	219 \pm 12.0	0.82
	-----Mass ratio-----		
C:N	45 \pm 2.68	52 \pm 1.17	0.028
N:P	50 \pm 3.92	41 \pm 2.86	0.11
C:P	2342 \pm 246	2170 \pm 138	0.57
	-----%-----		
Soluble fiber	56.8 \pm 1.31	63.1 \pm 2.27	0.03
Hemi-cellulose	6.10 \pm 0.98	5.91 \pm 0.33	0.86
Resistant	30.7 \pm 0.52	26.7 \pm 2.01	0.01
Ash	6.41 \pm 0.13	6.31 \pm 0.29	0.75
Resistant : N	27.3 \pm 2.38	28.4 \pm 2.38	0.75
Resistant : P	1403 \pm 142	1159 \pm 97.6	0.21

Table 2-3. Mean (\pm S.E.) of pre- and post-fire litter moisture, total biomass, and % litter loss measured in the herbivory and non-herbivory plots.

Variable	Fire	Herbivory	Non-herbivory	<i>P</i>
		-----%-----		
Moisture	Pre-Fire	49.1 \pm 2.30	47.5 \pm 2.68	0.62
	Post-Fire	1.74 \pm 0.43	2.51 \pm 0.53	0.27
		-----g m ⁻² -----		
Biomass	Pre-Fire	649 \pm 93.2	683 \pm 193	0.84
	Post-Fire	182 \pm 53.8	186 \pm 50.3	0.86
		-----%-----		
% Litter loss		72.6 \pm 9.17	79.7 \pm 7.87	0.80

Table 2-4. Mean (\pm S.E.) of pre- and post-fire soil moisture, bulk density (BD), and organic matter (OM) measured in the herbivory and non-herbivory plots.

Variable	Fire	Depth	Herbivory	Non-herbivory	<i>P</i>
-----%-----					
Moisture	Pre-Fire	0-5 cm	8.36 \pm 0.56	9.44 \pm 0.32	0.11
		5-15 cm	5.61 \pm 0.09	5.89 \pm 0.18	0.17
	Post-Fire	0-5 cm	1.36 \pm 0.24	1.94 \pm 0.48	0.30
		5-15 cm	3.07 \pm 0.17	2.80 \pm 0.22	0.34
-----g cm ⁻³ -----					
BD	Pre-Fire	0-5 cm	1.20 \pm 0.05	1.02 \pm 0.06	0.035
		5-15 cm	1.42 \pm 0.01	1.33 \pm 0.03	0.018
	Post-Fire	0-5 cm	1.08 \pm 0.04	1.00 \pm 0.05	0.22
		5-15 cm	1.50 \pm 0.03	1.45 \pm 0.03	0.31
-----%-----					
OM	Pre-Fire	0-5 cm	1.39 \pm 0.14	1.96 \pm 0.31	0.06
		5-15 cm	0.51 \pm 0.05	0.55 \pm 0.07	0.32
	Post-Fire	0-5 cm	2.23 \pm 0.30	3.35 \pm 0.51	0.06
		5-15 cm	0.94 \pm 0.06	1.04 \pm 0.06	0.26

Table 2-5. Mean (\pm S.E.) of pre- and post-fire litter and soil nutrient concentration measured in the herbivory and non-herbivory plots.

Variable	Fire	Depth	Herbivory	Non-herbivory	<i>P</i>
-----mg g ⁻¹ -----					
Carbon	Pre-Fire	Litter	461 \pm 25.1	410 \pm 7.08	0.07
		0-5 cm	6.23 \pm 0.83	9.01 \pm 1.61	0.07
		5-15 cm	1.36 \pm 0.17	1.36 \pm 0.23	0.99
	Post-Fire	Litter	240 \pm 25.1	290 \pm 38.3	0.40
		0-5 cm	9.42 \pm 1.53	11.0 \pm 0.92	0.16
		5-15 cm	2.63 \pm 0.27	3.42 \pm 0.31	0.07
Nitrogen	Pre-Fire	Litter	9.50 \pm 0.53	8.81 \pm 0.52	0.36
		0-5 cm	0.37 \pm 0.04	0.49 \pm 0.09	0.27
		5-15 cm	0.14 \pm 0.01	0.17 \pm 0.02	0.39
	Post-Fire	Litter	10.2 \pm 1.75	12.0 \pm 1.28	0.36
		0-5 cm	0.56 \pm 0.10	0.85 \pm 0.13	0.06
		5-15 cm	0.17 \pm 0.03	0.19 \pm 0.02	0.48
-----mg kg ⁻¹ -----					
Phosphorus	Pre-Fire	Litter	152 \pm 9.85	208 \pm 16.3	0.008
		0-5 cm	10.9 \pm 0.80	14.1 \pm 0.73	0.007
		5-15 cm	6.21 \pm 0.17	7.84 \pm 0.56	0.02
	Post-Fire	Litter	318 \pm 53.1	526 \pm 35.3	0.005
		0-5 cm	12.5 \pm 1.10	31.0 \pm 4.24	0.0001
		5-15 cm	10.3 \pm 1.35	9.59 \pm 0.81	0.89

Table 2-6. Mean (\pm S.E.) of pre- and post-fire of litter nutrient storage measured in the herbivory and non-herbivory plots.

Variable	Fire	Herbivory	Non-herbivory	<i>P</i>
-----g m ⁻² -----				
Carbon	Pre-Fire	319 \pm 50.8	295 \pm 83.0	0.81
	Post-Fire	59.8 \pm 20.8	71.7 \pm 19.1	0.68
Nitrogen	Pre-Fire	6.21 \pm 0.92	6.16 \pm 1.71	0.98
	Post-Fire	2.65 \pm 0.95	2.93 \pm 0.72	0.82
-----mg m ⁻² -----				
Phosphorus	Pre-Fire	96.3 \pm 14.6	149 \pm 45.4	0.28
	Post-Fire	85.2 \pm 31.7	123 \pm 30.8	0.41

Table 2-7. Mean (\pm S.E.) of pre- and post-fire specifically mineralizable nitrogen (SMN) and specifically mineralizable phosphorus (SMP) levels measured in the herbivory and non-herbivory plots.

Variable	Fire	Soil Depth	Herbivory	Non-herbivory	<i>P</i>
----- $\mu\text{g PMN mg}^{-1}$ N soil -----					
SMN	Pre-Fire	0-5 cm	15.3 \pm 1.88	18.6 \pm 2.07	0.26
		5-15 cm	6.99 \pm 2.85	4.07 \pm 1.49	0.38
	Post-Fire	0-5 cm	39.7 \pm 4.26	36.1 \pm 6.99	0.46
		5-15 cm	57.1 \pm 10.6	31.3 \pm 5.56	0.05
----- $\mu\text{g PMP mg}^{-1}$ P soil -----					
SMP	Pre-Fire	0-5 cm	15.8 \pm 7.51	3.53 \pm 0.46	0.2
		5-15 cm	12.5 \pm 3.38	4.16 \pm 2.06	0.09
	Post-Fire	0-5 cm	12.5 \pm 6.32	8.17 \pm 1.63	0.55
		5-15 cm	11.2 \pm 5.27	6.33 \pm 0.65	0.42

Table 2-8. Mean (\pm S.E.) of pre- and post-fire soil microbial biomass carbon measured in the herbivory and non-herbivory plots.

Variable	Fire	Soil Depth	Herbivory	Non-herbivory	<i>P</i>
			-----mg MBC kg ⁻¹ -----		
MBC	Pre-Fire	0-5 cm	720 \pm 121	1016 \pm 189	0.21
		5-15 cm	215 \pm 46.7	392 \pm 67.1	0.03
	Post-Fire	0-5 cm	110 \pm 15.6	132 \pm 18.5	0.39
		5-15 cm	124 \pm 31.7	106 \pm 19.1	0.86



Figure 2-1. Maps of the study site in southwest Florida (large photograph credit - South Florida Water Management District, inset photograph credit – Google Earth).

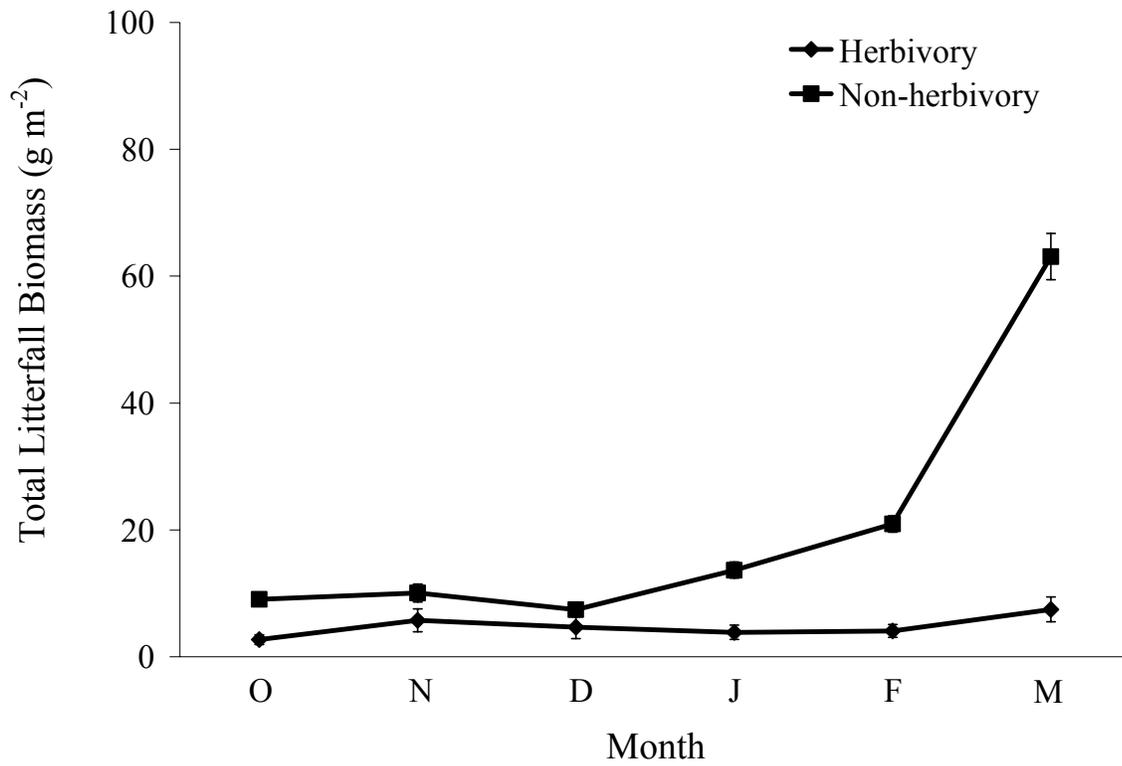


Figure 2-2. Mean (\pm S.E.) of total litterfall measured during each sampling period in the herbivory and non-herbivory plots.

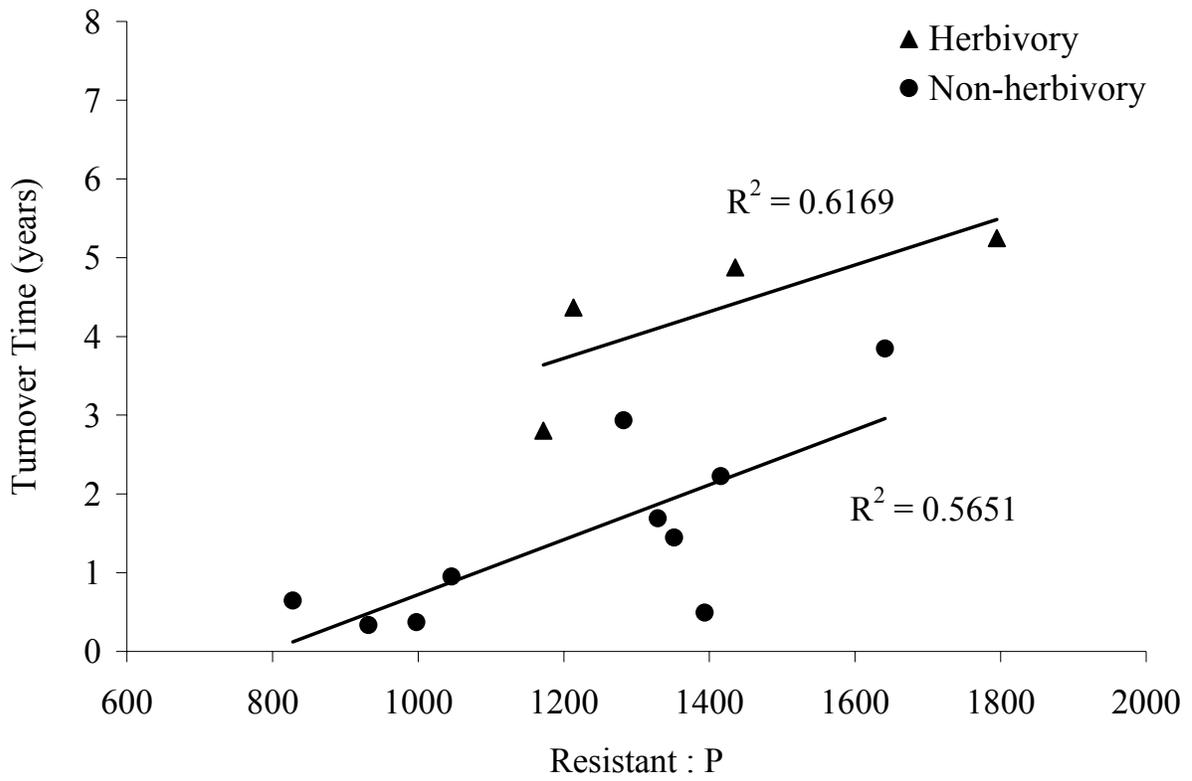


Figure 2-3. Relationship between turnover time of litter and resistant:P ratio of *Melaleuca quinquenervia* litterfall in the non-herbivory and herbivory plots.

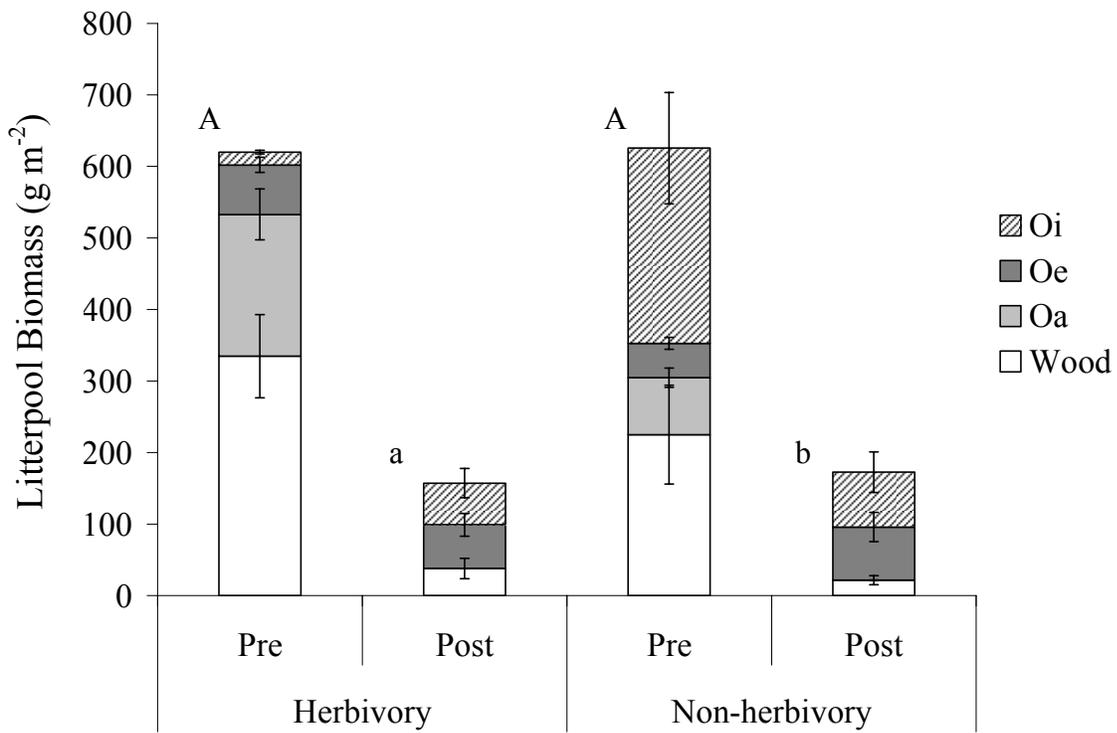


Figure 2-4. Mean (\pm S.E.) of pre- and post-fire litterpool biomass (woody, undecomposed Oi, moderately decomposed Oe, and humified Oa) in the herbivory and non-herbivory plots (lower and capital letters indicate significant differences for each analysis).

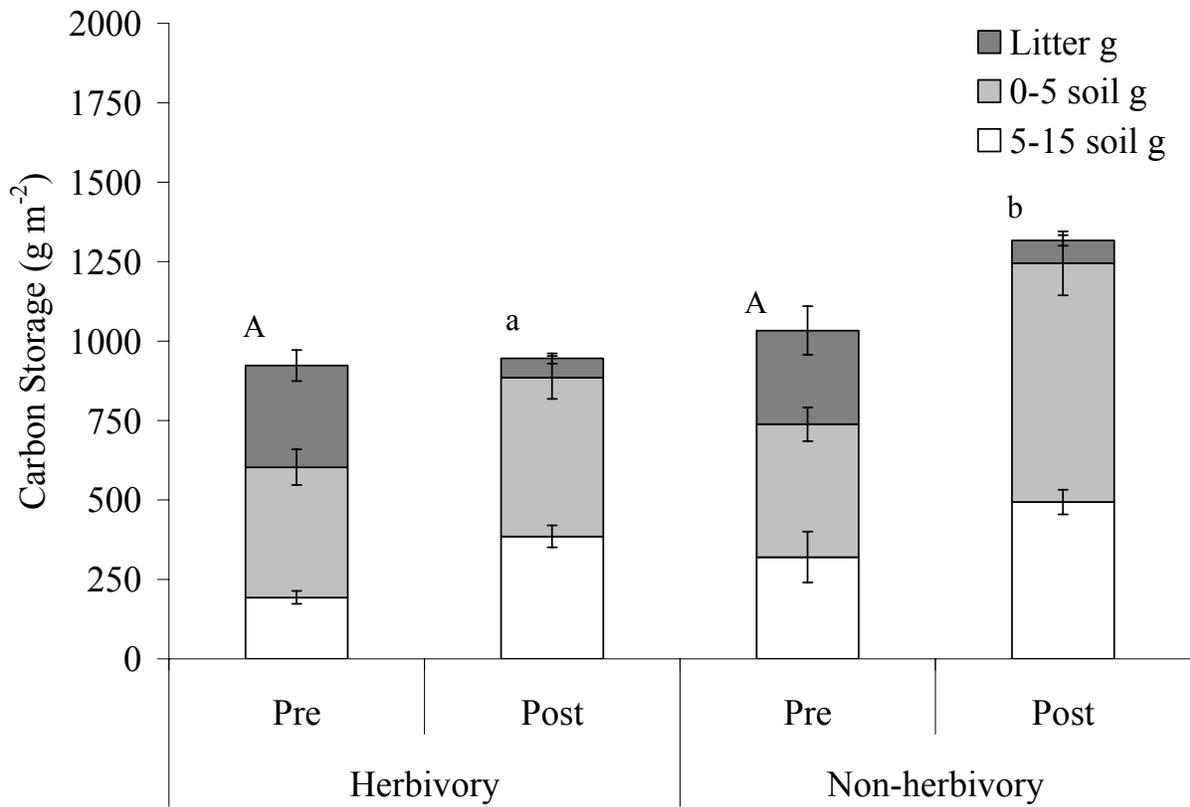


Figure 2-5. Mean (\pm S.E.) of pre- and post-fire total carbon storage measured in the herbivory and non-herbivory plots (lower and capital letters indicate significant differences for each analysis).

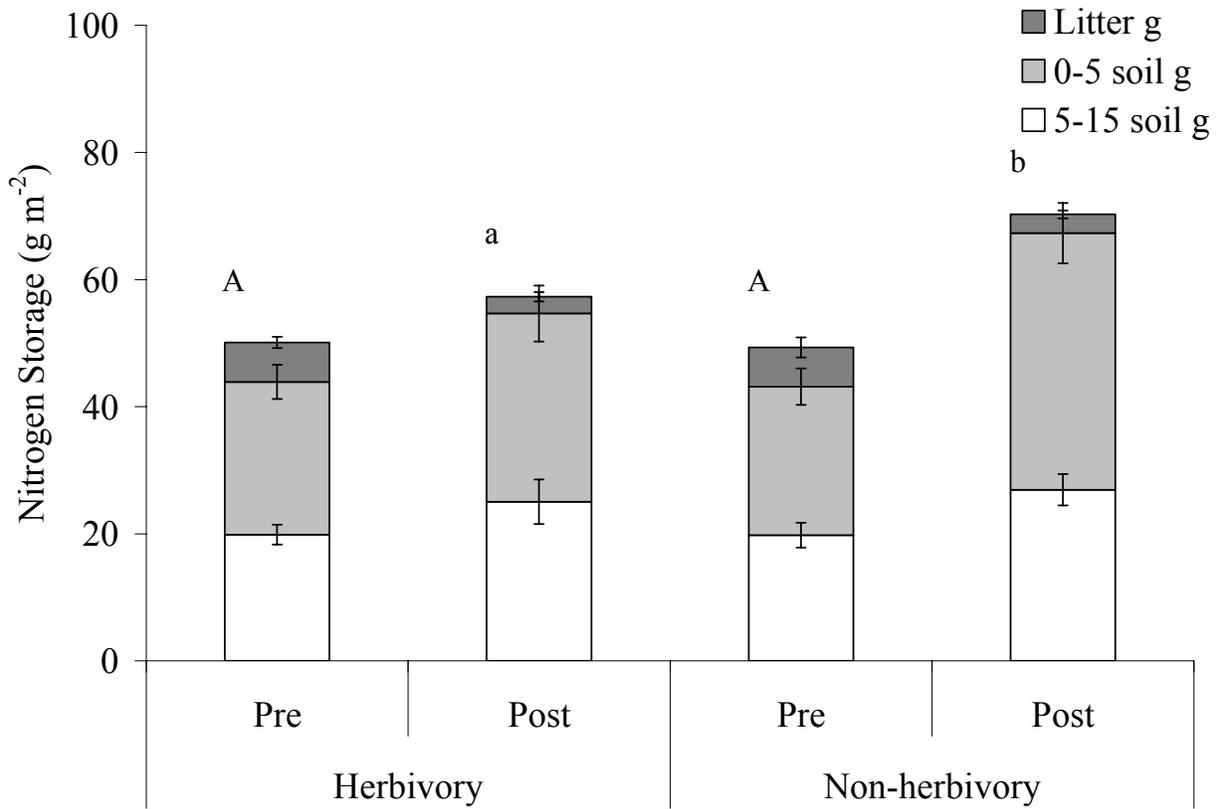


Figure 2-6. Mean (\pm S.E.) of pre- and post-fire total nitrogen storage measured in the herbivory and non-herbivory plots (lower and capital letters indicate significant differences for each analysis).

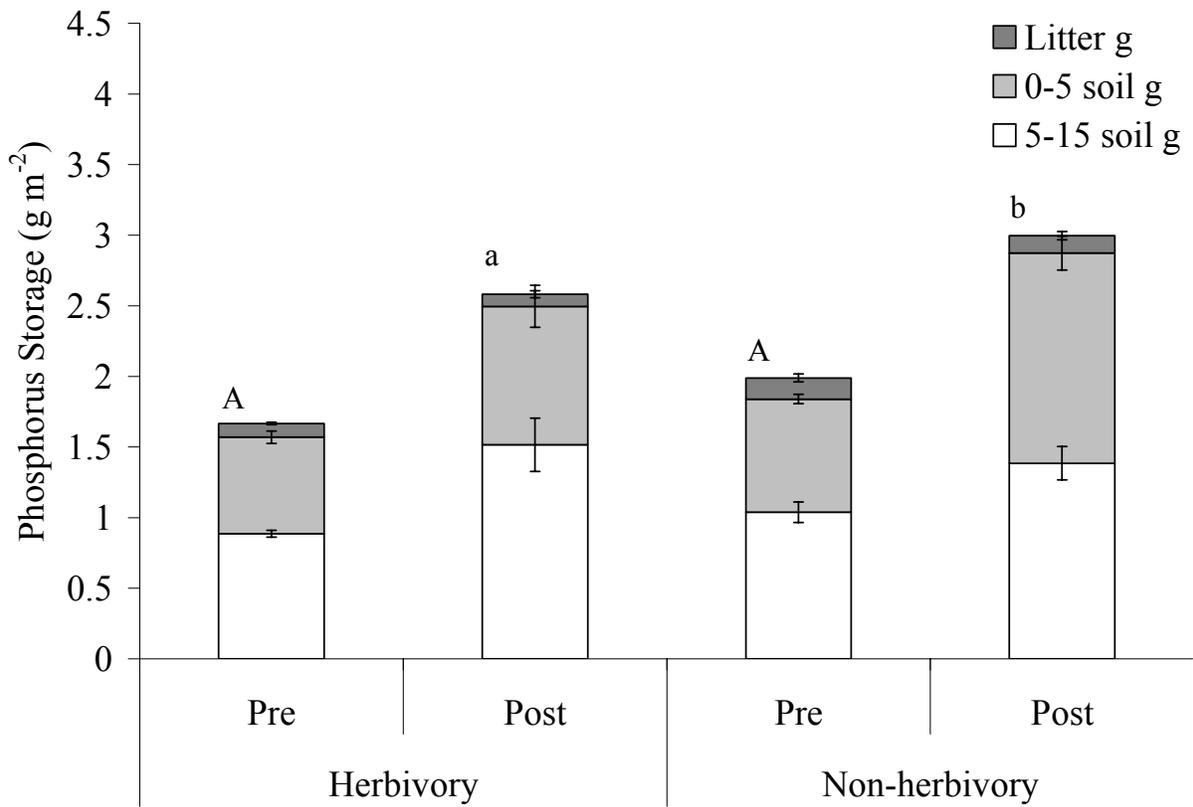


Figure 2-7. Mean (\pm S.E.) of pre- and post-fire total phosphorus storage measured in the herbivory and non-herbivory plots (lower and capital letters indicate significant differences for each analysis).

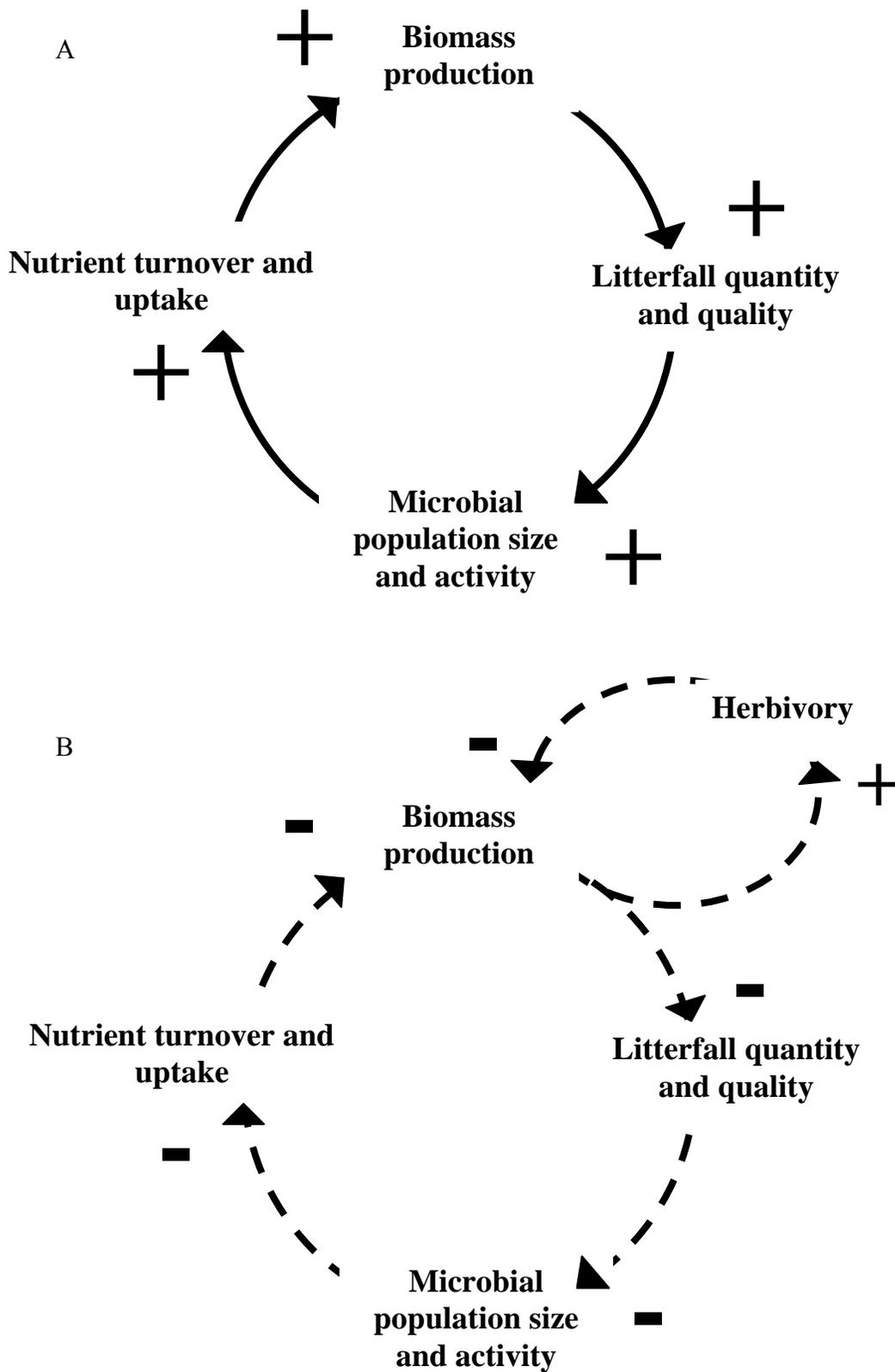


Figure 2-8. Conceptual models of the feedback cycle of *Melaleuca quinquenervia* biomass production in the two treatment plots. A) A positive feedback cycle without herbivory (solid line). B) A negative feedback cycle with herbivory (dashed line).

CHAPTER 3
ASSESSING THE IMPACT OF NATIVE DISTURBANCE REGIMES IN FORESTS
MANAGED TO CONTROL THE INVASION OF AN EXOTIC TREE

Introduction

The invasion of exotic species alters the basic structure of native plant communities with unpredictable consequences for ecosystem functions (Mack and D'Antonio 1998, Mack et al. 2000). Studies have found both positive and negative changes in the rates of nutrient storage and cycling of invaded ecosystems, two crucial ecosystem services (Ehrenfeld 2003). For example, grassland invasion by woody plants can increase the storage of carbon in standing biomass (Jackson et al. 2002). Exotic plants may also differ in the relative nutrient concentration and decomposability of their litter, so called litter “quality” (Ehrenfeld 2003). A sample of 30 invasive species from Hawaii had higher foliar nutrient levels compared to native plants, potentially altering the rate of ecosystem nutrient fluxes (Baruch and Goldstein 1999).

Federal, state, and local governments have created comprehensive weed control programs to reduce the populations of exotic plants. The most common method of controlling exotic plants is by using herbicides. Often, applications must be made in perpetuity to maintain satisfactory control and several programs have touted the “maintenance control” concept whereby annual costs are reduced by maintaining populations at relatively low densities by regular and consistent herbicide applications (Ramey and Hassell 2005). However, herbicides can injure adjacent native vegetation and, despite the “maintenance control” concept, require large, repeated investments of resources. Mechanical control, or the physical removal of exotic populations, is costly and time consuming thereby limiting its effectiveness for large scale efforts. This approach can also have significant negative collateral effects on local flora and fauna.

Classical biological control attempts to reunite weeds with their coevolved natural enemies, most of which are insects (Center and Hill 2002). Although there have been some notable successes with this self-sustaining method, progress can be slow, taking up to a decade to implement. In addition, this method can be incompatible with current herbicide management practices by preventing the establishment and building up of bio-control agents because of dramatic and unpredictable declines in their food supply (Center et al. 1999). While the goal of all of these approaches is to reduce exotic populations and restore ecosystem integrity, little work has been done to monitor and evaluate their impact on ecosystem function.

Perhaps one of the most successful integrated pest management projects to date has been the effort to control *Melaleuca quinquenervia* (Cav.) Blake in the Florida Everglades. This Australian tree was introduced into South Florida in 1886 and has since colonized and thrived in most natural areas of South Florida, including bayhead tree islands, sawgrass prairies, pine flatwoods, pastures, and cypress forests (Bodel et al. 1994, Dray et al. 2006). A high growth rate, early reproductive maturity, multiple annual flowering periods, and serotiny increase the population potential of this plant following perturbations like fires (Bodel et al. 1994). The high concentrations of essential oils found in mature *M. quinquenervia* trees can fuel more destructive canopy fires that can kill native vegetation which are adapted to cooler ground fires. Simultaneous and massive releases of *M. quinquenervia* seed from the canopy seed bank occur after fires, invariably leading to the creation of *M. quinquenervia* monocultures in many areas (Serbesoff-King 2003).

Inter-agency cooperation promoted the integration of chemical, mechanical, and biological control methods to reduce the impact of *M. quinquenervia* (Ferriter et al. 2005). The biological control component began in 1986 with the United States Department of Agriculture, Agricultural

Research Service (ARS) taking the lead. Research conducted at the USDA-ARS Invasive Plant Research Lab in Fort Lauderdale led to the release of four biological control agents (Ferriter et al. 2005). Two of the biological agents, *Oxyops vitiosa* Pascoe (Coleoptera: Curculionidae) and *Boreioglycaspis melaleucae* Moore (Hemiptera: Psyllidae), have successfully established and are suppressing *M. quinquenervia* reproduction, growth, and recruitment on a landscape scale (Tipping et al. 2009). The other two species have only recently been released so information on their impact is unavailable. Although these programs have been evaluated based on the quantity of plant biomass removed or reduction in rates of exotic population spread, other evaluation factors need to be considered including the impact on non-target vegetation, recovery of native plant communities, alteration of ecosystem function, and interactions with native disturbance regimes like seasonal fires (Denslow and D'Antonio 2005).

Many of Florida's natural areas that have been invaded by *M. quinquenervia* depend on regular disturbances like fires to maintain community structure and function. Native plant communities in these areas depend on seasonal fires to open canopies and trigger the seed release and germination of plant species, provide temporary pulses of soluble nutrients, and reduce plant competition (Wade et al. 1980, Neary et al. 1999). The invasion of *M. quinquenervia* and other exotic plants have altered native fire patterns which may have long-term consequences for ecosystem function (Wade et al. 1980). While understanding the consequences of fire on aboveground processes is vital, understanding belowground alterations to ecosystem functions is no less important particularly after the invasion and management of exotic plants.

The major objective of this work was to elucidate above- and belowground changes to a *Taxodium distichum* (L.) L.C. Rich var. *nutans* (Ait.) Sweet dominated eco-tone forest after the invasion by and subsequent management of *M. quinquenervia*. In particular, we were interested

in the management consequences for nutrient storage and availability before and after a seasonal fire. Two main hypotheses were tested: 1) *M. quinquenervia* invasion and treatment with an herbicide will reduce the quantity and availability of nutrients before and after a seasonal fire compared to a non-invaded site; 2) *M. quinquenervia* invasion and treatment with biological control agents will not alter the quantity and availability of nutrients before and after a seasonal fire compared to a non-invaded site.

Materials and Methods

Experimental and Statistical Justification

In order to assure the proper assignment of treatment causality in experiments several fundamental assumptions must be met including: random assignment of treatments across experimental units and treatment replication (Beyers 1998). Random assignment of treatments reduces the impact of non-treatment factors that could confound results and replication reduces the likelihood that random variation is the cause of measured differences between treatments. Although the most effective field studies have randomly assigned, replicated experimental treatments many times limitations of money, labor, and time make these conditions impossible. Without a proper experimental design, the use of inferential statistics may only reveal differences between un-replicated plots and not the desired treatment effect (Hurlbert 1984). In other words, the null hypothesis becomes that there is no difference between plots NOT that the treatment has no effect (Hurlbert 1984).

In ecosystems all over the world land managers are manipulating natural areas in an attempt to restore function, provide habitat, or mitigate anthropogenic disturbance. Often times these treatments are done on one large tract of land or single experimental unit. Scientific analysis of these areas can be complex because both of the assumptions mentioned above are violated. Still large-scale field studies investigating these treatments must be done in order to

assess the impact of natural resource management decisions. There is nothing to be gained from limiting scientific investigation when management must continue. Insight gained from determining large-scale treatment effects can be used to guide further research and prevent undesirable consequences of management decisions.

Site Description

The study site was located in the Belle Meade Tract of the Picayune Strand State Forest in Collier County, Florida (Figure 2-1). This area consists of nearly level, poorly drained, low fertility soils which are loamy, siliceous, hyperthermic Arenic Glassoqualfs. The soil series is Pineda-Boca-Hallandale which is characterized by moderately to poorly drained sands which overly limestone bedrock to a depth of approximately 1.4 m (USDA 1998). The water table fluctuates annually between greater than 15 cm below the soil surface to approximately 25 cm above. The area has a distinct wet season from about July to December and a dry season from January to June. Average annual rainfall in this region is approximately 1.36 m (SERC 2007). Historically, the vegetation in this area was a mixed *T. distichum*-*Pinus elliottii* Englem forest with a hardwood under-story. Over the past several decades, many areas in this landscape have been invaded with *M. quinquenervia* and are now comprised of sparse populations of mature trees with dense understories of seedlings and saplings that can exceed densities of 100 plants per square meter.

On March 27, 2007, twenty-five, 1 m² plots were established along five transects in each of three contiguous study areas (Figure 3-1). The areas sampled were: area #1) reproductive *M. quinquenervia* treated with herbicide in the summer of 2003 (hereafter referred to as “herbicide site”), area #2) reproductive *M. quinquenervia* treated with biological control (hereafter referred to as “biological site”), and area #3) native forest with no *M. quinquenervia* (hereafter referred to as “non-invaded site”). The two biological control agents mentioned above, *O. vitiosa* and *B.*

melaleuca, were common in all areas. The herbicide site consisted of reproductive *M. quinquenervia* that was treated aerially with Velpar® (Hexazinone, 3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5-triazine-2,4(1H,3H)-dione) in 2003. The biological site consisted of reproductive *M. quinquenervia* which was not treated with herbicides and has been under attack by *O. vitiosa* since 1998 and *B. melaleuca* since 2002. The non-invaded site was a *P. elliotii*-*T. distichum* forest with no history of *M. quinquenervia* invasion. Plots were re-visited and all parameters re-sampled after a seasonal fire on May 15, 2007.

In early May of 2007 the Great Basal fire burned approximately 8,000 hectares in southwest Florida and all of the established experimental plots. As the fire was not planned no direct measurements of the intensity of the fire were taken. However, all of the plots were equally affected as well as the entire surrounding landscape. The above- and belowground samples were taken 24 to 48 hours after the fire.

Litter and Soil Sampling

The litterpool was sampled in every m² plot (n=25 in each study site) by placing two 0.1 m² frames on the surface of the soil and collecting all of the organic material therein. Pre-fire litterpool samples were separated into undecomposed Oi, moderately decomposed Oe, humified Oa, and woody biomass layers. Post-fire litterpool samples were also separated into an additional “after” layer which sampled leaves that fell from the tree after the fire. Litterpool samples were air dried to a constant weight and reported on a dry weight basis. Fire intensity was estimated by calculating the percentage of the total litterpool that was lost after the May 2007 fire. One 5 cm diameter soil core was taken in each plot and separated into 0-5 cm and 5-15 cm depths. Soil samples were returned to the laboratory, sieved to remove roots and large plant debris, homogenized, and kept at 4°C for a maximum of 10 days before microbial analysis.

Litter Quality Analysis

Litter quality was measured with a sequential extraction using an Ankom A200 Fiber Analyzer (Rowland and Roberts 1994). 0.5 g of coarsely ground litter material was weighed and sealed into Ankom filter bags. The bags were extracted with a neutral detergent to remove soluble cellular contents (sugars, carbohydrates, lipids, etc.) followed by an acid detergent to removal hemi-cellulose. Cellulose was removed by soaking the bags in 72% sulfuric acid (H_2SO_4) for 3 hours. The residual (lignin and ash) was combusted at 550°C for 4 hours to determine ash content. Litter quality was calculated on a dry mass basis.

Soil Characteristics

Percent moisture and bulk density of soils were determined by drying 20-30 g sub-samples of field-moist, sieved, and homogenized soil at 70°C for three days. Bulk density and percent moisture were determined on a wet soil weight basis and pH was measured on a 2:1 water:soil slurry with an Accumet Research, AR50 dual channel pH/ion/conductivity meter. Soil organic matter was measured by loss on ignition from 0.2 to 0.5 g samples of dried and ground soils, which were first measured into 50 mL beakers (Luczak et al. 1997). The beakers were placed in a muffle furnace and brought to 250°C for 30 minutes. The furnace temperature was then increased to 550°C for 4 hours. Organic matter content was calculated as the mass loss on ignition on a dry weight basis.

Nutrient Analyses

Dried and ground soil and plant material were analyzed for percent carbon and nitrogen on a Thermo-Electron, 1112 Series elemental analyzer. Total phosphorus was determined by a two-phase acid extraction after loss on ignition (Andersen 1976). The ash remaining in the 50 mL beaker was moistened with 2 to 3 mL distilled de-ionized water and then extracted with 20 mL of 6 N hydrochloric acid (HCl). All of the water was removed and the hot plate was placed on

high for 30 minutes to completely dry the samples. After cooling, 2.25 mL of 6 N HCl was added to each beaker and the beakers placed on a hot plate until almost boiling. Extracts were then filtered through a #41 Whatman filter into 50 mL volumetric flasks that were then brought to volume with distilled de-ionized water. Total phosphorus was measured with an automated ascorbic acid method on a Bran and Luebbe Auto Analyzer 3, Digital Colorimeter (Method 365.4; USEPA 1993).

Microbial Biomass

Microbial biomass carbon (MBC) was measured by a modified chloroform-fumigation extraction method (Vance et al. 1987). Two replicates of 1 g field-moist soil samples were weighed into 50 mL centrifuge tubes. One of the duplicates was immediately extracted with 25 mL of 0.5 M potassium sulfate (K_2SO_4), shaken for 1 hour, and then filtered through a Whatman #41 filter. The second replicate of soil underwent chloroform fumigation where 0.5 mL of chloroform was added to each tube and the tubes were placed in a dessicator with a beaker containing 30 mL of chloroform and boiling chips. The dessicator was then vacuum-sealed for 24 hours then alternatively filled with air and evacuated ten times to remove all residual chloroform. The tubes were extracted as described above and all extracts were stored at 4°C until analysis for MBC. This was calculated as the difference between the total carbon in the fumigated and un-fumigated soil extracts as measured on a Shimadzu TOC 5050C, total organic carbon analyzer.

Nutrient Availability

Potentially mineralizable nitrogen (PMN) was measured with a modified incubation-extraction method (White and Reddy 2000) that calculates a mineralization potential based on the net production of ammonium during a 10 day anaerobic incubation. In order to determine the initial amount of ammonium in the soil, a set of 1 g field-moist soil samples were weighed into

50 mL centrifuge tubes. The tubes received 25 mL of 0.5 M K₂SO₄, shaken on a longitudinal shaker for one hour, and extracts were filtered through a #41 Whatman filter. An additional set of 1 g field-moist soil samples were weighed into 50 mL serum bottles with 5 mL of deionized water. These bottles were sealed with butyl rubber stoppers and aluminum crimps and their head-space was purged with oxygen (O₂)-free nitrogen (N₂) gas for 2-5 minutes. Bottles were incubated in the dark at 35°C for 10 days then extracted as described above with 25 mL of 0.5 M K₂SO₄ to determine final ammonium concentration. Total ammonium was determined with an automated colorimetric method on a Bran and Luebbe Auto Analyzer 3, Digital Colorimeter (Method 353.2; USEPA 1993). Specifically mineralizable nitrogen (SMN) was determined by dividing PMN by the concentration on nitrogen in the soil ($SMN = PMN * TN^{-1}$).

Potentially mineralizable phosphorus (PMP) was measured with a modified incubation-extraction method under aerobic conditions (Grierson et al. 1999). Soils were incubated at a temperature of 35°C for a period of 10 days in capped 125 mL polyethylene bottles that contained 5 g of soil held under optimal percent moisture conditions (4-7%). Soils were aerated every three days and moisture content was adjusted if necessary. On day 10, soil sub-samples were collected from each incubation bottle and analyzed for available phosphorus. Soil samples were extracted with 0.1 M potassium chloride (KCl) at a ratio of 10:1, shaken for one hour, and then filtered with 0.45 µm membrane filters. Available phosphorus was measured with an ascorbic acid method on a Shimadzu Spectrophotometer UV-160 (Method 365.4; USEPA 1993). Specifically mineralizable phosphorus (SMP) was determined by dividing PMP by the concentration on phosphorus in the soil ($SMP = PMP * TP^{-1}$).

Statistical Analyses

Values of measured soil and vegetation characteristics, as well as microbial population size and activity, were calculated as a mean for each plot. ANOVA and Tukey means separation tests

were used to detect any differences among the measured parameters. Differences are reported as significant for tests with p values ≤ 0.05 . Data that varied from normal distributions were transformed with square root(x), log(x), or log(x+1) functions. The datasets that were transformed with the square root(x) function were pre- and post-fire moisture (0-5 and 5-15 cm), pre- and post-fire litterpool biomass and moisture, pre- and post-fire nitrogen concentration (0-5 and 5-15 cm), pre- and post-fire phosphorus concentration (0-5 and 5-15 cm), pre- and post-fire SMN (5-15 cm), pre- and post-fire nitrogen storage (0-5 and 5-15 cm), pre- and post-fire phosphorus storage (5-15 cm), and pre- and post-fire SMP (5-15 cm). The datasets that were transformed with the log(x+1) function were pre- and post-fire organic matter (0-5 and 5-15 cm), pre- and post-fire carbon concentration (0-5 and 5-15 cm), and pre- and post-fire carbon storage (0-5 and 5-15 cm). The datasets that were transformed with the log(x) function were pre- and post-fire microbial biomass carbon (0-5 and 5-15 cm). All statistical analyses were performed using JMP 7.0.1 software (SAS Institute, North Carolina, USA).

Results

Full model results for the main effects and interactions are reported in Tables A-11 through A-18. Based on the magnitude of the results the main effects of treatment, site, and depth were the most important determinants of the measured response variables. There were no consistent transect or plot effects for any of the measured variables.

The litter in the non-invaded site had the highest percent moisture followed by the herbicide and then the biological sites. All sites had lower levels of litter moisture and nutrient storage after the fire (-91, -96, and -92% for the non-invaded, herbicide, and biological sites, respectively) (Tables 3-1 and 3-4). Litter biomass was greatest in the non-invaded site, both before and after the fire (Figure 3-1). Percent biomass loss was greater in the herbicide site

compared to the non-invaded and biological sites (Table 3-1). Pre- and post-fire values for soil moisture, bulk density, and organic matter are reported in Table 3-2.

The litter in the non-invaded site had the highest concentration of carbon before and after the fire (Table 3-3). Among sites the soil in the herbicide site had a lower concentration of carbon, nitrogen, and phosphorus at both depths before and after the fire compared to the non-invaded and biological sites (Tables 3-3). Conversely, the soil in the biological site had the highest concentration of nitrogen and phosphorus both before and after the fire compared to the other two sites (Table 3-3).

The concentration of carbon in the 0-5 cm soil depth was lower after the fire within all sites (-20, -55, and -16% in the non-invaded, herbicide, and biological sites, respectively) whereas in the 5-15 cm soil depth carbon concentration was lower in the non-invaded and herbicide sites but higher in the biological site after the fire (-1, -2, and +35%, respectively) (Table 3-3). Within sites, nitrogen concentration in the 0-5 cm soil depth was lower after the fire (-16, -30, and -3% in the non-invaded, herbicide, and biological sites after the fire, respectively) but was only lower in the herbicide site while being higher in the non-invaded and biological site in the 5-15 cm soil depth (-13, +15, and +5%, respectively) (Table 3-3). With sites, phosphorus concentration in the 0-5 cm soil depth soil was higher after the fire (+27, +31, and +2% in the non-invaded, herbicide, and biological sites, respectively) while in the 5-15 cm soil depth it was lower in the herbicide site but higher in the non-invaded and biological sites (-1, +16, and +35% respectively) (Table 3-3).

There were no differences in SMN among sites in the 0-5 cm or 5-15 cm soil depths before or after the fire (Table 3-5). However, SMN in the 0-5 cm soil depth was higher in all sites after the fire (+20, +102, and +52% in the non-invaded, herbicide, and biological sites after the fire,

respectively) (Table 3-5). SMN was lower in the 5-15 cm soil depth in the herbicide site but higher in the non-invaded and herbicide site after the fire (+23, -6, and +5%, respectively).

Pre-fire SMP was highest in the non-invaded site in the 0-5 cm soil depth and in the biological site in the 5-15 cm soil depth (Table 3-5). However, post-fire there were no differences among sites in the 0-5 cm soil depth and the herbicide site had the highest availability of phosphorus at both depths. Within sites, SMP in the 0-5 cm soil depth was higher post-fire in the herbicide and biological sites but lower in the non-invaded site (+107, +46, and -1%, respectively). SMP in the 5-15 cm soil depth was lower in the biological site but higher in the non-invaded and herbicide sites after the fire (-78, +41, and +76%, respectively) (Table 3-5).

Microbial biomass carbon (MBC) was lower in the 0-5 cm soil depth in the herbicide site compared to the non-invaded and biological sites, both before and after the fire (Table 3-6). Before the fire, MBC was lower in the 5-15 cm soil depth in the herbicide site compared to the non-invaded and biological sites (Table 3-6). However, MBC was lower in the non-invaded site after the fire. Within sites, MBC at in the 0-5 cm soil depth was lower in the non-invaded, herbicide, and biological sites after the fire (-76, -68, and -78%, respectively). The same was true in the 5-15 cm soil depth after the fire (-76, -63, and -20%, respectively) (Table 3-6).

Before the fire, the non-invaded site contained a larger pool of total carbon compared to the herbicide and biological sites (Figure 3-4). However, after the fire, the biological site had the larger pool of total carbon compared to the herbicide and non-invaded sites (Figure 3-4). The pool of total nitrogen was largest in the non-invaded site compared to the herbicide and biological sites, both before and after the fire (Figure 3-5). Before the fire, the non-invaded site contained the largest pool of total phosphorus, while after the fire the largest pool occurred in the biological site (Figure 3-6).

Discussion

Alteration of Aboveground Components

Many natural systems are managed to maximize the delivery of ecosystem services such as space for recreational activities, wildlife habitat, and maintenance of biological diversity. However, few studies have evaluated the effects of management programs on the delivery of less obvious ecosystem services like nutrient storage. In this study, the invasion and management of *M. quinquenervia* caused significant and persistent changes in the aboveground litter storage of a sub-tropical wetland forest. Litter accumulates on the forest floor when organic matter inputs (e.g. litterfall) exceed outputs (e.g. decomposition of organic matter). The main source of the organic matter input to the litter in these forests was from litterfall. Before the release of the two biological control agents, litterfall in a mature *M. quinquenervia* forest measured 750 to 930 g dry weight m⁻² year⁻¹ (Van et al. 2002). In Australia, where *M. quinquenervia* is attacked by many insect herbivores, litterfall ranged from 675 to 809 g dry weight m⁻² year⁻¹ in seasonally inundated sites (Greenway 1994). Litterfall by *M. quinquenervia* was not measured in this study although rates in the biological site were presumed to be lower than reported by the previous studies because of the smaller sized trees. Martin et al. (2009) reported litterfall rates of 257.5 g dry weight m⁻² year⁻¹ in a *T. distichum* forest adjacent to the non-invaded study area. The herbicide site had no new litterfall inputs, as all the trees were killed with the treatment and had not yet re-grown.

The main source of the organic matter output from the litter in these forests is from litter decomposition. Previous studies have shown that *M. quinquenervia* has a lower rate of litter decay compared to *T. distichum* because leaves of *M. quinquenervia* contain antibacterial phenolics which hinder microbial decomposition (Greenway 1994). Although no direct measurements of *M. quinquenervia* decomposition have been published, we re-analyzed litterfall

and litter accumulation data from Greenway (1994) to obtain an estimate of 4.3 years for the turnover time of *M. quinquenervia* litter. Nessel and Bayley (1984) estimated 3 years for the turnover time of *T. distichum* litter, the dominant litterfall component in the non-invaded study area. The proposed higher litterfall and lower decomposition rates would suggest that greater amounts of litter would accumulate in the biological and non-invaded areas compared to the herbicide area.

As hypothesized, there was a reduction in both litter biomass and nutrient concentration in the herbicide treated site despite the fact that it was treated four years ago (Figure 3-1). These differences resulted in the herbicide site storing 10 times less carbon, 10 times less nitrogen, and 9 times less phosphorus in the litter compared to the non-invaded site. This is most likely due to the relative composition of the litter between the sites where 62% of the litter in the herbicide site consisted of relatively low-nutrient wood material compared to only 13% in the non-invaded and 26% in the biological sites ($p = 0.02$) (Figure 3-2). However, in contrast to our hypotheses, the biological site also contained less litter biomass and stored less nutrients compared to the non-invaded site (2 times less carbon, nitrogen, and phosphorus). We suggest two possible explanations for the observed differences: 1) the biological control agents may be altering quality of nutrient inputs to the biological site accelerating the decomposition of the *M. quinquenervia* litter and/or 2) another low quality litterfall component in the non-invaded area is slowing litter decomposition rates.

Franks et al. (2006) found that higher densities of the biological control agent *B. melaleucae* caused *M. quinquenervia* seedlings to drop leaves prematurely, which could interrupt the natural cycle of nutrient resorption during senescence and result in higher quality leaf litter inputs. In addition, the frass produced by both biological agents may be rich in nitrogen and

phosphorus thereby potentially short-circuiting the nutrient limitations and accelerating litter decomposition (Frost and Hunter 2007). The second possibility is that the accumulation of *P. elliotii* needles on the forest floor in the non-invaded area is slowing the decomposition of the litter. Martin et al. (2009) found that 7% of the litterfall in the adjacent non-invaded area was *P. elliotii* needles. *P. elliotii* needles decompose at a much slower rate than *T. distichum* and may accumulate on the forest floor (Gholz et al. 1985). This could increase total biomass inputs while slowing the decomposition rate of the *T. distichum* litter, resulting in greater litter accumulation than expected.

All of the sites lost a significant amount of litter biomass and aboveground nutrient storage after the fire (Tables 3-1 and 3-4). However, the herbicide site lost more of the total biomass compared to the other two sites ($p = 0.001$). This may indicate that the intensity of the fire was greatest in the herbicide site. Unfortunately, as this fire was not planned, there were no intensity measurements taken during the burn. The herbicide site also lost the largest percentage of the litter carbon (95%, $p = 0.27$), nitrogen (88%, $p = 0.21$), and phosphorus (86%, $p = 0.03$) pools (Table 3-1). Other studies have reported similar losses of aboveground nitrogen after fires (Kauffman et al. 1993, Hughes et al. 2000, Wan et al. 2001, Wanthongchai et al. 2008). However, phosphorus losses in the herbicide site were higher than previously reported (Kauffman et al. 1993, Hughes et al. 2000, Wanthongchai et al. 2008). Nutrient losses from aboveground storages after fire can be caused by volatilization and particulate transport, transformation of organic to inorganic forms, and transport by wind and water (Neary et al. 1999, Certini 2005). Before the fire, the landscape in the herbicide site consisted of sparsely distributed herbaceous plants and large amounts of dry woody debris on the soil surface. The fire reduced woody debris by 94% and killed most of the standing vegetation, leaving bare

mineral soil that was extremely vulnerable to wind transport. While some of the litter phosphorus was incorporated into the mineral soil after the fire, it is possible that some was blown off site by wind (Neary et al. 1999, Certini 2005).

Alteration of Belowground Components

The invasion and treatment of *M. quinquenervia* significantly altered the biotic and abiotic components of the surface soils both before and after the fire. Before the fire, the herbicide site had significantly less moisture at 0-5 cm compared to the biological and non-invaded sites. This may be explained by the litter composition in the herbicide site which, unlike the mostly undecomposed and moderately decomposed leaves in the non-invaded and biological sites, consisted primarily of woody material that left large portions of the mineral soil exposed to wind and solar radiation (Figure 3-2). Post-fire the herbicide site had lower levels of soil moisture at 0-5 cm compared to the non-native and biological sites. This may be the result of lower initial soil moisture and increased fire intensity in the herbicide site.

The herbicide site also had the lowest storages of carbon, nitrogen, and phosphorus pre- and post-fire at both soil depths (Figure 3-4, 3-5, and 3-6). The largest differences were recorded in the storages of nitrogen and phosphorus at 0-5 cm before the fire where the biological and non-invaded sites stored approximately 1.6 and 2 times more nitrogen, respectively, and 1.5 times more phosphorus than the herbicide site. Findlay et al. (2003) noted a similar pattern with the invasive reed *Phragmites australis* whose removal from a marsh by herbicides and cutting disrupted the system's ability to process and store nitrogen. Similarly, the chemical treatment and cutting of the invasive plant *Pteridium aquilinum* led to a loss of ecosystem carbon storage in an European moorland (Marrs et al. 2007). In this study, despite a trend of increased phosphorus storage after the fire in every site and soil depth, the only significant increase was found in the herbicide site at 0-5 cm. As discussed above the high intensity fire in this site

probably caused the significantly higher loss of the litter phosphorus. It is likely that the phosphorus rich ash produced from the combustion of the litter was incorporated into the 0-5 cm soil depth by wind events and microbial communities (Neary et al. 1999, Carter and Foster 2004, Certini 2005).

Nitrogen availability increased in all sites after the fire in every soil depth (Table 3-5). Several studies have found similar results with increasing nitrogen availability after fire (Carter and Foster 2004, Wanthongchai et al. 2008). Giardina and Rhoades (2001) found that nitrogen availability increased significantly after a prescribed fire in a pine forest. In contrast, although the availability of phosphorus was consistently lower at 0-5 cm in the biological site, the fire did not alter the availability in any site or soil depth. These changes in the storage and availability of nutrients may have unpredictable effects on ecosystem structure and function in the future. For example, minimum levels of nitrogen and phosphorus availability are needed for maintenance of soil microbial communities and re-vegetation of native plants after disturbances such as fire. However, any nitrogen or phosphorus produced in excess of these needs may be vulnerable to loss by leaching and erosion. Further study is required to determine the current requirements of the plant and microbial communities in these sites to ensure that invasive species management strategies do not lead to leaching of nutrients with negative consequences for downstream ecosystems.

In addition to alterations to nutrient cycling and storage caused by the invasion and management of exotic species, microbial communities also exhibit changes that may ultimately influence future ecosystem services. Wardle et al. (2004) detailed how plant community structure drives changes in soil microbial community size and composition via a series of aboveground-belowground feedback loops. In this study, MBC was lower at 0-5 cm in the

herbicide site both before and after the fire (Table 3-6). Nutrient availability did not differ significantly between sites suggesting that environmental factors such as soil moisture and temperature controlled levels of MBC. Although pre-fire levels of MBC were highly correlated with soil moisture, no relationship existed post-fire (Figure 3-3). This lack of a relationship post-fire may reflect higher soil temperatures normally found right after a fire that would reduce MBC (Neary et al. 1999, Certini 2005). Prieto-Fernandez et al. (1998) found a significant decrease in the size of the soil microbial biomass after a fire in a pine forest. In this study all sites lost approximately 70% of the microbial biomass in the 0-5 cm soil depth and 65% in the 5-15 cm soil depth after the fire. Changes in microbial community structure may significantly affect the ability of these systems to recover after the fire.

Conclusions

Determining the best management practices for exotic species requires consideration of a broad array of factors and their potential interactions, including future interactions with natural events like fires. Most efforts to date have emphasized above ground factors like plant and animal diversity and richness, with little to no consideration of below ground factors like nutrient storage, nutrient cycling, and microbial community diversity. This study clearly shows how these foundational ecosystem components were affected by the management of exotics in the backdrop of a natural fire event.

Biological control of *M. quinquenervia* using insect herbivores has proven to be effective at controlling plant growth and reproduction (Tipping et al. 2009). The results of this study suggest that this method had less of an impact on nutrient storage and cycling than herbicides. Additional questions remain including how both methods affect re-vegetation over the longer term. Although herbicides remain a valuable tool in the management of invasive species, more attention needs to be paid to the resulting consequences for ecosystem structure and function.

Practices such as active re-vegetation with native plants may mitigate the deleterious impacts of the treatment and help to prevent future invasion. If evaluations of the below-ground side effects of exotic plant management remain rare, then advancing our understanding of basic ecosystem structure and restoration will suffer and any alterations to foundational communities like microbes may permanently and negatively alter ecosystem function.

Tables and Figures

Table 3-1. Mean (\pm S.E.) of pre- and post-fire litter moisture, biomass, and fire intensity in the non-invaded, herbicide, and biological sites (lower case letters indicate significant differences for each analysis).

Variable	Fire	Non-invaded	Herbicide	Biological	<i>P</i>
			----- % -----		
Moisture	Pre-fire	38.7 \pm 1.40 a	25.8 \pm 11.4 b	17.1 \pm 6.69 c	<0.0001
	Post-fire	3.33 \pm 0.40 a	1.15 \pm 0.53 b	1.42 \pm 0.15 b	<0.0001
			----- kg m ⁻² -----		
Biomass	Pre-fire	2.24 \pm 0.29 a	0.71 \pm 0.08 c	1.36 \pm 0.13 b	<0.0001
	Post-fire	0.35 \pm 0.04 a	0.12 \pm 0.04 c	0.18 \pm 0.03 b	<0.0001
			----- % -----		
Litter Loss		81.5 \pm 2.27 b	93.7 \pm 2.15 a	85.9 \pm 2.24 b	0.001

Table 3-2. Mean (\pm S.E.) of pre- and post-fire fire soil moisture, bulk density (BD), and organic matter (OM) in the non-invaded, herbicide, and biological sites (lower case letters indicate significant differences for each analysis).

Variable	Fire	Depth	Non-invaded	Herbicide	Biological	<i>P</i>
----- % -----						
Moisture	Pre-fire	0-5	11.2 \pm 1.17 a	7.05 \pm 0.65 b	11.3 \pm 1.64 a	0.048
		5-15	7.86 \pm 0.46 a	6.07 \pm 0.17 b	5.48 \pm 0.37 b	<0.0001
	Post-fire	0-5	1.37 \pm 0.25 a	0.29 \pm 0.06 b	1.17 \pm 0.20 a	<0.0001
		5-15	3.96 \pm 0.25 a	2.54 \pm 0.13 b	3.17 \pm 0.21 b	<0.0001
----- g cm ⁻³ -----						
BD	Pre-fire	0-5	1.11 \pm 0.06 a	1.20 \pm 0.05 a	0.89 \pm 0.05 b	0.0004
		5-15	1.30 \pm 0.05 b	1.43 \pm 0.16 a	1.35 \pm 0.03 ab	0.017
	Post-fire	0-5	1.13 \pm 0.60 a	1.19 \pm 0.03 a	0.88 \pm 0.03 b	<0.0001
		5-15	1.49 \pm 0.03 a	1.60 \pm 0.02 b	1.49 \pm 0.03 a	0.004
----- % -----						
OM	Pre-fire	0-5	1.87 \pm 0.22 b	1.70 \pm 0.17 b	3.71 \pm 0.49 a	0.0001
		5-15	0.95 \pm 0.09 a	0.52 \pm 0.04 b	0.82 \pm 0.07 a	0.0001
	Post-fire	0-5	2.46 \pm 0.32 b	1.07 \pm 0.04 c	3.49 \pm 0.37 a	<0.0001
		5-15	1.38 \pm 0.14 a	0.68 \pm 0.05 b	1.05 \pm 0.10 a	<0.0001

Table 3-3. Mean (\pm S.E.) of pre- and post-fire fire nutrient concentrations in the non-invaded, herbicide, and biological sites (lower case letters indicate significant differences for each analysis).

Variable	Fire	Depth	Non-invaded	Herbicide	Biological	<i>P</i>
-----mg g ⁻¹ -----						
Carbon	Pre-fire	Litter	470 \pm 9.79 a	460 \pm 8.82 a	421 \pm 8.82 b	0.008
		0-5	12.9 \pm 1.80	8.45 \pm 1.06	16.8 \pm 2.82	0.08
		5-15	3.77 \pm 0.61 a	1.74 \pm 0.21 b	1.92 \pm 0.2 b	0.003
	Post-fire	Litter	273 \pm 29.6	203 \pm 26.7	300 \pm 26.8	0.07
		0-5	10.3 \pm 1.56 a	3.78 \pm 0.33 b	14.1 \pm 1.79 a	<0.001
		5-15	3.73 \pm 0.55 a	1.70 \pm 0.16 b	2.59 \pm 0.34 a	0.008
Nitrogen	Pre-fire	Litter	9.45 \pm 0.29 b	7.98 \pm 0.40 c	11.1 \pm 0.28 a	<0.001
		0-5	0.93 \pm 0.14 a	0.43 \pm 0.07 b	0.96 \pm 0.19 a	0.01
		5-15	0.33 \pm 0.05 a	0.15 \pm 0.02 b	0.19 \pm 0.03 b	0.002
	Post-fire	Litter	12.3 \pm 0.75 a	8.94 \pm 1.19 b	13.2 \pm 0.96 ab	0.01
		0-5	0.78 \pm 0.13 a	0.30 \pm 0.04 b	0.93 \pm 0.13 a	<0.001
		5-15	0.38 \pm 0.06 a	0.13 \pm 0.01 b	0.20 \pm 0.02 b	<0.001
-----mg kg ⁻¹ -----						
Phosphorus	Pre-fire	Litter	135 \pm 6.33 b	141 \pm 8.83 b	197 \pm 6.66 a	<0.001
		0-5	15.8 \pm 1.98 ab	10.3 \pm 0.98 b	23.5 \pm 3.09 a	0.004
		5-15	9.03 \pm 0.83	7.26 \pm 0.52	8.64 \pm 0.65	0.21
	Post-fire	Litter	296 \pm 5.54 b	280 \pm 37.1 b	387 \pm 24.3 a	0.006
		0-5	20.1 \pm 2.64 ab	13.4 \pm 1.55 b	23.9 \pm 2.49 a	0.006
		5-15	10.5 \pm 1.03 ab	7.18 \pm 0.50 b	11.7 \pm 1.36 a	0.01

Table 3-4. Mean (\pm S.E.) of pre- and post-fire litter nutrient storages in the non-invaded, herbicide, and biological sites (lower case letters indicate significant differences for each analysis).

Variable	Fire	Non-invaded	Herbicide	Biological	<i>P</i>
----- g m ⁻² -----					
Carbon	Pre-fire	1076 \pm 125 a	367 \pm 52.4 c	592 \pm 60.4 b	<0.0001
	Post-fire	65.0 \pm 10.5	33.6 \pm 65.9	40.4 \pm 7.89	0.12
Nitrogen	Pre-fire	22.5 \pm 2.96 a	6.15 \pm 1.03 c	15.0 \pm 1.40 b	<0.0001
	Post-fire	3.35 \pm 0.46 a	1.41 \pm 0.58 b	1.74 \pm 0.31 b	0.01
----- mg m ⁻² -----					
Phosphorus	Pre-fire	322 \pm 26.4 a	96.9 \pm 13.4 b	260 \pm 26.4 a	<0.0001
	Post-fire	77.0 \pm 9.15	46.6 \pm 18.7	53.2 \pm 9.36	0.26

Table 3-5. Mean (\pm S.E.) of pre- and post-fire specifically mineralizable nitrogen (SMN) and specifically mineralizable phosphorus (SMP) levels measured in the non-invaded, herbicide, and biological sites (lower case letters indicate significant differences for each analysis).

Variable	Fire	Depth	Native	Herbicide	Biological	<i>P</i>
----- $\mu\text{g PMN mg}^{-1}$ N soil -----						
SMN	Pre-fire	0-5	18.7 \pm 3.35	14.8 \pm 1.67	18.1 \pm 4.01	0.66
		5-15	12.4 \pm 2.45	12.6 \pm 2.76	16.0 \pm 2.41	0.55
	Post-fire	0-5	22.5 \pm 3.53	29.8 \pm 4.01	27.6 \pm 3.04	0.33
		5-15	15.2 \pm 3.11	11.9 \pm 2.24	16.9 \pm 3.07	0.45
----- $\mu\text{g PMP mg}^{-1}$ P soil -----						
SMP	Pre-fire	0-5	16.3 \pm 2.14 a	8.38 \pm 4.31 ab	4.49 \pm 1.01 b	0.03
		5-15	3.41 \pm 0.99	8.69 \pm 2.89	12.6 \pm 5.88	0.31
	Post-fire	0-5	16.1 \pm 4.81	17.3 \pm 3.50	6.54 \pm 0.82	0.09
		5-15	4.82 \pm 2.14 a	15.3 \pm 4.56 b	2.73 \pm 0.69 a	0.04

Table 3-6. Mean (\pm S.E.) of pre- and post-fire microbial biomass carbon levels measured in the non-invaded, herbicide, and biological sites (lower case letters indicate significant differences for each analysis).

Variable	Fire	Depth	Native	Herbicide	Biological	<i>P</i>
			-----mg C kg ⁻¹ -----			
MBC	Pre-fire	0-5	785 \pm 116	330 \pm 46.4	791 \pm 150	0.08
		5-15	408 \pm 45.4 a	295 \pm 29.5 a	181 \pm 34.3 b	0.001
	Post-fire	0-5	186 \pm 20.4 a	104 \pm 9.75 b	174 \pm 19.5 a	0.0018
		5-15	99.3 \pm 10.7	108 \pm 18.5	144 \pm 24.92	0.495

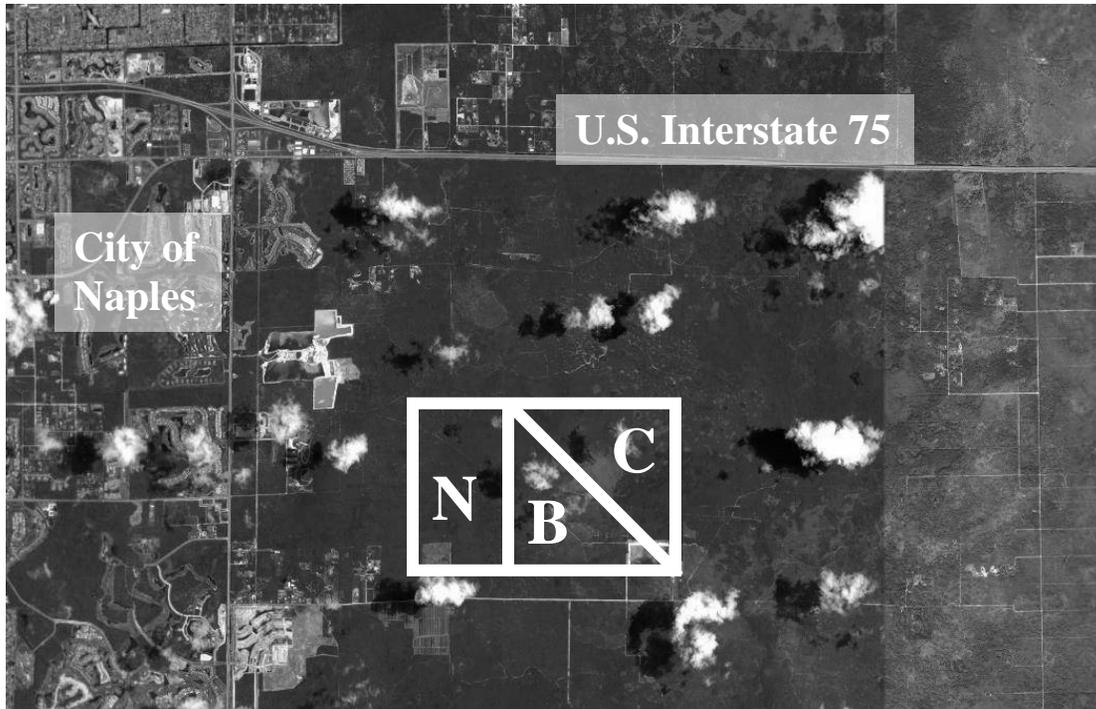


Figure 3-1. Map of the study site in southwest Florida showing the (N) non-invaded, (C) chemically controlled, and (B) biologically controlled sites. Diagram not to scale (photograph credit – Google Earth).

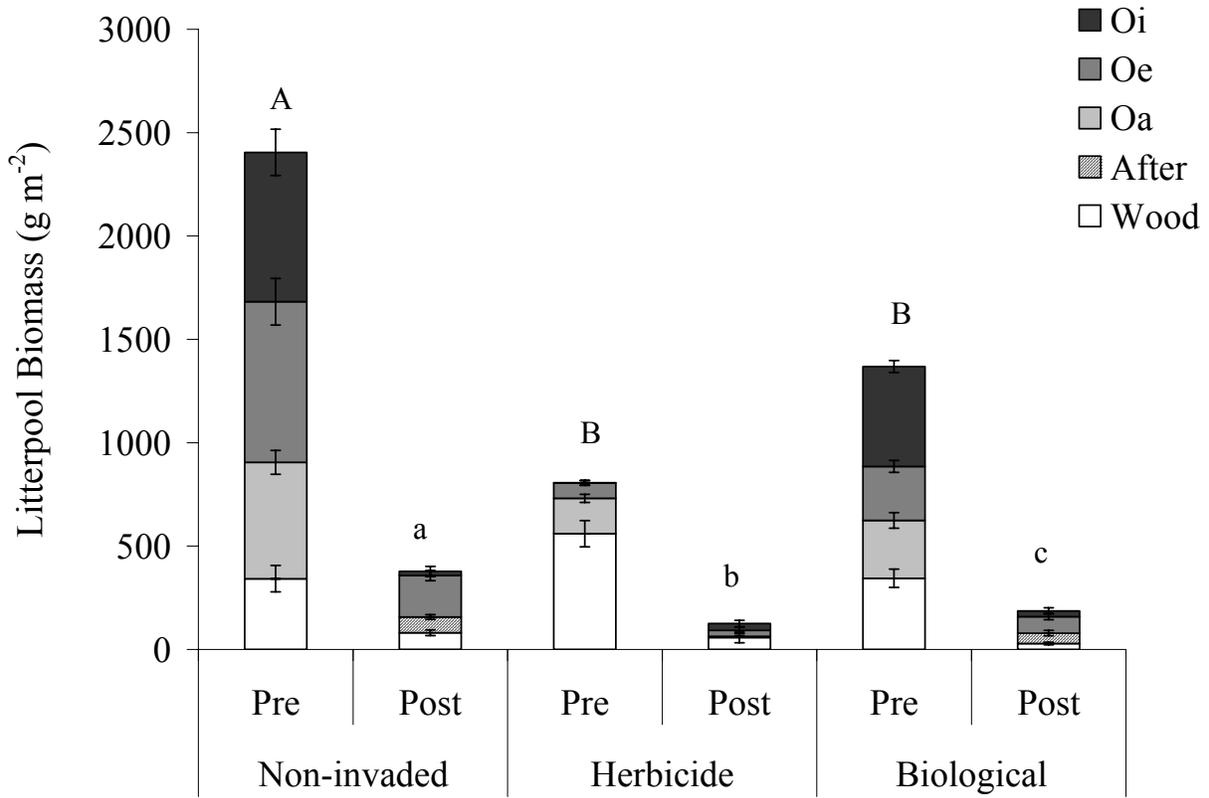


Figure 3-2. Mean (\pm S.E.) of pre- and post-fire litterpool biomass by components (after, wood, undecomposed Oi, moderately decomposed Oe, and humified Oa) measured in the non-invaded, herbicide, and biological sites (different capital and lower case letters indicate significant differences for pre- and post-fire means, respectively).

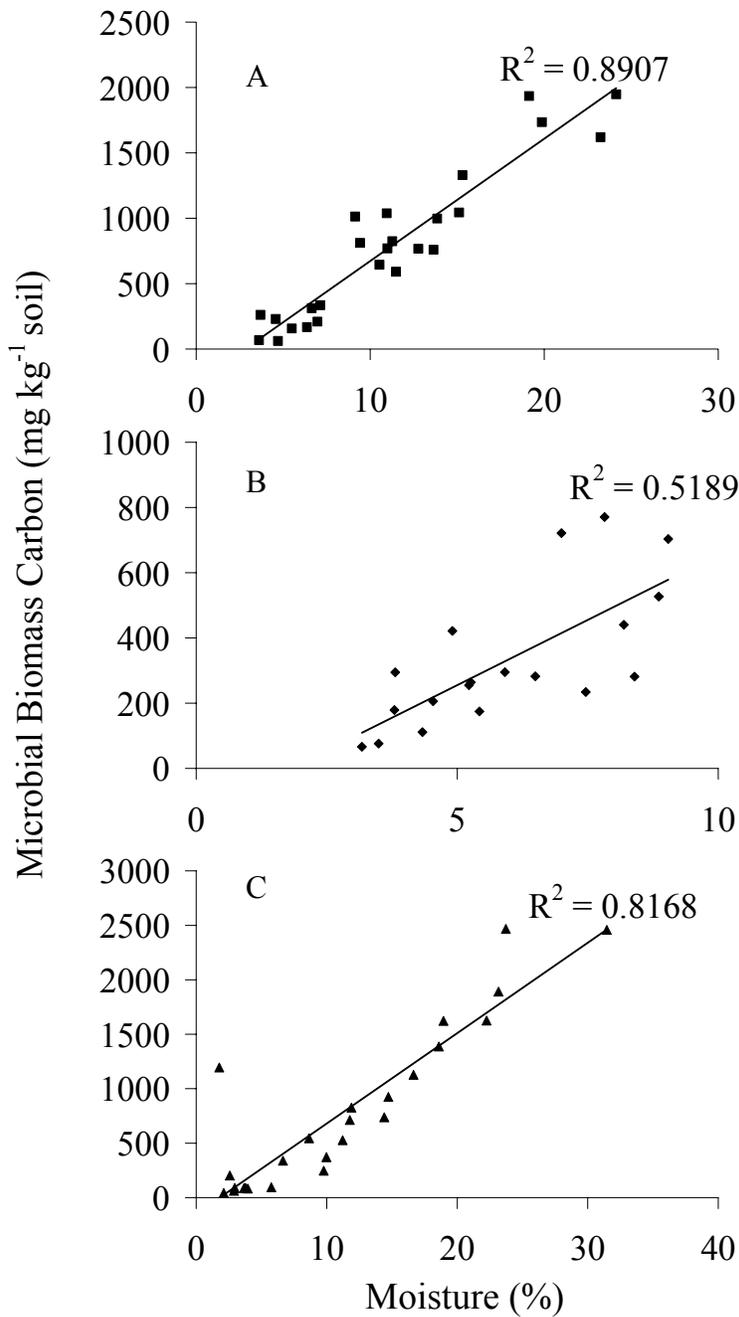


Figure 3-3. Relationship between microbial biomass carbon (MBC) levels and % soil moisture in the three treatment sites. A) The relationship in the non-invaded site. B) The relationship in the herbicide site. C) The relationship in the biological site.

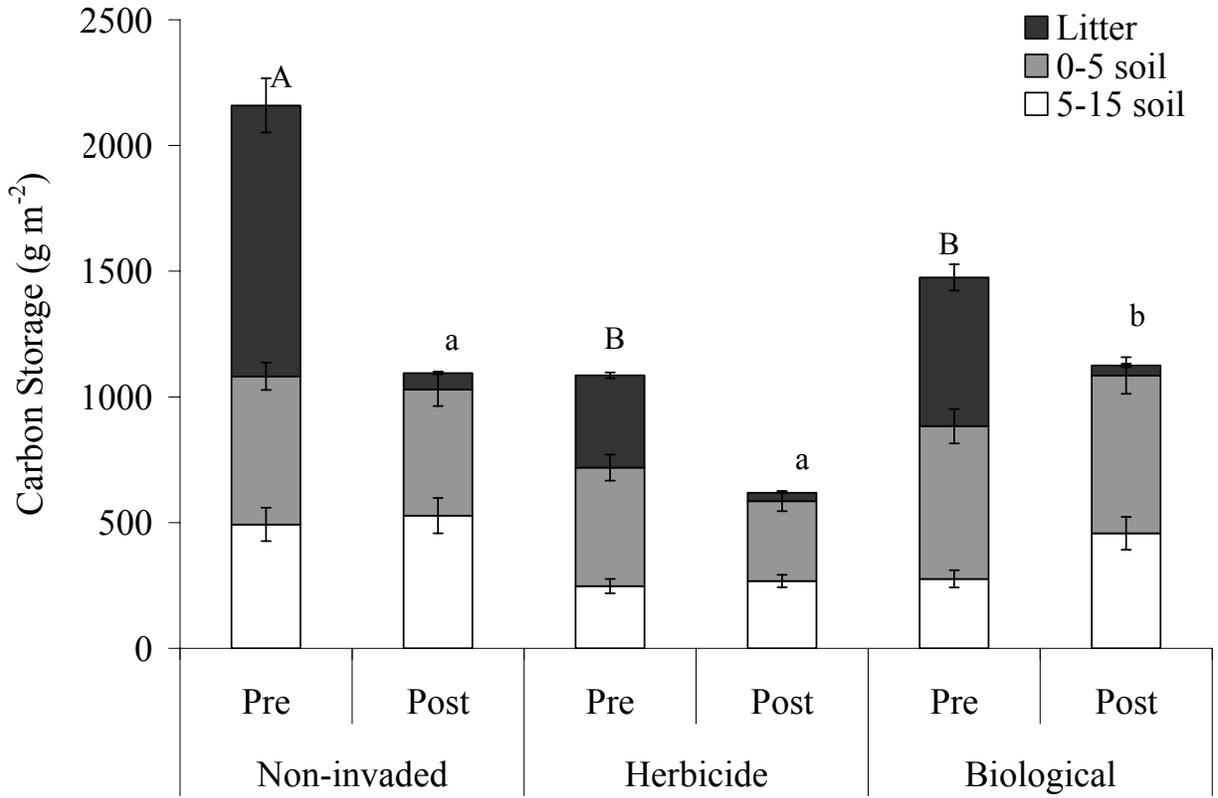


Figure 3-4. Mean (\pm S.E.) of pre- and post-fire total storages of carbon measured in the non-invaded, herbicide, and biological sites (different capital and lower case letters indicate significant differences for pre- and post-fire means, respectively).

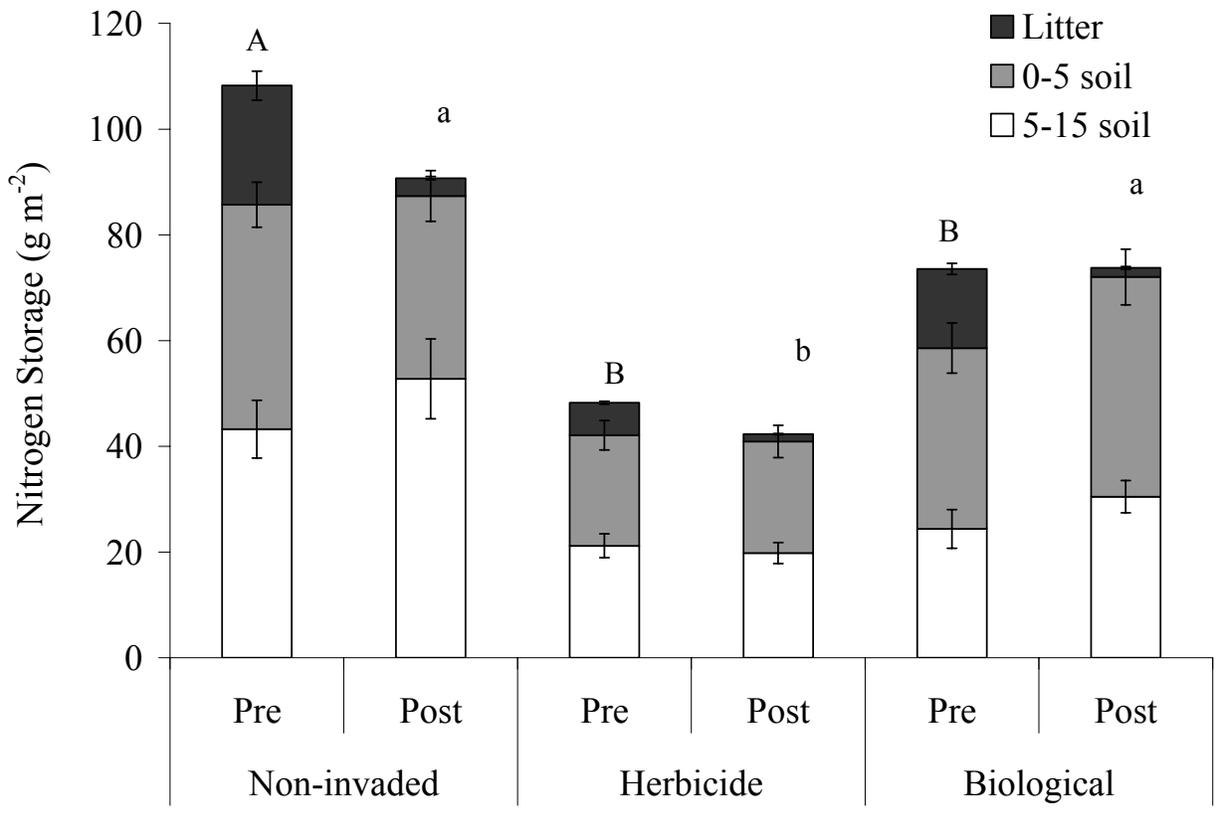


Figure 3-5. Mean (\pm S.E.) of pre- and post-fire storages of nitrogen measured in the non-invaded, herbicide, and biological sites (different lower and capital letters indicate significant differences for each analysis).

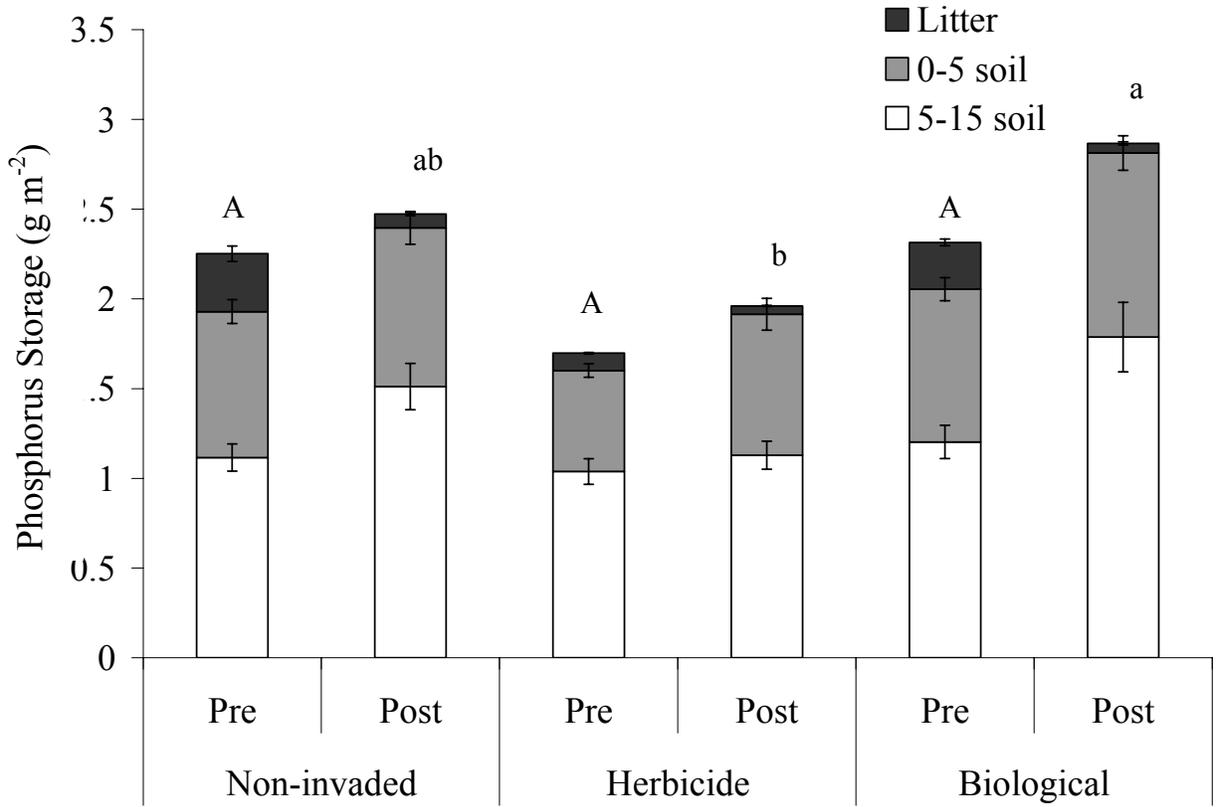


Figure 3-6. Mean (\pm S.E.) of pre- and post-fire storages of phosphorus measured in the non-invaded, herbicide, and biological sites (different lower case and capital letters indicate significant differences for each analysis).

CHAPTER 4 COMPARING NATIVE AND EXOTIC PLANT QUALITY: IMPLICATIONS FOR NUTRIENT TURNOVER

Introduction

Organic matter decomposition and the subsequent release of plant available nutrients is a vital ecosystem process. The decomposition of plant derived organic matter occurs in three phases: 1) initial losses due to the leaching of soluble chemical compounds, 2) microbial colonization and degradation, and 3) physical and biological fragmentation (Chapin et al. 2002). All three phases of decomposition are controlled by both biotic and abiotic factors (Berg 2000). For example, in general, plant residues with higher concentrations of nitrogen and phosphorus and lower ratios of resistant materials (e.g. lignin) to soluble fibers (e.g. sugars and carbohydrates) may have faster decomposition rates (Berg 2000, Chapin et al. 2002, Mack and D'Antonio 2003). In addition, environmental factors such as temperature, moisture, and pH can alter the structure and function of microbial communities that process organic matter (Couteaux et al. 1995, Katterer et al. 1998, Chapin et al. 2002). Several studies have shown that the alteration of organic inputs after a disturbance, such as exotic plant invasions, can alter decomposition rates resulting in changes in the structure and function ecosystems (Ehrenfeld 2003, Mack and D'Antonio 2003).

Melaleuca quinquenervia (Cav.) Blake, otherwise known as the paper-bark tree, cajeput, punk tree, or white bottlebrush tree, is a member of the Myrtaceae family, sub-family Leptospermoidae. This tall evergreen tree historically occupies tropical wetland sites throughout its native range along the eastern coast of Australia (Kaufman and Smouse 2001). It was introduced into South Florida in 1886 (Dray et al. 2006), originally for sale as an ornamental, but later was used for erosion control, as a forestry crop, and as an agricultural windrow plant (Meskimen 1962, Stocker and Sanders Sr. 1981, Bodel et al. 1994). The exotic tree colonized

and thrived in most natural areas of South Florida, including bayhead tree islands, sawgrass prairies, pine flatwoods, pastures, and cypress forests (Bodel et al. 1994).

Myers (1984) described the *Pinus elliottii* Englem-*Taxodium distichum* (L.) L.C. Rich var. *nutans* (Ait.) Sweet ecotone in South Florida. This is the transition zone between upland *P. elliottii*-dominated sites and depressional *T. distichum* dominated swamps where both trees co-dominate but neither grows to its full potential (Myers 1983). This ecotone has also been extensively invaded by *M. quinquenervia* (Myers 1984). These infestations have been managed using a combination of chemical, mechanical, and biological methods. However, to date, no research has been done on the rate of *M. quinquenervia* litter decomposition and its effect on nutrient turnover in South Florida ecosystems like this one.

A 1999 study suggested that ecosystem invasion by *M. quinquenervia* alters rates of decomposition and increases the storage of organic material (Anonymous 1999). *Melaleuca alternifolia*, a close relative of *M. quinquenervia*, is known to produce volatile essential oils with antimicrobial properties (Carson et al. 2006). In addition, DiStefano and Fisher (1983) found that extracts of *M. quinquenervia* leaves reduced fungal infections of plant embryos. The antimicrobial properties of litter are often cited as a mechanism through which *M. quinquenervia* dominates ecosystems.

The objective of this work, therefore, was to elucidate temporal changes in the litter quality of *M. quinquenervia*, *T. distichum*, and *P. elliottii* and quantify their effects on nutrient turnover. Two main hypotheses were tested: 1) *M. quinquenervia* will have the slowest rate of decomposition; and 2) *M. quinquenervia* litter will release least amount of carbon, nitrogen, and phosphorus compared to *T. distichum* and *P. elliottii* litter.

Materials and Methods

Site Description

The study site was located in the Belle Meade Tract of the Picayune Strand State Forest in Collier County, Florida (Figure 2-1). This area consists of nearly level, poorly drained, low fertility soils which are loamy, siliceous, hyperthermic Arenic Glassoqualfs. The soil series is Pineda-Boca-Hallandale which is characterized by moderately to poorly drained sands which overly limestone bedrock to a depth of approximately 1.4 m (USDA 1998). The water table fluctuates annually between greater than 15 cm below the soil surface to approximately 25 cm above. The area has a distinct wet season from approximately July to December and a dry season from January to June. Average annual rainfall in this region is approximately 1.36 m (SERC 2007). Historically, the vegetation in this area was a mixed *T. distichum*-*Pinus elliottii* forest with a hardwood under-story. Over the past several decades, many areas in this landscape have been invaded with *M. quinquenervia* and are now comprised of sparse populations of mature trees with dense understories of seedlings and saplings that can exceed densities of 100 plants per square meter.

Experimental Approach

Six by six inch litter bags were constructed using 1 mm mesh fiberglass screen. Leaves or needles that were senescent but still attached were collected from *M. quinquenervia*, *T. distichum* and *P. elliottii* and air dried to a constant weight. Leaves from *M. quinquenervia* were collected in an area that is dominated by mature *M. quinquenervia* trees while *T. distichum* and *P. elliottii* needles were collected from an adjacent non-invaded area. Two gram samples of leaves or needles from each species were placed into separate litter bags which were then deployed at three locations within a non-invaded, non-burned, mixed *T. distichum*-*P. elliottii* forest. Each species was replicated 3 times within a location and held in place using staples. Samples were

collected from each location at 6 week, 3 month, 6 month, and 12 month intervals. The decomposition constants (k) were determined for each plant species by assuming an exponential rate of mass loss ($M_f = M_i e^{-kt}$) where M_i is the initial mass of the litter, M_f is the final mass of the litter, and t is the time at M_f . The mean residence time, or time required for the litter to decompose under steady state, was calculated as $1/k$ (Chapin et al. 2002).

Litter Component Analyses

Percent organic matter was measured by loss on ignition from 0.2 to 0.5 g samples of dried and ground plant material, which were first measured into 50 mL beakers (Luczak et al. 1997). The beakers were placed in a muffle furnace and brought to 250°C for 30 minutes. The furnace temperature was then increased to 550°C for 4 hours. Organic matter content was calculated as the mass loss on ignition on a dry weight basis.

Litter quality was measured with a sequential extraction using an Ankom A200 Fiber Analyzer (Rowland and Roberts 1994). Half of a gram of coarsely ground litter material was weighed and sealed into Ankom filter bags. The bags were extracted with a neutral detergent to remove soluble cellular contents (sugars, carbohydrates, lipids, etc.) followed by an acid detergent to removal hemi-cellulose. Cellulose was removed by soaking the bags in 72% sulfuric acid (H_2SO_4) for 3 hours. The residual (lignin and ash) was combusted at 550°C for 4 hours to determine ash content. Litter quality was calculated on a dry mass basis.

Nutrient Analyses

Dried and ground plant material was analyzed for percent carbon and nitrogen on a Thermo-Electron, 1112 Series elemental analyzer. Total phosphorus was determined by a two-phase acid extraction after loss on ignition (Andersen 1976). The ash remaining in the 50 mL beaker was moistened with 2 to 3 mL distilled de-ionized water and then extracted with 20 mL of 6 N hydrochloric acid (HCl). All of the water was removed and the hot plate was placed on

high for 30 minutes to completely dry the samples. After cooling, 2.25 mL of 6 N HCl was added to each beaker and the beakers placed on a hot plate until almost boiling. Extracts were then filtered through a #41 Whatman filter into 50 mL volumetric flasks that were then brought to volume with distilled de-ionized water. Total phosphorus was measured with an automated ascorbic acid method on a Bran and Luebbe Auto Analyzer 3, Digital Colorimeter (Method 365.4; USEPA 1993). Nutrient ratios were all calculated on a mass basis.

Statistical Analyses

Values of measured vegetation characteristics and decomposition rates were calculated as a mean for each sample date. ANOVA and Tukey means separation tests were used to detect any differences between the measured parameters. Differences are reported as significant for tests with p values ≤ 0.05 . All statistical analyses were performed using JMP 7.0.1 software (SAS Institute, North Carolina, USA).

Results

Full model results for the main effects and interactions are reported in Tables A-19 through A-22. Based on the magnitude of the results the main effects of species and week were the most important determinants of the measured response variables. There were consistent block effects for many of the measured variables however in no circumstances did this effect change the pattern between the three plants species over time.

The tissue concentrations of carbon, nitrogen, and phosphorus for each plant species are presented in Table 4-1. Although there was no difference in the initial concentration of carbon among the three species, there was more initial nitrogen in the *T. distichum* and *M. quinquenervia* litter compared to the *P. elliotii* litter (Table 4-1). The phosphorus concentration was highest in the *T. distichum* litter. The concentration of nitrogen and phosphorus increased over time for each plant species. Prior to placement in the field, the *P. elliotii* litter had the

highest ratio of carbon to nitrogen followed by the *T. distichum* and then *M. quinquenervia* litter (Table 4-2). *Pinus elliottii* litter had the lowest ratio of nitrogen to phosphorus compared to the other two species. There was no difference in the initial ratio of carbon to phosphorus among any of the plant species. The ratio of carbon to nitrogen, nitrogen to phosphorus, and carbon to phosphorus decreased in all plant species over time.

The *T. distichum* litter had the highest decomposition constant compared to both the *M. quinquenervia* and *P. elliottii* litter (Table 4-3, Figure 4-1). It also had the shortest residence time or fastest rate of decomposition followed by *M. quinquenervia* and then *P. elliottii* (Table 4-3, Figure 4-1). At the end of the year, the *T. distichum* litter lost 53%, the *M. quinquenervia* litter lost 37%, and the *P. elliottii* litter lost 31% (Figure 4-1).

The *M. quinquenervia* litter initially had the highest percentage of soluble fiber, followed by the *T. distichum* litter, and then *P. elliottii* litter ($p = <0.0001$, Figure 4-2). This relationship was maintained in the final sample where soluble fiber was also highest in the *M. quinquenervia* litter, followed by the *T. distichum*, and then *P. elliottii* ($p = <0.0001$, Figure 4-2). The *P. elliottii* litter had the highest percentage of lignin both initially and in the last sampling date, followed by the *T. distichum* litter, and then *M. quinquenervia* litter ($p = 0.0001$, Figure 4-2).

Each plant species lost carbon compared to the initial pool at each sample period (Figure 4-5a). At 6 weeks and 1 year, the *M. quinquenervia* litter lost nitrogen compared to the initial pool (Figure 4-5b). However, *M. quinquenervia* litter gained nitrogen at 3 and 6 months. In contrast, *T. distichum* litter lost nitrogen at each sample period. *Pinus elliottii* litter gained nitrogen at 6 weeks, 3 months, and 6 months compared to the initial pool but lost nitrogen at 1 year. Each plant species gained phosphorus compared to the initial pool at each sample period (Figure 4-5c).

Discussion

Organic Matter Turnover

Baruch and Goldstein (1999) and Ehrenfeld (2003) found that the litter of exotic plants may differ from native species in chemical composition, which could alter the rate of ecosystem nutrient fluxes. For example, the ratio of soluble fibers (e.g. sugars and carbohydrates) to resistant materials (e.g. lignin) in organic matter can affect the rate of decomposition and subsequent release of plant available nutrients. In this study, differences were found among the chemical compositions of the *M. quinquenervia*, *T. distichum*, and *P. elliotii* litters. However, contrary to our hypothesis that *M. quinquenervia* would have the highest concentrations of lignin, *M. quinquenervia* had the highest concentration of soluble materials and the lowest concentration of lignin, both initially and at the one year sample period (Figure 4-2). Lignin increased in all three plant species by end of one year, probably as a result of the preferential degradation of soluble carbon compounds during organic matter decomposition (Chapin et al. 2002).

As hypothesized, the residence time of the *M. quinquenervia* litter was significantly longer than the *T. distichum* litter (Table 4-3). However, contrary to our hypotheses, the residence time of the *M. quinquenervia* litter was significantly shorter compared to *P. elliotii* litter (Table 4-3). Many studies have found that ecosystem invasion by exotic plants significantly alters rates of organic matter decomposition (Pidgeon and Cairns 1981, Baruch and Goldstein 1999, Ehrenfeld 2003, Rothstein et al. 2004, Standish et al. 2004). Standish et al. (2004) found that the invasion of the exotic herb *Tradescantia fluminensis* increased rates of organic matter decomposition and nutrient availability in a remnant forest. However, these data indicate that invasion by *M. quinquenervia* into a *P. elliotii*-*T. distichum* ecotone forest may not significantly alter rates of

organic matter turnover. Further study is needed to investigate the effects of mixed litter decomposition in areas dominated by exotic plants.

The residence time of all three species was somewhat faster than reported in the literature (Table 4-3). Reported estimates of the turnover time of *T. distichum* litter range 1.2 to 3.1 years compared to the 1.34 years in this study. Although no direct measurements of *M. quinquenervia* decomposition have been published, we reanalyzed litterfall and litter accumulation data from Greenway (1994) and calculated a residence time of 4.3 years, compared to the 2.19 years in this study. Wienand and Stock (1995) found that the decomposition of *P. elliotii* needles can be relatively slow compared to co-existing native species. For example, Gholz et al. (1985) reported that *P. elliotii* litter lost only 13-17% of the dry litter in one year. However, decomposition of *P. elliotii* litter was faster in this study where 31% of the litter had decomposed after 12 months. This faster rate may have been caused by the seasonal hydro-period of the study area. The largest losses of organic material occurred during or directly after inundation (Figure 4-1). These fluctuations in the water table may have increased the leaching of soluble compounds and provided moisture to the microbial communities.

Nutrient Turnover

Nutrient storage and cycling in the decomposing organic matter was different among the three plant species. Nitrogen was immobilized at every sample period in the *T. distichum* and *M. quinquenervia* litter which led to an increase in the nitrogen concentration of the litter at the 1 year sample period (1.72 and 1.53 times greater for *T. distichum* and *M. quinquenervia*, respectively, Table 4-1). In contrast, nitrogen was immobilized in the *P. elliotii* litter for the first 6 months, then mineralized at the 1 year sample, for an overall increase in nitrogen concentration (1.31 times greater, Table 4-1). Despite the increase in nitrogen concentration with *T. distichum* at every sample period, the significant mass loss of litter led to an overall

decline in nitrogen storage (Figure 4-5b). In contrast, the storage of nitrogen increased in *M. quinquenervia* and *P. elliotii* litter at the 3 month and 6 month sample periods and then decreased at 1 year (Figure 4-5b). Overall, differences in nutrient concentration offset mass loss and led to the greater total nitrogen storage of nitrogen in the *T. distichum* and *M. quinquenervia* litter compared to the *P. elliotii* litter ($p = <0.0001$, Figure 4-6b). The rates of nitrogen storage and cycling can differ between native and exotic plant dominated ecosystems (Mack and D'Antonio 2003, Rothstein et al. 2004, Standish et al. 2004). Rothstein et al. (2004) found that the invasion of the exotic tree *Fraxinus uhdei* into the Hawaiian rainforest doubled the release of nitrogen of the litter compared to a native forest. However, in this study invasion by *M. quinquenervia* should not significantly alter the storage and cycling of nitrogen in a *P. elliotii*-*T. distichum* ecotone forest.

All three plant species immobilized phosphorus at every sample period and increased overall phosphorus storage indicating a phosphorus limitation in the system (Table 4-1 and Figure 4-5c). At the one year sample period, the total storage of phosphorus was highest in the *T. distichum* followed by *M. quinquenervia* and then *P. elliotii* litter ($p = 0.012$, Figure 4-6c). The measured differences in nutrient dynamics explain the differences in the residency times of the litter, namely the final nitrogen concentration, phosphorus concentration, and the final nutrient ratios of the litter material (Figure 4-3 and 4-4). These relationships suggest that both nitrogen and phosphorus limitations, as well as, organic matter quality may be controlling the decomposition of the litter material of all three species.

Another mechanism whereby *M. quinquenervia* litter could alter nutrient turnover rates is through changes in microbial communities. Microbes are responsible for the decomposition of organic matter and cycling of nutrients critical to plant growth (Chapin et al. 2002). However,

before a nutrient is released into the ecosystem, internal needs of microbial communities must be met. For example, it is estimated that microbial communities will immobilize nitrogen in order to meet internal needs if the C:N molar ratio of the substrate is greater than 25:1 to 30:1. This figure is based on two assumptions: 1) a microbial substrate use efficiency of 40% and 2) a C:N microbial biomass ratio of 10:1 (Chapin et al. 2002). Martin et al. (2009) found that *M. quinquenervia* altered the soil microbial community composition, which in turn may change rates of ecosystem nutrient cycling. For example, if fungal biomass were to become more prevalent in the invaded soils, then substrate use efficiency could be greater thereby increasing the availability of carbon substrates (Davet 2004). In addition, microbial communities with higher C:N biomass ratios have lower requirements for nitrogen and will therefore mineralize nitrogen at lower concentrations (Eviner and Chapin 2003). Further research is needed to assess the structure of microbial communities growing on the various litter types.

Conclusion

The invasion of *M. quinquenervia* has been shown to alter ecosystem structure and function (Myers 1983, 1984, Bodel et al. 1994, Martin et al. 2009). However, this work has shown that *M. quinquenervia* may not significantly alter the basic ecosystem processes of organic matter decomposition and nutrient turnover in invaded *P. elliotii*-*T. distichum* ecotone forests. This indicates the need for ecosystem-specific studies to evaluate the impact of plant invasions. Although *M. quinquenervia* has colonized and thrived in most natural areas of South Florida, the consequences for ecosystem function may not be the same for each community (Bodel et al. 1994). Currently there is an integrated plant management program to control *M. quinquenervia* in South Florida ecosystems. Mechanical, chemical, and biological control programs have contained the spread and eliminated the invasive potential of existing *M. quinquenervia* populations (Ferriter et al. 2005, Tipping et al. 2008, Tipping et al. 2009).

However, live non-invasive *M. quinquenervia* trees remain part of vegetative landscape and are targets for future management. Treatment of remnant *M. quinquenervia* populations with chemical or mechanical methods may cause significant collateral damage to native plant communities and may negatively influence ecosystem function. Further work is needed to determine if communities would actually benefit from the removal of this exotic, but now less invasive plant.

Tables and Figures

Table 4-1. Mean (\pm S.E.) of litter nutrient concentrations at every sample time for each plant species (lower case letters indicate significant differences for each analysis).

Sample period	<i>M. quinquenervia</i>	<i>T. distichum</i>	<i>P. Elliottii</i>	<i>P</i>
Carbon	----- mg g ⁻¹ -----			
initial	479 \pm 12.3	523 \pm 28.4	475 \pm 10.80	0.22
6 weeks	484 \pm 2.92 a	464 \pm 1.81 b	470 \pm 5.39 b	0.0035
3 months	483 \pm 3.50 a	459 \pm 2.07 b	470 \pm 4.00 b	<0.0001
6 months	472 \pm 2.41 a	457 \pm 2.03 b	469 \pm 1.63 a	<0.0001
12 months	494 \pm 3.10 a	461 \pm 3.26 b	463 \pm 4.89 b	<0.0001
Nitrogen				
initial	7.44 \pm 0.18 a	9.06 \pm 0.68 a	5.38 \pm 0.11 b	0.002
6 weeks	8.44 \pm 0.20 b	12.1 \pm 0.21 a	6.62 \pm 0.03 c	<0.0001
3 months	9.20 \pm 0.40 b	13.8 \pm 0.34 a	6.75 \pm 0.22 c	<0.0001
6 months	9.70 \pm 0.31 b	14.5 \pm 0.42 a	8.44 \pm 0.41 b	<0.0001
12 months	11.4 \pm 0.71 b	15.6 \pm 0.34 a	7.03 \pm 0.26 c	<0.0001
Phosphorus	----- mg kg ⁻¹ -----			
initial	103 \pm 1.56 b	127 \pm 3.10 a	106 \pm 1.73 b	0.0006
6 weeks	188 \pm 11.0 c	526 \pm 19.8 a	266 \pm 18.3 b	<0.0001
3 months	284 \pm 14.4 b	650 \pm 50.7 a	321 \pm 35.7 b	<0.0001
6 months	289 \pm 15.2 b	623 \pm 38.7 a	322 \pm 23.7 b	<0.0001
12 months	410 \pm 48.8 b	660 \pm 42.0 a	338 \pm 16.8 b	<0.0001

Table 4-2. Mean (\pm S.E.) of mass nutrient ratios at every sample time for each plant species (lower case letters indicate significant differences for each analysis).

Variable	<i>M. quinquenervia</i>	<i>T. distichum</i>	<i>P. elliotii</i>	<i>P</i>	
C : N	0 weeks	64.4 \pm 0.24 b	57.9 \pm 1.15 c	88.3 \pm 1.42 a	<0.0001
	6 weeks	57.5 \pm 1.15 b	38.6 \pm 0.69 c	72.0 \pm 2.80 a	<0.0001
	3 months	53.3 \pm 2.17 b	33.0 \pm 0.93 c	67.2 \pm 3.19 a	<0.0001
	6 months	49.1 \pm 1.55 b	31.9 \pm 1.00 c	56.7 \pm 2.83 a	<0.0001
	12 months	44.4 \pm 2.51 b	29.7 \pm 0.60 c	66.4 \pm 1.90 a	<0.0001
N : P	0 weeks	72.4 \pm 2.38 a	71.9 \pm 6.86 a	50.8 \pm 1.67 b	0.019
	6 weeks	46.0 \pm 2.22 a	23.1 \pm 0.66 b	25.8 \pm 1.88 b	<0.0001
	3 months	32.7 \pm 1.52 a	22.0 \pm 1.43 b	21.8 \pm 1.26 b	<0.0001
	6 months	34.2 \pm 1.67 a	23.6 \pm 0.96 b	26.8 \pm 1.23 b	<0.0001
	12 months	29.4 \pm 2.14 a	24.1 \pm 1.05 b	21.0 \pm 0.58 b	0.0009
C : P	0 weeks	4662 \pm 151	4143 \pm 306	4486 \pm 171	0.31
	6 weeks	2646 \pm 149 a	892 \pm 32.2 c	1862 \pm 174 b	<0.0001
	3 months	1649 \pm 62.5 a	733 \pm 60.4 c	1435 \pm 119 b	<0.0001
	6 months	1676 \pm 93.5 a	757 \pm 47.9 b	1534 \pm 132 a	<0.0001
	12 months	1325 \pm 146 a	718 \pm 41.4 b	1397 \pm 68.9 a	<0.0001

Table 4-3. Mean (\pm S.E.) of litter decomposition constants and residence times for each plant species reported in literature and this study (lower case letters indicate significant differences for each analysis).

Citation	Species	Decomposition constant (k)	Residence time years (1/k)
Greenway 1994	<i>Melaleuca quinquenervia</i>	0.23	4.3
Gholtz et al. 1984	<i>Pinus elliottii</i>	0.13	7.7
Hendricks et al. 2002	<i>Pinus elliottii</i>	0.10	10.3
Polglase et al. 1992	<i>Pinus elliottii</i>	0.27	3.7
Wienand and Stock 1995	<i>Pinus elliottii</i>	0.21	4.8
Wienand and Stock 1995	<i>Pinus elliottii</i>	0.35	2.9
Battle and Golladay 2001	<i>Taxodium distichum</i>	0.62	1.6
Day 1982	<i>Taxodium distichum</i>	0.33	3.1
Deghi et al. 1980	<i>Taxodium distichum</i>	0.83	1.2
Middleton 1994	<i>Taxodium distichum</i>	0.32	3.1
Nessel and Bayley 1984	<i>Taxodium distichum</i>	0.33	3.0
This study	<i>Melaleuca quinquenervia</i>	0.47 \pm 0.03 b	2.19 \pm 0.13 b
	<i>Taxodium distichum</i>	0.76 \pm 0.04 a	1.34 \pm 0.07 c
	<i>Pinus elliottii</i>	0.37 \pm 0.02 b	2.75 \pm 0.13 a
	<i>P</i>	<0.0001	<0.0001

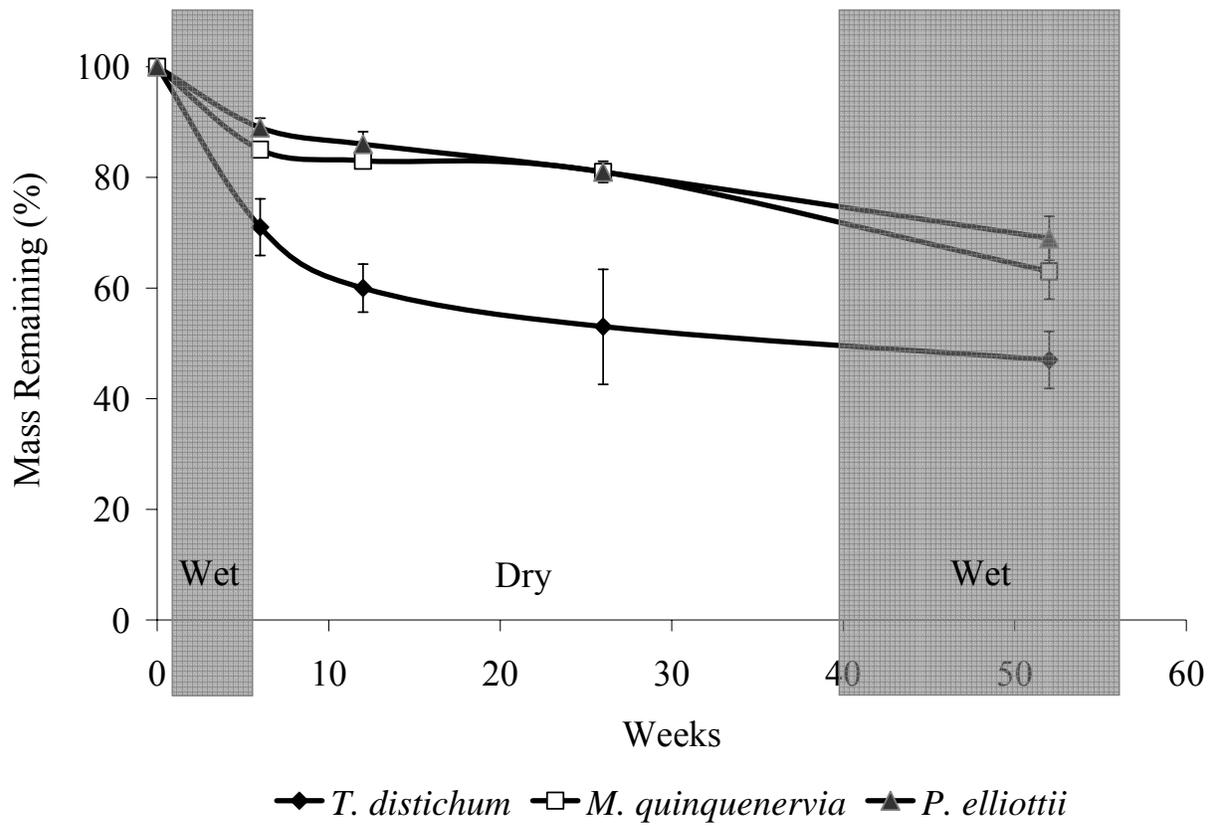


Figure 4-1. Mean (\pm S.E.) of litter mass remaining at every sample time for each plant species.

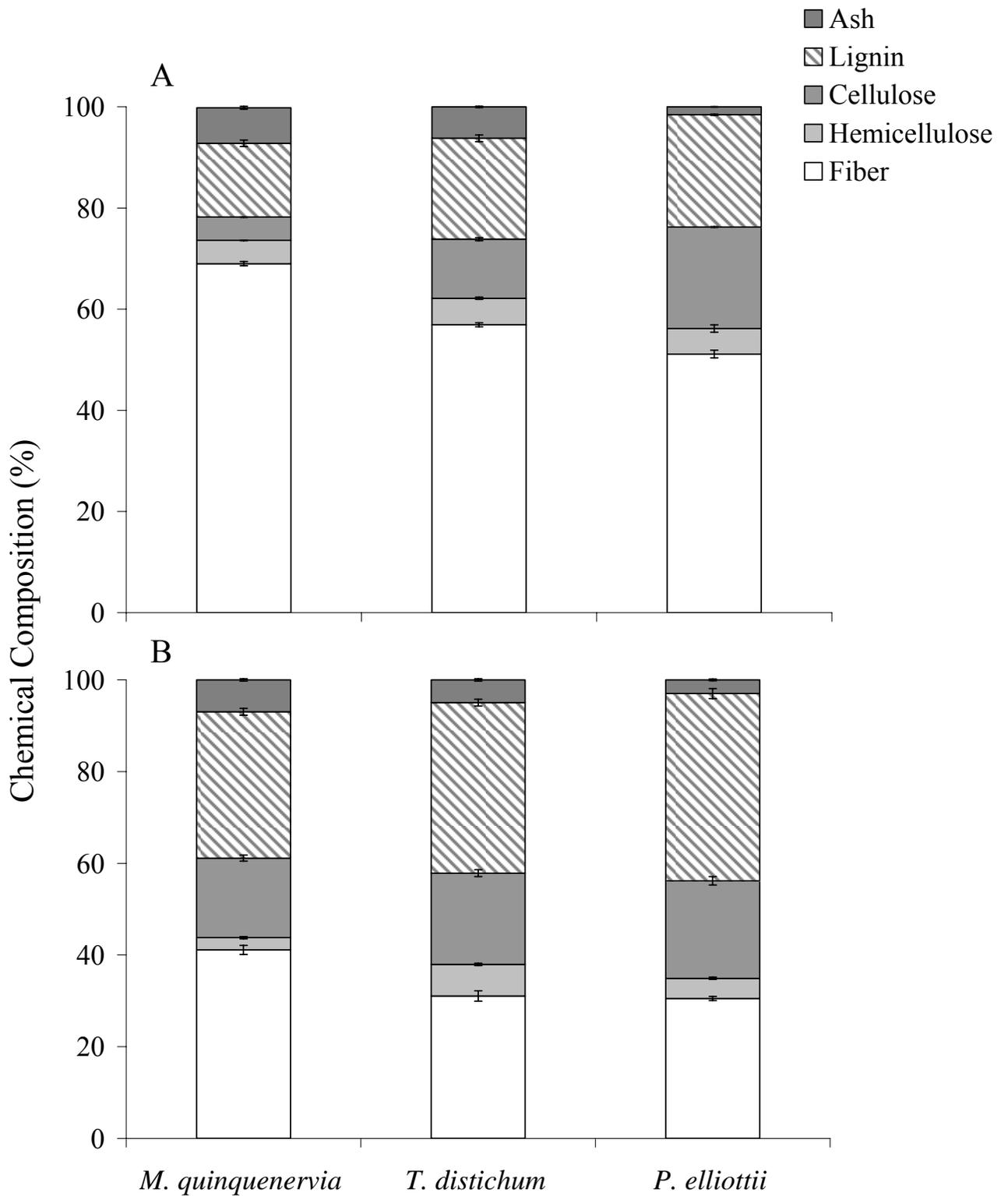


Figure 4-2. Mean (\pm S.E.) of the chemical composition for each plant species. A) The chemical composition at the initial sample period. B) The chemical composition at the final sample period.

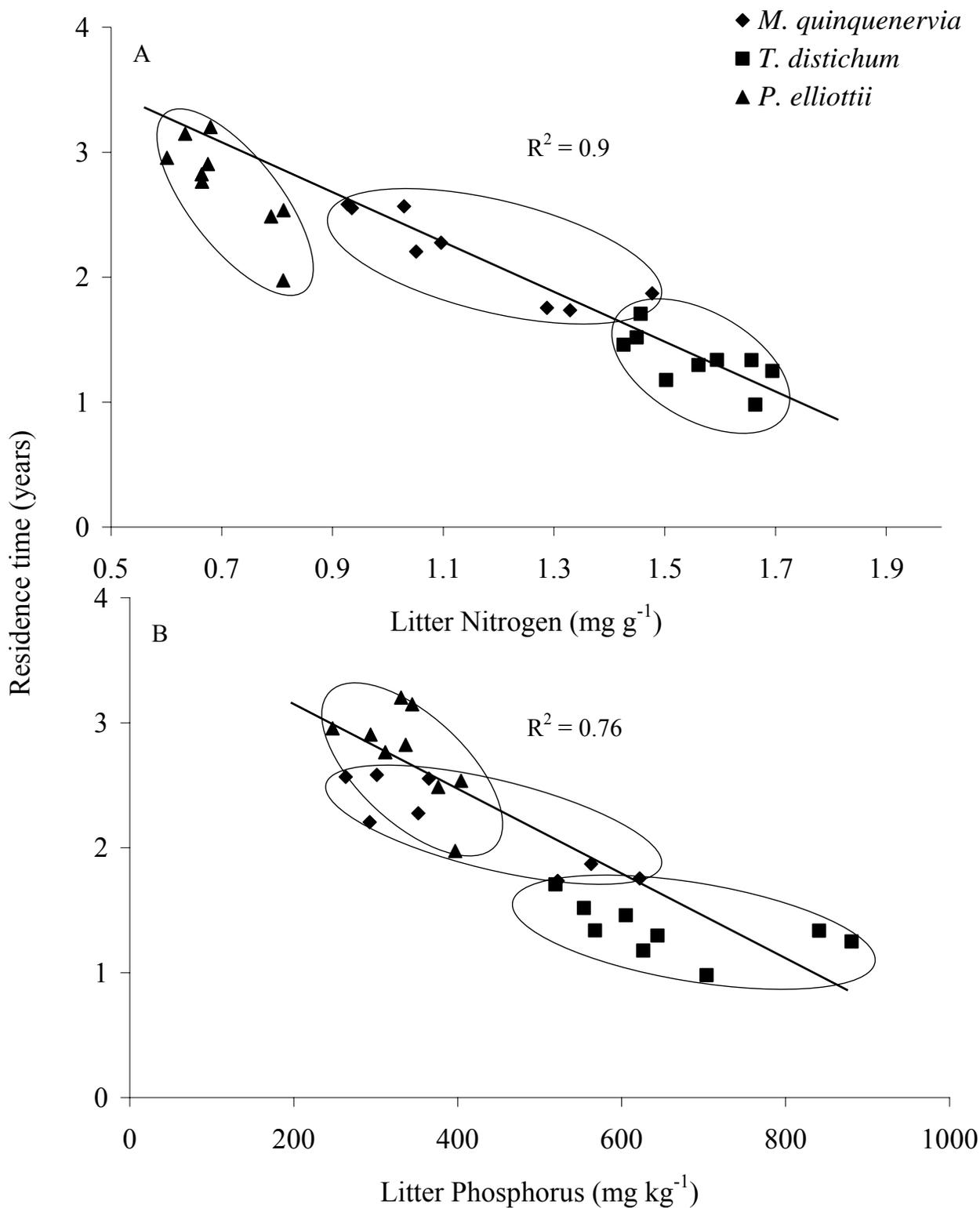


Figure 4-3. Relationship between litter residence time and final nutrient concentration for each plant species. A) Relationship between residence time and litter nitrogen concentration at the final sample period. B) Relationship between residence time and litter phosphorus concentration at the final sample period (circles indicate individual plant species).

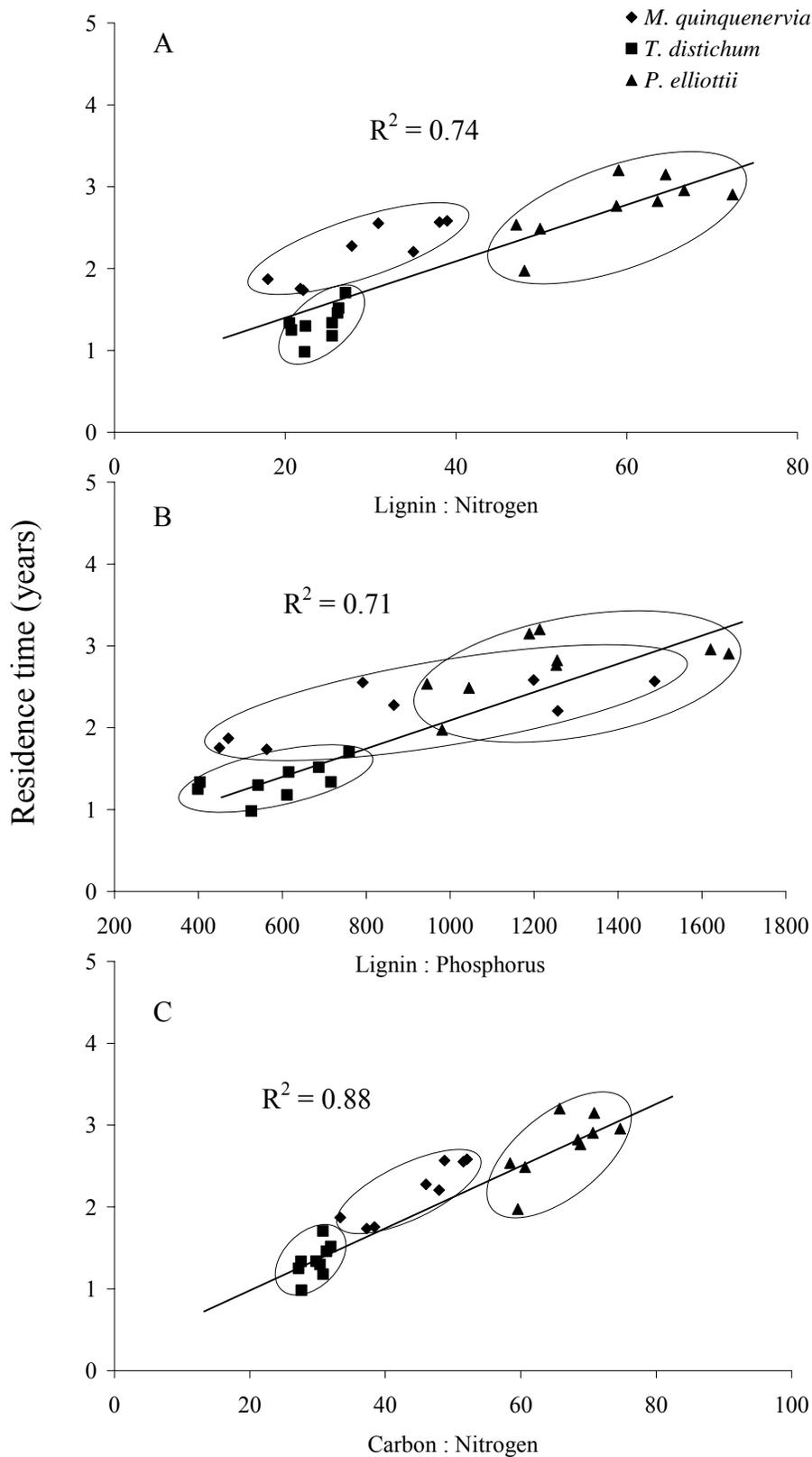


Figure 4-4. Relationship between litter residence time and chemical and nutrient ratios at the final sample period for each plant species. A) Relationship between residence time and lignin to nitrogen ratios. B) Relationship between residence time and lignin to phosphorus ratios. C) Relationship between residence time and carbon to nitrogen ratios (circles indicate individual plant species).

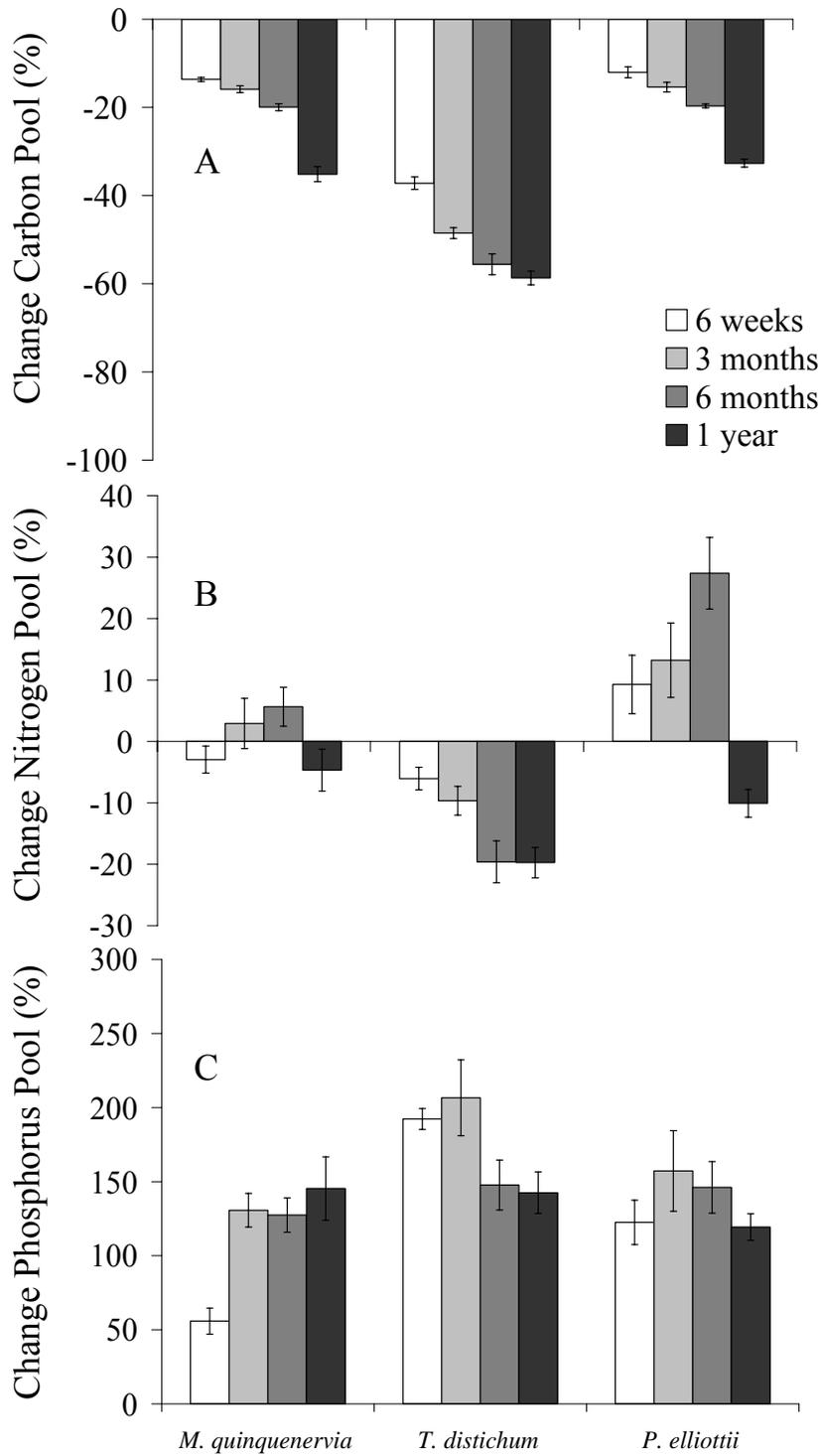


Figure 4-5. Mean (\pm S.E.) percent change in the pools of nutrients from the initial storage at every sample time for each plant species. A) Change in carbon pool. B) Change in nitrogen pool. C) Change in phosphorus pool.

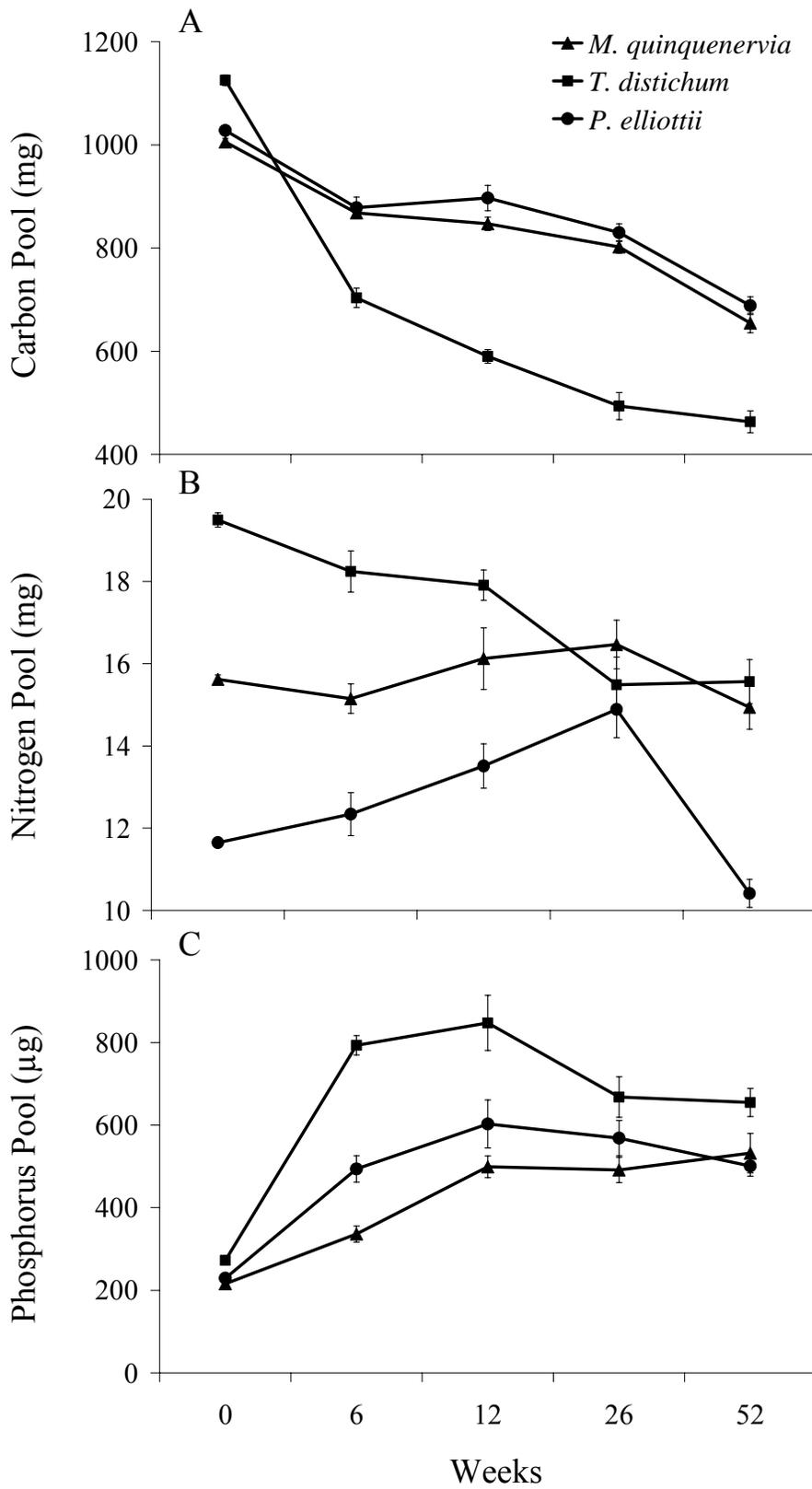


Figure 4-6. Mean (\pm S.E.) pools of nutrients at every sample time for each plant species. A) Carbon pool. B) Nitrogen pool. C) Phosphorus pool.

CHAPTER 5 RECOVERY OF PLANT COMMUNITY STRUCTURE AFTER A SEASONAL FIRE

Introduction

Ecosystem invasion by exotic plant species poses a significant threat to community diversity, function, and stability (Mack and D'Antonio 1998, Mack et al. 2000, Fenn et al. 2003, Kourtev et al. 2003). Although this issue is of global concern, the invasion of exotic plants has been a significant problem in the State of Florida, especially South Florida, which is home to Everglades. The Everglades is an extensive forest and graminoid wetland community that once occupied 4,000 square miles of the state's lower peninsula, over twice its present day land area (Gunderson 1994). This complex ecosystem has proved an ideal habitat for many exotic plant species. The Florida Exotic Pest Plant Council has compiled a list of Florida's 125 most invasive exotic plants and separated them into two categories (Doren 2002). Sixty-six plants received a category I designation, which indicates they are considered "highly disruptive to native plant communities".

Arguably one of the worst category I invasive plants is *Melaleuca quinquenervia* (Cav.) Blake, otherwise known as the paper-bark tree, cajeput, punk tree, or white bottlebrush tree (Doren 2002). Due to its fire adapted nature and copious seed production, *M. quinquenervia* is able to out-compete and replace many native species. It is estimated that *M. quinquenervia* populations currently cover over 161, 874 hectares in the State of Florida (Anonymous 2007). This large evergreen tree (25-30 m tall) is native to coastal areas of eastern Australia, southern New Guinea, and New Caledonia where it occurs typically along freshwater streams and swamps (Boland et al. 1987). It was introduced into South Florida in 1886 (Dray et al. 2006), originally for sale as an ornamental, but later was used for erosion control, as a forestry crop, and as an agricultural windrow plant (Meskimen 1962, Stocker and Sanders Sr. 1981, Bodel et al. 1994).

This exotic tree has colonized and thrived in most of the natural areas of South Florida, including bayhead tree islands, sawgrass prairies, pine flatwoods, pastures, and cypress forests (Bodel et al. 1994). DiStefano and Fisher (1983) found that the relative density, frequency, and dominance of several native plant species were significantly diminished in sites invaded by *M. quinquenervia*.

A management plan was cooperatively developed by local, state, and federal agencies to reduce the impact of *M. quinquenervia* using chemical, mechanical, and biological methods (Ferriter et al. 2005). The South Florida Water Management District (SFWMD) has sustained a multi-year campaign to chemically and mechanically control *M. quinquenervia* on public lands. In 2003 alone the SFWMD chemically treated 1,795 hectares of *M. quinquenervia* with ground application and 4,118 hectares using aerial application (Ferriter et al. 2005). In addition, the SFWMD partially funded a biological control project headed by the United States Department of Agriculture, Agricultural Research Service (ARS) (Ferriter et al. 2005). This project, begun in 1986 at the ARS Invasive Plant Research Lab in Fort Lauderdale, is responsible for the release of four biological control agents to reduce or eliminate the capacity of *M. quinquenervia* to invade (Ferriter et al. 2005). Two of the biological agents, *Oxyops vitiosa* Pascoe (Coleoptera: Curculionidae) and *Boreioglycaspis melaleucae* Moore (Hemiptera: Psyllidae), have successfully established and are suppressing *M. quinquenervia* reproduction, growth, and recruitment on a landscape scale (Tipping et al. 2009).

Although management schemes aim to reduce or remove the competitive advantage of invasive plants in order for native plant communities to recover, little work has been done evaluating the impact of treatment methods on plant community structure, especially in the context of native disturbance regimes. Many of Florida's natural areas that have been invaded by *M. quinquenervia* depend on regular disturbances like fires to maintain community structure

and function. Native plant communities in these areas depend on seasonal fires to open canopies and trigger the seed release and germination of plant species, provide temporary pulses of soluble nutrients, and reduce plant competition (Wade et al. 1980, Neary et al. 1999). The invasion of *M. quinquenervia* and other exotic plants have altered native fire patterns which may have long-term consequences for ecosystem function (Wade et al. 1980, Serbesoff-King 2003).

The objective of this work was to elucidate changes in plant community structure in a *Pinus elliottii* Englem-*Taxodium distichum* (L.) L.C. Rich var. *nutans* (Ait.) Sweet ecotone forest after the invasion and management of *M. quinquenervia*. Two main hypotheses were tested: after a seasonal fire 1) plant community structure will not be different in the invaded and biologically controlled but will be different in the invaded and chemically treated site compared to the non-invaded site and 2) the re-invasion of *M. quinquenervia* will be most severe in the chemically treated site compared to the biologically controlled and non-invaded sites.

Materials and Methods

Experimental and Statistical Justification

In order to assure the proper assignment of treatment causality in experiments several fundamental assumptions must be met including: random assignment of treatments across experimental units and treatment replication (Beyers 1998). Random assignment of treatments reduces the impact of non-treatment factors that could confound results and replication reduces the likelihood that random variation is the cause of measured differences between treatments. Although the most effective field studies have randomly assigned, replicated experimental treatments many times limitations of money, labor, and time make these conditions impossible. Without a proper experimental design, the use of inferential statistics may only reveal differences between un-replicated plots and not the desired treatment effect (Hurlbert 1984). In other words,

the null hypothesis becomes that there is no difference between plots NOT that the treatment has no effect (Hurlbert 1984).

In ecosystems all over the world land managers are manipulating natural areas in an attempt to restore function, provide habitat, or mitigate anthropogenic disturbance. Often times these treatments are done on one large tract of land or single experimental unit. Scientific analysis of these areas can be complex because both of the assumptions mentioned above are violated. Still large-scale field studies investigating these treatments must be done in order to assess the impact of natural resource management decisions. There is nothing to be gained from limiting scientific investigation when management must continue. Insight gained from determining large-scale treatment effects can be used to guide further research and prevent undesirable consequences of management decisions.

Site Description

The study site was located in the Belle Meade Tract of the Picayune Strand State Forest in Collier County, Florida. This area consists of nearly level, poorly drained, low fertility soils which are loamy, siliceous, hyperthermic Arenic Glassoqualfs. The soil series is Pineda-Boca-Hallandale which is characterized by moderately to poorly drained sands which overly limestone bedrock to a depth of approximately 1.4 m (USDA 1998). The water table fluctuates annually between greater than 15 cm below the soil surface to approximately 25 cm above. In an average year, the area has a distinct wet season from approximately July to December and a dry season from January to June. Average annual rainfall in this region is approximately 1.36 m (SERC 2007). Historically, the vegetation in this area was a mixed *T. distichum*-*P. elliotii* forest with a hardwood under-story. Over the past several decades, many areas in this landscape have been invaded with *M. quinquenervia* and are now comprised of sparse populations of mature trees

with dense understories of seedlings and saplings that can exceed densities of 100 plants per square meter.

In early May of 2007 the Great Basal fire burned approximately 8,000 hectares in southwest Florida and all of the established experimental plots. As the fire was not planned no direct measurements of fire intensity were taken. However, all of the plots were equally affected as well as the entire surrounding landscape. Diversity measurements were taken 1 year after the fire.

Diversity Plots

On May 15, 2007, after a seasonal fire, twenty-five, 1 m² plots were established along five transects in each of three contiguous study areas. The areas sampled were: area #1) reproductive *M. quinquenervia* treated with herbicide in the summer of 2003 (hereafter referred to as “herbicide site”), area #2) reproductive *M. quinquenervia* treated with biological control (hereafter referred to as “biological site”), and area #3) native forest with no *M. quinquenervia* (hereafter referred to as “non-invaded site”). The two biological control agents mentioned above, *O. vitiosa* and *B. melaleuca*, were common in all areas. The herbicide site consisted of reproductive *M. quinquenervia* that was treated aerially with Velpar® (Hexazinone, 3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5-triazine-2,4(1H,3H)-dione) in 2003. The biological site consisted of reproductive *M. quinquenervia* which was not treated with herbicides and has been under attack by *O. vitiosa* since 1998 and *B. melaleuca* since 2002. The non-invaded site was a *P. elliotii*-*T. distichum* ecotone forest with no history of *M. quinquenervia* invasion. Non-woody diversity was measured in each plot (n = 25) on February 12-14, 2008. Four, 100 m² plots were established between the five transects in each of the sites and woody diversity was measured in each plot (n = 4) on February 17-19, 2008. Diversity was expressed by Simpson’s Index, $1/D = 1 / (\sum p_i^2)$, and Shannon’s Index, $H = - \sum p_i (\ln p_i)$, where p_i is the

relative (decimal) cover of the *i*th species (Peet 1974). Frequency is measured as the number of plots within each site where the species occurred divided by the total number of plots.

Statistical Analyses

Values of measured woody and non-woody diversity and species abundance were calculated as a mean for each plot. ANOVA and Tukey means separation tests were used to detect any differences among the plots. Differences are reported as significant for tests with p values ≤ 0.05 . All statistical analyses were performed using JMP 7.0.1 software (SAS Institute, North Carolina, USA).

Results

Full model results for the main effects and interactions are reported in Tables A-23 and A-24. Based on the magnitude of the results the main effect of site was the most important determinant of the measured response variables. There were no consistent transect or plot effects for any of the measured variables.

A total of 51 plant species were found across the three study sites with 37 species both in the non-invaded and biological sites, and 28 species in the herbicide site (Table 5-1). There was considerable overlap in species between the biological site and non-invaded sites with 68% of non-woody species, 100% of woody species, and 70% of all plant species found in both sites. The herbicide site had fewer plants in common with the non-invaded: 59% of non-woody species, 66% of woody species, and 57% of all plant species.

Overall, the non-woody plant species richness was highest in the non-invaded and herbicide sites compared to the biological site (Table 5-2). Woody plant species richness was highest in the non-invaded site followed by the biological site and then the herbicide site. Both the Simpson's and Shannon's indices for non-woody vegetation were highest in the non-invaded compared to the herbicide and biological sites. There was no difference in the Simpson's index

for woody vegetation among the sites. Shannon's index for woody vegetation was highest in the non-invaded site compared to the biological and herbicide sites.

The abundance of *M. quinquenervia* live and dead seedlings was highest in the biological compared to the non-invaded and herbicide sites (Table 5-3). Many of the *M. quinquenervia* seedlings measured in the biological were dead (37%) followed by 5% in the non-invaded site and 0% in the herbicide site. The non-invaded site had highest abundance of *T. distichum* and *P. elliotii* mature trees compared to the herbicide and biological sites. Figure 1 shows the frequency occurrence of each species in the three sites.

Discussion

Plant Community Structure

Approaches to restoring communities after the management of exotics can run the gamut from passive to active. The most passive approach relies on native plant communities recovering on their own, while more active methods involve directed efforts like replanting natives. Selecting the best approach depends on several factors including cost and the impact of the management itself on the native plant community. However, little work has been done evaluating the effects of current management programs on native community recovery in South Florida ecosystems.

Smith et al. (2002) experimentally evaluated the concept of "passive" restoration as part of the Comprehensive Everglades Restoration Plan (CERP). The main focus of the CERP is to "get the water right" which would "passively" restore the Everglades plant communities. In this study vegetation responses to increased hydroperiod length were measured to assess if the restoration of historic water flow patterns would result in control of invasive plants and a rebound of native plant communities. Their results indicated that restoration of native plant communities will not be solely dependant on water flow patterns and, therefore, more active

management strategies may be necessary in the future to restore historical plant communities (Smith et al. 2002). In contrast, MacDougall and Turkington (2007) managed weeds using fire, cutting and raking, and weeding and noted reductions in several common, invasive agricultural weeds, coupled with increases in native plants.

In this study, chemical and biological management of *M. quinquenervia* resulted in lower levels of plant diversity after a seasonal fire when compared to an unmanaged, non-invaded site (Table 5-2). Although the herbicide site contained levels of species richness comparable to the non-invaded site, only 57% of the plant species were found in common compared to 70% of species in biological site. Similarly, Mason and French (2007) found that despite significant reductions of *Chrysanthemoides monilifera* ssp. *rotundata*, dune systems were unable to passively return to pre-invasion levels of native plant diversity. They attributed this deficit to collateral damage from aerial herbicide applications which prevented recovery of dune communities. Further work is needed to evaluate the long-term consequences of the treatment of *M. quinquenervia* on native plant recruitment.

Plant Community Re-invasion

The density of *M. quinquenervia* seedlings was highest in the biological site compared to the non-invaded and herbicide sites (Table 5-3). However, 37% of those seedlings were dead compared to only 5% in the non-invaded site and 0% in the herbicide site. The rate of *M. quinquenervia* re-invasion in the all sites is significantly lower than experienced in the same site prior to the introduction of the biological control agents. After a fire in 1998, 591 *M. quinquenervia* seedlings per square meter germinated compared to the 34 seedlings in this study (Tipping et al., unpublished data). The lower rate of post-fire *M. quinquenervia* seedling recruitment is the result of the aforementioned biological control program. Tipping et al. (2008)

found that herbivory for the two established biological agents has reduced the seed production of *M. quinquenervia* by 99%.

However, management of one exotic species may lead to its replacement by another. Ogden and Rejmanek (2005) used fire and herbicides to significantly decrease the cover of the invasive fennel *Foeniculum vulgare*, only to have it replaced by non-native Mediterranean annual grasses. Another study found that riparian systems managed to control *Impatiens glandulifera* invasion were more readily invaded after management (Hulme and Bremner 2006). Although it was not one of the most abundant species, the invasive grass *Panicum repens* or torpedo grass (ID #25) was found in both the herbicide and biological sites (Table 5-1, Figure 5-1). This species is a serious pest in the State of Florida, has proven resistant to management programs, and may out-compete natives in the two treatment sites (David 1999). The potential for re-invasion following management reveals a need for a more active management approach that considers site specific environmental conditions (MacDougall and Turkington 2007). For example, a multi-habitat analysis of the control of the invasive plant *Tamarix* spp. identified several site characteristics that promoted greater cover and richness of natives (Bay and Sher 2008). Such analyses should extend to both above- and belowground alterations to ecosystem function caused by exotics and the tactics to manage them.

Conclusion

It is clear that plant invasions can result in devastating changes in natural systems, which justifies management operations designed to reduce or eliminate their effects (Mack and D'Antonio 1998, Mack et al. 2000, Fenn et al. 2003). Invasive species also pose significant direct and indirect challenges to ecosystem-wide restoration projects like CERP. Despite the fact that CERP will cost at least 30 billion dollars, require 30 years to complete, involve many agencies from all levels and jurisdictions, and affect 18,000 square miles over sixteen Florida

counties, the management of exotics has been something of an afterthought. The United States Army Corps of Engineers, the managerial agency for CERP, stated that “once hydrology is restored to the Everglades, invasive exotic species, such as *Melaleuca*...will continue to degrade the system by displacing native species” (Anonymous 2004). While the ultimate goal of management programs is to restore ecosystem integrity, this work has shown that passive restoration may not be enough to restore plant community structure in this system. More detailed studies which incorporate ecosystems services are needed to evaluate and value the role of native plant communities in overall ecosystem health, thereby guiding management decisions designed to protect and maintain them.

Tables and Figures

Table 5-1. Species list of all plants identified in the non-invaded, herbicide, and biologically controlled plots.

ID	Species Name	Non-invaded	Herbicide	Biological
		-----non-woody-----		
1.	unknown spp. 1	X	X	X
2.	<i>Pluchea rosea</i>	X	X	X
3.	<i>Andropogon glomeratus</i>	X	X	X
4.	<i>Leptochola spp.</i>	X	X	X
5.	<i>Cyperus elegans</i>	X	X	X
6.	<i>Cyperus haspan</i>	X	X	X
7.	<i>Scoparia dulcis.</i>	X	X	X
8.	<i>Eupatorium capillifolium</i>	X	X	X
9.	<i>Gamochaeta purpurea</i>	X	X	X
10.	<i>Diodia virginiana</i>	X	X	X
11.	<i>Symphyotrichum spp.</i>	X	X	X
12.	<i>Pluchea odorata</i>	X	X	X
13.	<i>Rhynchospora colorata</i>	X	X	X
14.	<i>Heloptropium spp.</i>	X	X	X
15.	<i>Rhynchospora divergens</i>	X		
16.	<i>Fuirena breviseta</i>		X	
17.	<i>Mikania scandens</i>	X	X	X
18.	<i>Dichantherium dichotomum</i>	X	X	X
19.	<i>Agalinis purpurea</i>		X	X
20.	<i>Solanum americanum</i>	X	X	X
21.	<i>Ludwigia leptocarpa</i>	X	X	X
22.	<i>Hypericum fasciculatum</i>	X	X	
23.	<i>Erechtites hieracifolia</i>	X	X	X
24.	<i>Juncus scirpodes</i>		X	
25.	<i>Panicum repens</i>		X	X
26.	<i>Dichantherium spp.</i>	X		X
27.	unknown spp. 2			X

Table 5-1. continued.

ID	Species Name	Non-invaded	Herbicide	Biological
-----non-woody-----				
28.	<i>Cyperus odoratus</i>			X
29.	<i>Eragrostis elliottii</i>			X
30.	<i>Gratiola ramosa</i>	X		X
31.	<i>Panicum hians</i>			X
32.	<i>Erechtites hieracifolius</i>			X
33.	<i>Blechnum serrulatum</i>			X
34.	<i>Fuirena spp.</i>	X		X
35.	<i>Cyperus polystachyos</i>			X
36.	<i>Oldenlandia uniflora</i>	X		X
37.	<i>Viola lanceolata</i>	X		
38.	<i>Pteridium aquilinum</i>	X		
39.	<i>Centella asiatica</i>	X		
40.	<i>Hyptis alata</i>	X		
41.	unknown spp. 3	X		
42.	<i>Sarcostemma clausum</i>	X		
43.	<i>Conoclinium coelestinum</i>	X		
44.	<i>Bigelovia nudata</i>	X		
45.	<i>Mitreola petiolata</i>	X		
46.	unknown spp. 4	X		
47.	<i>Xyris platylepis</i>	X	X	X
48.	<i>Cladium jamaicense</i>			X
-----woody-----				
49.	<i>Melaleuca quinquenervia</i>	X	X	X
50.	<i>Pinus elliottii</i>	X	X	X
51.	<i>Taxodium distichum</i>	X		X

Table 5-2. Diversity indices for the non-invaded, herbicide, and biologically controlled plots.

Variable	Plant type	Non-invaded	Herbicide	Biological	<i>P</i>
Richness	Non-woody	9.40 ± 0.63 a	9.83 ± 0.54 a	7.21 ± 0.55 b	0.004
	Woody	3.00 ± 0.00 a	1.00 ± 0.00 c	2.25 ± 0.25 b	<0.0001
Simpson	Non-woody	4.17 ± 0.43 a	2.47 ± 0.17 b	2.41 ± 0.23 b	0.0001
	Woody	1.77 ± 0.16 a	1.00 ± 0.00 b	1.07 ± 0.10 b	0.0005
Shannon	Non-woody	1.59 ± 0.07 a	1.18 ± 0.07 b	1.04 ± 0.11 b	<0.0001
	Woody	0.68 ± 0.09 a	0.00 ± 0.00 b	0.16 ± 0.02 b	<0.0001

Table 5-3. Woody species abundance for the non-invaded, herbicide, and biologically controlled plots.

Species	Plant Stage	Non-invaded	Herbicide	Biological	<i>P</i>
		-----number of plants m ⁻² -----			
<i>Melaleuca quinquenervia</i>					
	Live Seedling (< 15cm)	5.24 ± 0.95 b	2.58 ± 0.47 b	22.83 ± 13.62 a	<0.0001
	Dead Seedling (< 15cm)	0.28 ± 0.15 b	0.00 ± 0.00 b	13.63 ± 5.87 a	0.007
	Mature (>15cm)	1.78 ± 0.99	2.27 ± 0.29	3.79 ± 0.94	0.24
<i>Taxodium distichum</i>					
	Live Seedling (< 15cm)	0.20 ± 0.08 a	0.00 ± 0.00 b	0.00 ± 0.00 b	0.004
	Dead Seedling (< 15cm)	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	
	Mature (>15cm)	0.53 ± 0.04 a	0.00 ± 0.00 c	0.13 ± 0.01 b	<0.0001
<i>Pinus elliottii</i>					
	Live Seedling (< 15cm)	0.20 ± 0.13	0.04 ± 0.04	0.17 ± 0.10	0.47
	Dead Seedling (< 15cm)	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	
	Mature (>15cm)	0.06 ± 0.01 a	0.00 ± 0.00 b	0.003 ± 0.003 b	<0.0001

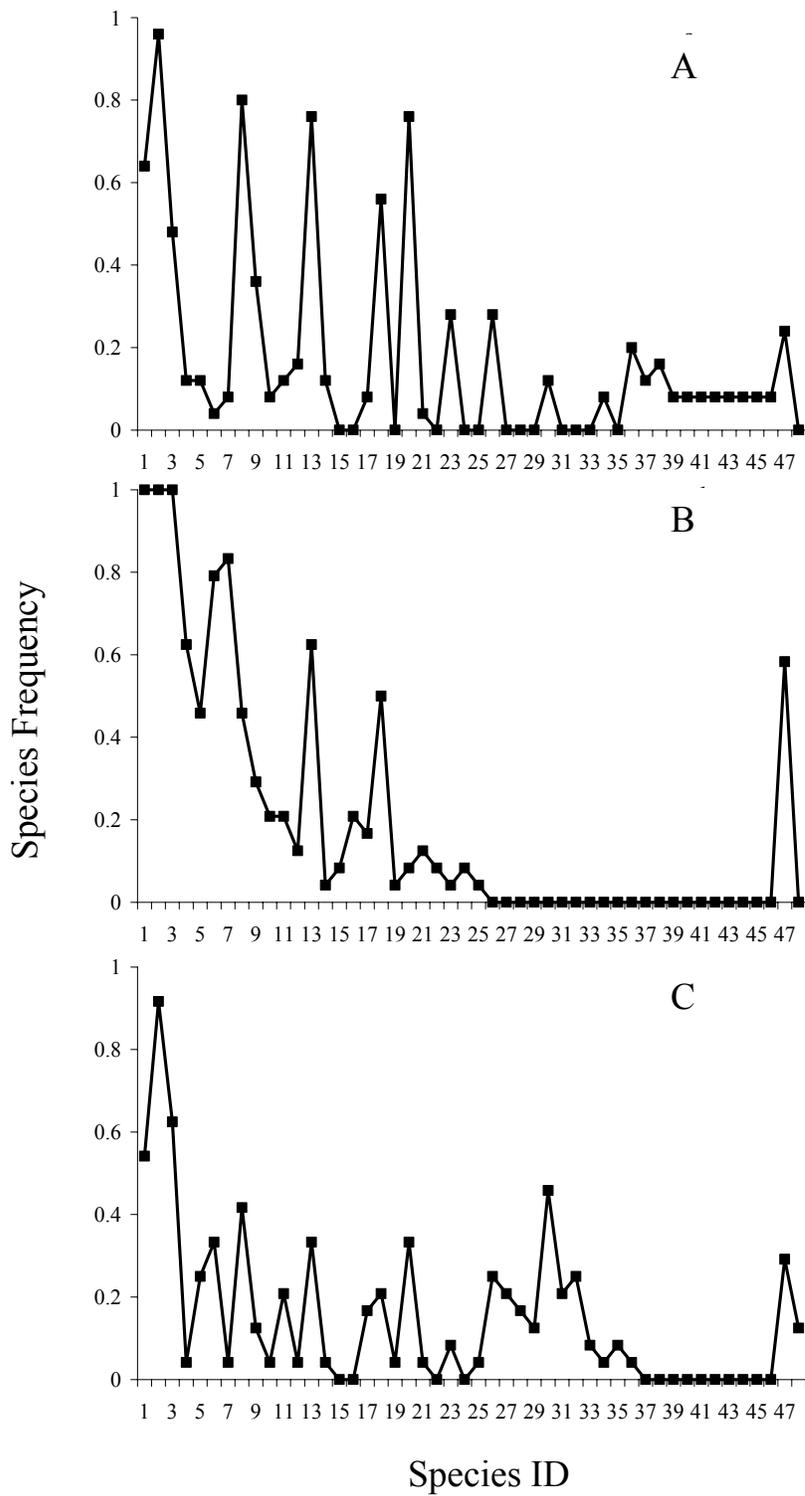


Figure 5-1. Frequency data for each non-woody plant species in the non-invaded, herbicide, and biological plots. A) Non-invaded site plant species frequency. B) Herbicide site plant species frequency. C) Biologically controlled site plant species frequency.

CHAPTER 6 SYNTHESIS

Objective 1. An Investigation of Ecosystem-Alteration after Management of *Melaleuca quinquenervia*.

The work presented in Chapter 2 tested two main hypotheses: 1) herbivory from the biological control agents will lower *M. quinquenervia* litter quality and rates of litter production and 2) herbivore-induced changes in litter quality will lower soil nutrient storage and availability before and after a seasonal fire.

This study identified an indirect mechanism whereby *M. quinquenervia* out-competes native plants and maintains a dominate position in low-resource ecosystems. When freed from the top-down regulation of herbivory, *M. quinquenervia* creates a positive feedback loop to growth and reproduction (Figure 2-7). Initially, high above- and below-ground biomass production allows *M. quinquenervia* to out-compete native plants for nutrient and light resources. Higher rates of nutrient uptake produce greater amounts of high quality standing biomass, which eventually falls to the soil at a much higher volume. This high quality litter maintains a larger population of soil microbial biomass that processes litter and soil nutrients at a faster rate. The resultant mineralized nutrients are quickly taken up by the extensive *M. quinquenervia* root biomass, further increasing the production of vegetative and reproductive biomass.

The no herbivory advantages formerly experienced by *M. quinquenervia* have now been removed with the introduction and establishment of two specialized herbivores. As a result, all ages of *M. quinquenervia* are now under continuous attack by insect herbivores, from the most recently recruited seedlings to the tallest and fully mature trees. This relentless herbivory slows the rate of above-ground biomass production and reduces the size of the root zone (Figure 2-7). In addition, herbivores remove a significant amount of standing biomass, thereby preventing it from falling to the forest floor. The remaining litterfall has higher concentrations of resistant

materials such as lignin which, in turn, increases its turnover time. Concomitantly smaller pools of soil microbial biomass are supported, which further reduces the rate of nutrient turnover. This is clear evidence of how herbivory not only controls populations of *M. quinquenervia* directly by reducing plant growth and reproduction, but also indirectly by interrupting its positive feedback growth cycle which would otherwise maintain its dominance in the ecosystem.

We predict that *M. quinquenervia* populations exposed to herbivory will be less invasive after native disturbances such as fire. A post-fire census of the experimental plots revealed that 73% of the trees were killed in the herbivory plots compared to only 41% of the trees in the non-herbivory plots (Tipping, unpublished data). Surviving trees in the herbivory plots may have been weakened by herbivory perhaps resulting in less root biomass which should reduce their ability to efficiently scavenge the pulse of available nutrients produced immediately after the fire. Native plants should benefit from the reduced competition for light, space, and nutrients. In contrast, without herbivory, populations of *M. quinquenervia* will likely benefit disproportionately from the increases in storage and availability of nutrients, compared to native plants. Although some plant mortality would be expected from fires, over the longer term populations may actually benefit from reduced intra-specific competition. Thus *M. quinquenervia* would continue to invade and dominate high and low resource plant communities.

Objective 2. Assessing the Impact of a Seasonal Fire on Native, Invaded, and Managed Plots.

The work presented in Chapter 3 tested two main hypotheses were tested: 1) *M. quinquenervia* invasion and treatment with an herbicide will reduce the quantity and availability of nutrients before and after a seasonal fire compared to a non-invaded site and 2) *M. quinquenervia* invasion and treatment with biological control agents will not alter the quantity and availability of nutrients before and after a seasonal fire compared to a non-invaded site.

Determining the best management practices for exotic species requires consideration of a broad array of factors and their potential interactions, including future interactions with natural events like fires. Most efforts to date have emphasized above ground factors like plant and animal diversity and richness, with little to no consideration of below ground factors like nutrient storage, nutrient cycling, and microbial community diversity. This study clearly shows how these foundational ecosystem components were affected by the management of exotics in the backdrop of a natural fire event. The data collected on the storages of carbon, nitrogen, and phosphorus were compiled to give a broader ecosystem picture (Figures 3-4, 3-5, and 3-6). Before the fire, both the herbicide and biological treatment areas stored less carbon and nitrogen compared to the native site. The observed differences were mostly due to the smaller litter nutrient storages. In contrast, post-fire the biological site stored the most carbon and no longer had higher levels of nitrogen compared to the non-invaded site. Total storages of phosphorus were not different before the fire while every site experienced an increase of phosphorus after the fire.

Biological control of *M. quinquenervia* using insect herbivores has proven to be effective at controlling plant growth and reproduction (Tipping et al. 2009). The results of this study suggest that this method had less of an impact on nutrient storage and cycling than herbicides. Additional questions remain including how both methods affect re-vegetation over the longer term. Although herbicides remain a valuable tool in the management of invasive species, more attention needs to be paid to the resulting consequences for ecosystem structure and function. Practices such as active revegetation with native plants may mitigate the deleterious impacts of the treatment and help to prevent future invasion. If evaluations of the below-ground side effects of exotic plant management remain rare, then advancing our understanding of basic ecosystem

structure and restoration will suffer and any alterations to foundational communities like microbes may permanently and negatively alter ecosystem function.

Objective 3. An Analysis of Native and Non-native Litter Quality.

The work presented in Chapter 4 tested two main hypotheses were tested: 1) *M. quinquenervia* will have the slowest rate of decomposition and 2) *M. quinquenervia* litter will release least amount of carbon, nitrogen, and phosphorus compared to *T. distichum* and *P. elliotii* litter.

The invasion of *M. quinquenervia* has been shown to alter ecosystem structure and function (Myers 1983, 1984, Bodel et al. 1994, Martin et al. 2009). However, this work has shown that *M. quinquenervia* may not significantly alter the basic ecosystem processes of organic matter decomposition and nutrient turnover in invaded *P. elliotii*-*T. distichum* ecotone forests. This indicates the need for ecosystem-specific studies to evaluate the impact of plant invasions. Although *M. quinquenervia* has colonized and thrived in most natural areas of South Florida, the consequences for ecosystem function may not be the same for each community (Bodel et al. 1994). Currently there is an integrated plant management program to control *M. quinquenervia* in South Florida ecosystems. Mechanical, chemical, and biological control programs have contained the spread and eliminated the invasive potential of existing *M. quinquenervia* populations (Ferriter et al. 2005, Tipping et al. 2008, Tipping et al. 2009). However, live non-invasive *M. quinquenervia* trees remain part of vegetative landscape and are targets for future management. Treatment of remnant *M. quinquenervia* populations with chemical or mechanical methods may cause significant collateral damage to native plant communities and may interrupt ecosystem function. Further work is needed to determine if communities would actually benefit from the removal of this exotic, but now less invasive plant.

Objective 4. Recovery of Plant Community Structure after a Seasonal Fire

The work presented in Chapter 5 will test two main hypotheses: after a seasonal fire 1) plant community structure will not be different in an invaded and biologically controlled site but will be different in an invaded and chemically controlled site compared to the non-invaded site and 2) the re-invasion of *M. quinquenervia* will be most severe in the chemically controlled site compared to the biologically controlled and non-invaded sites.

It is clear that plant invasions can result in devastating changes in natural systems. Several control methods exist that can help stop the spread of invasive species and minimize the impact of established populations. While the goal of management programs is to reduce invasive populations and restore ecosystem integrity, this work has shown that passive restoration may not be enough to restore plant community structure. Plant community diversity was highest in the non-invaded site compared to both the biological and herbicides sites as measured by two diversity indices. In addition, the chemically treated site had the fewest number of mature native trees and the highest percentage of live *M. quinquenervia* seedlings. Further study is needed to evaluate both the long-term resilience and structure of managed ecosystems.

Overall Conclusions

Invasive species also pose significant direct and indirect challenges to ecosystem-wide restoration projects like CERP. Despite the fact that CERP will cost at least 30 billion dollars, require 30 years to complete, involve many agencies from all levels and jurisdictions, and affect 18,000 square miles over sixteen Florida counties, the management of exotics has been something of an afterthought. The United States Army Corps of Engineers, the managerial agency for CERP, stated that “once hydrology is restored to the Everglades, invasive exotic species, such as *Melaleuca*...will continue to degrade the system by displacing native species” (Anonymous 2004). While the ultimate goal of management programs is to restore ecosystem

integrity, this work has shown that passive restoration may not be enough to restore plant community structure and function. The results of this study were compiled into Figures 6-1, 6-2, 6-3, and 6-4 to illustrate the effects of the invasion and management of *M. quinquenervia* on basic ecosystem structure and function in a sub-tropical South Florida wetland site. More detailed studies of this kind are needed to evaluate and value the role of native plant communities in overall ecosystem health, thereby guiding management decisions designed to protect and maintain them.

Figures

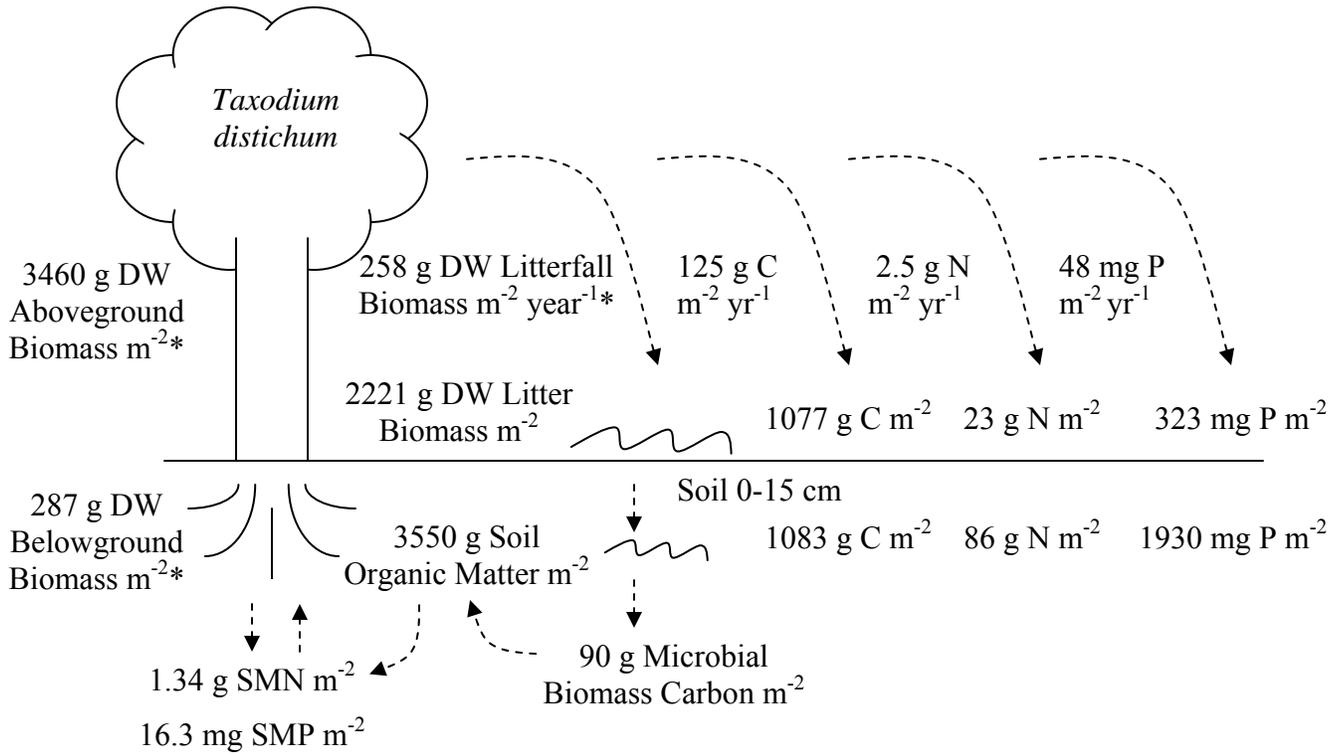


Figure 6-1. Conceptual model of a forest ecosystem dominated by mature *Taxodium distichum* trees (*data from Martin et al. 2009).

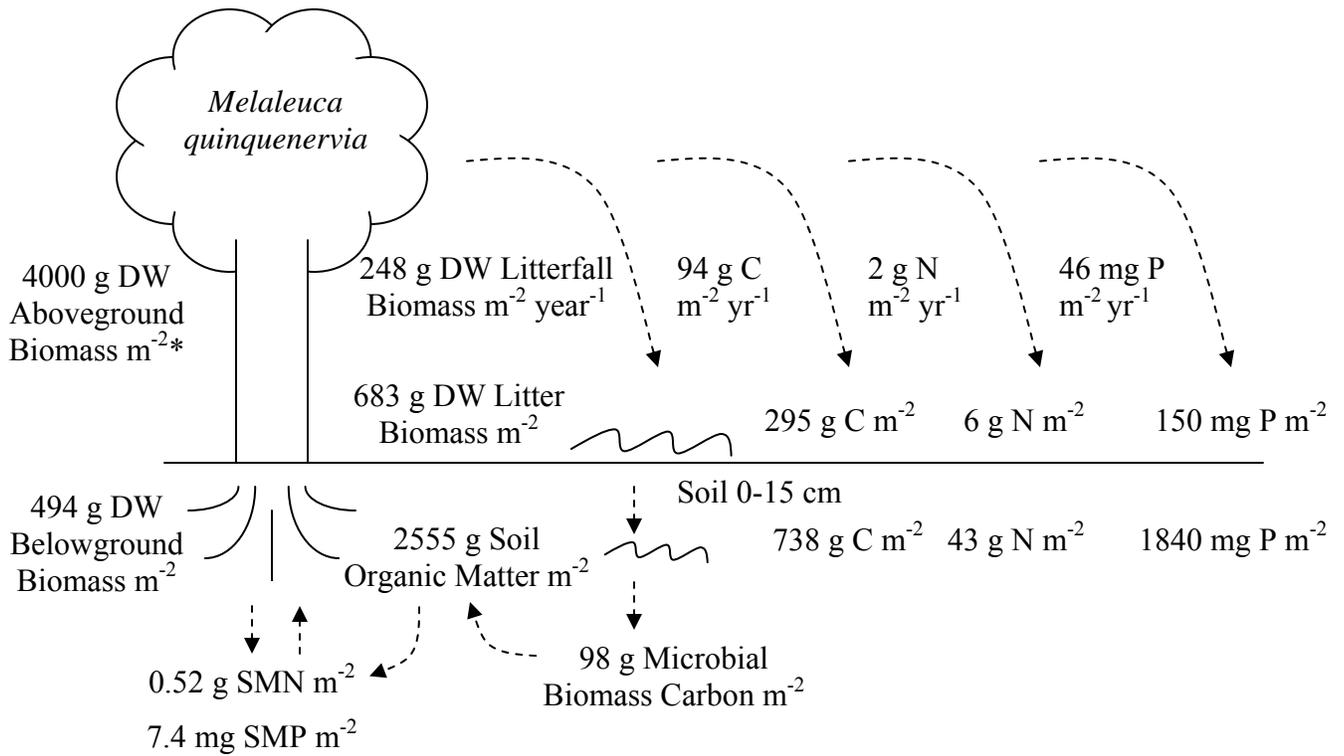


Figure 6-2. Conceptual model of a forest ecosystem dominated by early stage *Melaleuca quinquenervia* trees (*data from Tipping, unpublished data).

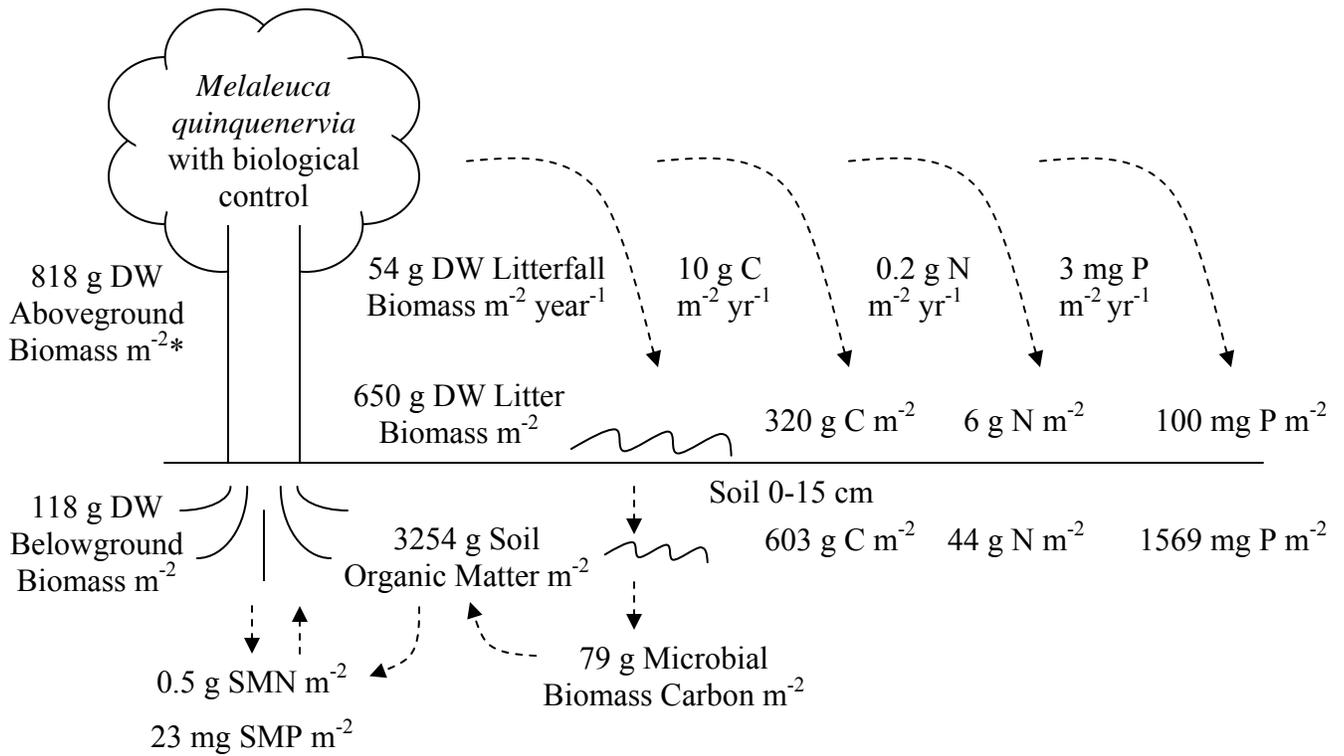


Figure 6-3. Conceptual model of a forest ecosystem dominated by early stage *Melaleuca quinquenervia* trees controlled with biological agents (*data from Tipping, unpublished data).

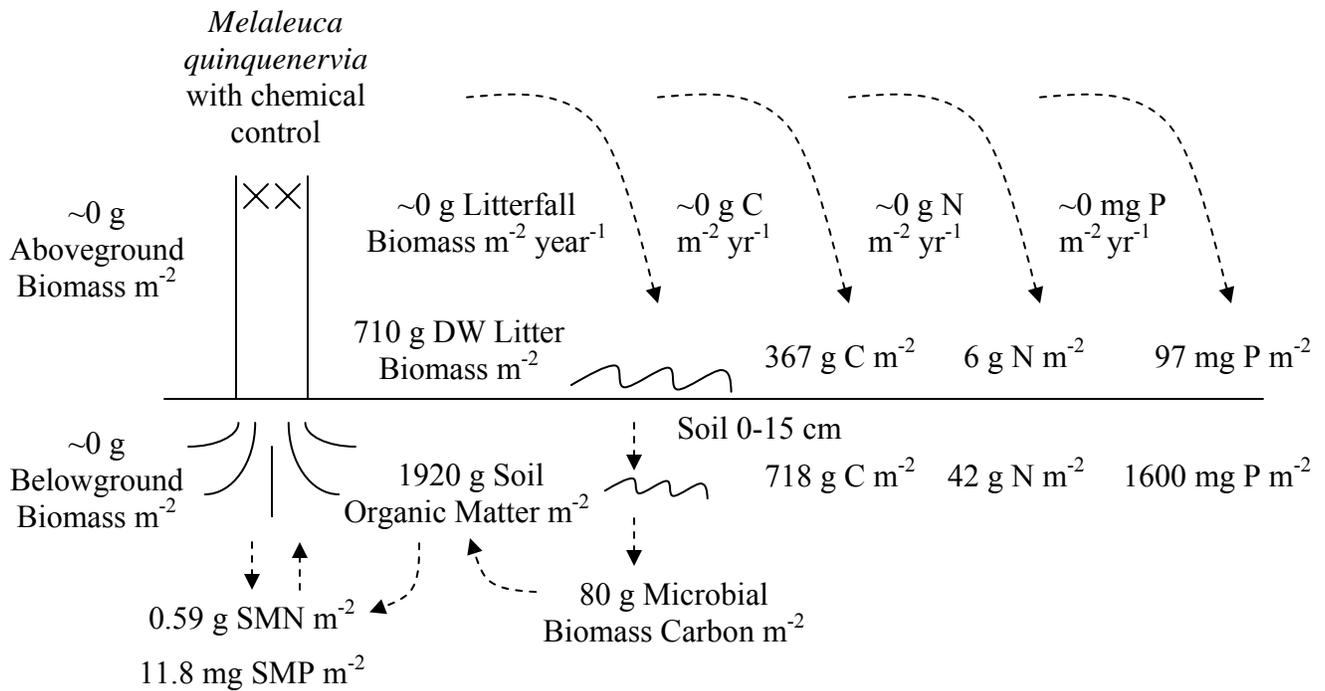


Figure 6-4. Conceptual model of a forest ecosystem dominated by early stage *Melaleuca quinquenervia* trees controlled with herbicides.

APPENDIX A
FULL MODEL STATISTICAL RESULTS

Chapter 2 Model Results

Table A-1. Full model results for main effects and interactions for *Melaleuca quinquenervia* (MQ) litterfall biomass and carbon, nitrogen, and phosphorus transfer in Chapter 2. Effects: site (herbivory and non-herbivory) and transect (N, E, S, W).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
MQ Litterfall Biomass					
	Site	1	56110	170	<0.0001
	Transect	3	480	0.49	0.70
	Site*Transect	3	304	0.31	0.82
MQ Litterfall Carbon Transfer					
	Site	1	11776	219	<0.0001
	Transect	3	159	0.99	0.42
	Site*Transect	3	88.4	0.55	0.66
MQ Litterfall Nitrogen Transfer					
	Site	1	4.21	177	<0.0001
	Transect	3	0.04	0.59	0.63
	Site*Transect	3	0.01	0.19	0.90
MQ Litterfall Phosphorus Transfer					
	Site	1	2757	93.2	<0.0001
	Transect	3	34.6	0.39	0.76
	Site*Transect	3	33.2	0.37	0.77

Table A-2. Full model results for main effects and interactions for litter % moisture, litter biomass, and % litter loss in Chapter 2. Effects: treatment (pre and post fire), site (herbivory and non-herbivory), and transect (N, E, S, W).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
% Litter Moisture					
	Treatment	1	3.79	1000	<0.0001
	Transect	3	0.04	3.10	0.04
	Site	1	0.0005	0.13	0.72
	Transect*Site	3	0.006	0.56	0.64
	Trt*Transect	3	0.004	0.35	0.79
	Trt*Site	1	0.005	1.40	0.24
	Trt*Trans*Site	3	0.002	0.15	0.92
Litter Biomass					
	Treatment	1	1767	21.2	<0.0001
	Transect	3	547	2.19	0.11
	Site	1	1.62	0.02	0.89
	Transect*Site	3	115	0.46	0.71
	Trt*Transect	3	130	0.52	0.67
	Trt*Site	1	12.0	0.14	0.71
	Trt*Trans*Site	3	65.1	0.26	0.85
% Litter Loss					
	Site	1	0.05	0.62	0.45
	Transect	3	0.32	1.34	0.31
	Site*Transect	3	0.09	0.36	0.78

Table A-3. Full model results for main effects and interactions for litter carbon, nitrogen, and phosphorus concentration in Chapter 2. Effects: treatment (pre and post fire), site (herbivory and non-herbivory), and transect (N, E, S, W).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
Litter Carbon Concentration					
	Treatment	1	314044	27.9	<0.0001
	Transect	3	38216	1.13	0.35
	Site	1	303	0.03	0.87
	Transect*Site	3	19916	0.59	0.63
	Trt*Transect	3	60583	1.79	0.17
	Trt*Site	1	20076	1.78	0.19
	Trt*Trans*Site	3	42893	1.27	0.30
Litter Nitrogen Concentration					
	Treatment	1	52.2	3.66	0.06
	Transect	3	72.4	1.69	0.19
	Site	1	1.95	0.14	0.71
	Transect*Site	3	33.4	0.78	0.51
	Trt*Transect	3	46.2	1.08	0.37
	Trt*Site	1	11.9	0.84	0.37
	Trt*Trans*Site	3	39.4	0.92	0.44
Litter Phosphorus Concentration					
	Treatment	1	752936	77.2	<0.0001
	Transect	3	42237	1.44	0.25
	Site	1	167401	17.2	0.0002
	Transect*Site	3	102707	3.5	0.03
	Trt*Transect	3	3376	0.12	0.95
	Trt*Site	1	46122	4.73	0.04
	Trt*Trans*Site	3	111402	3.81	0.02

Table A-4. Full model results for main effects and interactions for litter carbon, nitrogen, and phosphorus storage in Chapter 2. Effects: treatment (pre and post fire), site (herbivory and non-herbivory), and transect (N, E, S, W).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
Litter Carbon Storage					
	Treatment	1	431115	13.1	0.001
	Transect	3	152683	1.55	0.23
	Site	1	637	0.02	0.89
	Transect*Site	3	27282	0.28	0.84
	Trt*Transect	3	87838	0.89	0.46
	Trt*Site	1	5219	0.16	0.69
	Trt*Trans*Site	3	26524	0.27	0.85
Litter Nitrogen Storage					
	Treatment	1	75.0	5.48	0.03
	Transect	3	94.9	2.31	0.10
	Site	1	0.08	0.006	0.94
	Transect*Site	3	16.7	0.41	0.75
	Trt*Transect	3	43.7	1.06	0.38
	Trt*Site	1	1.39	0.10	0.75
	Trt*Trans*Site	3	22.9	0.56	0.65
Litter Phosphorus Storage					
	Treatment	1	477	0.05	0.83
	Transect	3	64501	2.06	0.13
	Site	1	15121	1.45	0.24
	Transect*Site	3	19291	0.62	0.61
	Trt*Transect	3	10798	0.35	0.79
	Trt*Site	1	6.18	0.0006	0.98
	Trt*Trans*Site	3	39145	1.25	0.31

Table A-5. Full model results for main effects and interactions for soil % moisture, bulk density, and organic matter in Chapter 2. Effects: treatment (pre and post fire), site (herbivory and non-herbivory), transect (N, E, S, W), and depth (0-5 and 5-15cm).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
% Soil Moisture					
	Treatment	1	0.05	369	<0.0001
	Transect	3	0.0004	0.99	0.40
	Site	1	0.0004	2.99	0.09
	Depth	1	0.002	13.9	0.0004
	Trt*Transect	3	0.00007	0.16	0.92
	Trt*Site	1	0.0002	1.27	0.26
	Trt*Depth	1	0.01	73.2	<0.0001
	Transect*Site	3	0.0002	0.45	0.72
	Transect*Depth	3	0.0003	0.72	0.54
	Site*Depth	1	0.0005	3.58	0.06
	Trt*Tran*Site	3	0.0003	0.66	0.58
	Trt*Tran*Depth	3	0.00006	0.14	0.94
	Trt*Site*Depth	1	0.000001	0.01	0.92
Bulk Density					
	Treatment	1	0.004	0.23	0.64
	Transect	3	0.22	3.91	0.01
	Site	1	0.22	11.9	0.0009
	Depth	1	3.05	163	< 0.0001
	Trt*Transect	3	0.05	0.87	0.46
	Trt*Site	1	0.02	1.08	0.30
	Trt*Depth	1	0.17	9.21	0.003
	Transect*Site	3	0.16	2.90	0.04
	Transect*Depth	3	0.05	0.80	0.50
	Site*Depth	1	0.02	1.31	0.26
	Trt*Tran*Site	3	0.07	1.17	0.33
	Trt*Tran*Depth	3	0.08	1.44	0.24
	Trt*Site*Depth	1	0.004	0.22	0.64
Organic Matter					
	Treatment	1	0.00004	0.13	0.72
	Transect	3	0.0007	0.72	0.54
	Site	1	0.002	4.75	0.03
	Depth	1	0.002	5.29	0.02
	Trt*Transect	3	0.002	2.54	0.06
	Trt*Site	1	0.00007	0.23	0.64
	Trt*Depth	1	0.002	7.01	0.01
	Transect*Site	3	0.002	1.90	0.14
	Transect*Depth	3	0.003	3.24	0.03
	Site*Depth	1	0.000006	0.02	0.89
	Trt*Tran*Site	3	0.002	2.51	0.07
	Trt*Tran*Depth	3	0.001	1.03	0.38
	Trt*Site*Depth	1	0.0006	1.82	0.18

Table A-6. Full model results for main effects and interactions for soil carbon, nitrogen, and phosphorus concentration in Chapter 2. Effects: treatment (pre and post fire), site (herbivory and non-herbivory), transect (N, E, S, W), and depth (0-5 and 5-15cm).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
Soil Carbon Concentration					
	Treatment	1	86.4	7.45	0.008
	Transect	3	61.1	1.76	0.16
	Site	1	33.6	2.89	0.09
	Depth	1	879	75.7	< 0.0001
	Trt*Transect	3	18.0	0.52	0.67
	Trt*Site	1	2.50	0.22	0.64
	Trt*Depth	1	3.75	0.32	0.57
	Transect*Site	3	23.3	0.67	0.57
	Transect*Depth	3	41.3	1.19	0.32
	Site*Depth	1	11.2	0.97	0.33
	Trt*Tran*Site	3	21.3	0.61	0.61
	Trt*Tran*Depth	3	11.2	0.32	0.81
	Trt*Site*Depth	1	7.53	0.65	0.42
Soil Nitrogen Concentration					
	Treatment	1	0.24	9.76	0.003
	Transect	3	0.16	2.09	0.11
	Site	1	0.16	6.20	0.02
	Depth	1	2.50	99.6	< 0.0001
	Trt*Transect	3	0.02	0.32	0.81
	Trt*Site	1	0.02	0.63	0.43
	Trt*Depth	1	0.13	5.15	0.03
	Transect*Site	3	0.07	0.95	0.42
	Transect*Depth	3	0.07	0.88	0.45
	Site*Depth	1	0.07	2.64	0.11
	Trt*Tran*Site	3	0.04	0.50	0.68
	Trt*Tran*Depth	3	0.03	0.34	0.80
	Trt*Site*Depth	1	0.02	0.64	0.42
Soil Phosphorus Concentration					
	Treatment	1	0.46	33.9	<0.0001
	Transect	3	0.06	1.58	0.20
	Site	1	0.37	27.2	<0.0001
	Depth	1	1.35	99.7	< 0.0001
	Trt*Transect	3	0.006	0.14	0.93
	Trt*Site	1	0.03	2.29	0.13
	Trt*Depth	1	0.01	1.06	0.31
	Transect*Site	3	0.05	1.15	0.33
	Transect*Depth	3	0.10	2.35	0.08
	Site*Depth	1	0.22	16.6	0.0001
	Trt*Tran*Site	3	0.11	2.76	0.05
	Trt*Tran*Depth	3	0.08	2.03	0.12
	Trt*Site*Depth	1	0.12	9.14	0.004

Table A-7. Full model results for main effects and interactions for soil carbon, nitrogen, and phosphorus storage in Chapter 2. Effects: treatment (pre and post fire), site (herbivory and non-herbivory), transect (N, E, S, W), and depth (0-5 and 5-15cm).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
Soil Carbon Storage					
	Treatment	1	990057	19.3	<0.0001
	Transect	3	273590	1.78	0.16
	Site	1	332266	6.47	0.01
	Depth	1	756964	14.7	0.0003
	Trt*Transect	3	127783	0.83	0.48
	Trt*Site	1	105413	2.05	0.16
	Trt*Depth	1	4566	0.09	0.77
	Transect*Site	3	240649	1.56	0.21
	Transect*Depth	3	74137	0.48	0.70
	Site*Depth	1	1817	0.04	0.85
	Trt*Tran*Site	3	74813	0.49	0.69
	Trt*Tran*Depth	3	37468	0.24	0.87
	Trt*Site*Depth	1	96998	1.89	0.17
Soil Nitrogen Storage					
	Treatment	1	1852	12.1	0.0008
	Transect	3	478	1.04	0.38
	Site	1	186	1.22	0.27
	Depth	1	1102	7.21	0.009
	Trt*Transect	3	113	0.25	0.86
	Trt*Site	1	303	1.99	0.16
	Trt*Depth	1	158	1.04	0.31
	Transect*Site	3	463	1.01	0.39
	Transect*Depth	3	82.2	0.18	0.91
	Site*Depth	1	110	0.72	0.40
	Trt*Tran*Site	3	54.7	0.12	0.95
	Trt*Tran*Depth	3	41.5	0.09	0.97
	Trt*Site*Depth	1	138	0.90	0.35
Soil Phosphorus Storage					
	Treatment	1	5600965	37.2	<0.0001
	Transect	3	173557	0.38	0.76
	Site	1	563197	3.74	0.06
	Depth	1	1234995	8.20	0.006
	Trt*Transect	3	40432	0.09	0.97
	Trt*Site	1	23821	0.16	0.69
	Trt*Depth	1	1690	0.01	0.92
	Transect*Site	3	711014	1.57	0.20
	Transect*Depth	3	773409	1.71	0.17
	Site*Depth	1	564850	3.75	0.06
	Trt*Tran*Site	3	918276	2.03	0.12
	Trt*Tran*Depth	3	975159	2.16	0.10
	Trt*Site*Depth	1	648115	4.30	0.04

Table A-8. Full model results for main effects and interactions for soil specifically mineralizable nitrogen and specifically mineralizable phosphorus in Chapter 2. Effects: treatment (pre and post fire), site (herbivory and non-herbivory), transect (N, E, S, W), and depth (0-5 and 5-15cm).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
Specifically Mineralizable Nitrogen					
	Treatment	1	21498	85.5	<0.0001
	Transect	3	5756	7.63	0.0002
	Site	1	919	3.65	0.06
	Depth	1	116	0.46	0.50
	Trt*Transect	3	3888	5.16	0.003
	Trt*Site	1	1002	3.99	0.05
	Trt*Depth	1	1909	7.59	0.007
	Transect*Site	3	1411	1.87	0.14
	Transect*Depth	3	1855	2.46	0.07
	Site*Depth	1	1002	3.99	0.05
	Trt*Tran*Site	3	708	0.94	0.43
	Trt*Tran*Depth	3	1102	1.46	0.23
	Trt*Site*Depth	1	231	0.92	0.34
Specifically Mineralizable Phosphorus					
	Treatment	1	2.40	0.03	0.86
	Site	1	445	6.22	0.02
	Depth	1	16.5	0.23	0.64
	Trt*Site	1	65.2	0.91	0.35
	Trt*Depth	1	0.10	0.001	0.97
	Site*Depth	1	5.61	0.08	0.78
	Trt*Site*Depth	1	10.1	0.14	0.71

Table A-9. Full model results for main effects and interactions for soil microbial biomass carbon in Chapter 2. Effects: treatment (pre and post fire), site (herbivory and non-herbivory), transect (N, E, S, W), and depth (0-5 and 5-15cm).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
Microbial Biomass Carbon					
	Treatment	1	3530	99.5	<0.0001
	Transect	3	272	2.55	0.06
	Site	1	164	4.63	0.03
	Depth	1	968	27.3	<0.0001
	Trt*Transect	3	327	3.07	0.03
	Trt*Site	1	124	3.49	0.07
	Trt*Depth	1	695	19.6	<0.0001
	Transect*Site	3	62.4	0.58	0.63
	Transect*Depth	3	15.9	0.15	0.93
	Site*Depth	1	0.03	0.0008	0.98
	Trt*Tran*Site	3	103	0.97	0.41
	Trt*Tran*Depth	3	51.8	0.49	0.69
	Trt*Site*Depth	1	7.18	0.20	0.65

Table A-10. Full model results for main effects and interaction for root biomass in Chapter 2. Effects: site (herbivory and non-herbivory) and depth (0-5 and 5-15cm).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
Root Biomass					
	Site	1	177893	13.6	0.002
	Depth	1	1768	0.14	0.72
	Site*Depth	1	112	0.009	0.93

Chapter 3 Model Results

Table A-11. Full model results for main effects and interactions for litter % moisture, litter biomass, and % litter loss in Chapter 3. Effects: treatment (pre and post fire), site (non-invaded, herbicide, and biological), transect nested in site (1, 2, 3, 4, and 5), and plot nested in site (1, 2, 3, 4, and 5).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
% Litter Moisture					
	Treatment	1	3.45	679	<0.0001
	Site	2	0.44	43.1	<0.0001
	Transect [Site]	12	0.13	2.16	0.02
	Plot [Site]	12	0.04	0.65	0.79
	Trt*Transect [Site]	12	0.11	1.86	0.05
	Trt*Plot [Site]	12	0.06	0.97	0.48
	Trt*Site	2	0.13	13.0	<0.001
Litter Biomass					
	Treatment	1	19.0	333	<0.0001
	Site	2	5.18	45.5	<0.0001
	Transect [Site]	12	2.15	3.15	0.0009
	Plot [Site]	12	2.56	3.75	0.0001
	Trt*Transect [Site]	12	0.97	1.42	0.17
	Trt*Plot [Site]	12	1.35	1.98	0.04
	Trt*Site	2	0.40	3.54	0.03
% Litter Loss					
	Site	2	1232	4.88	0.01
	Transect [Site]	12	676	0.45	0.93
	Plot [Site]	12	1162	0.77	0.68

Table A-12. Full model results for main effects and interactions for litter carbon, nitrogen, and phosphorus concentration in Chapter 3. Effects: treatment (pre and post fire), site (non-invaded, herbicide, and biological), transect nested in site (1, 2, 3, 4, and 5), and plot nested in site (1, 2, 3, 4, and 5).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
Litter Carbon Concentration					
	Treatment	1	979255	131	<0.0001
	Site	2	27985	1.87	0.16
	Transect [Site]	12	21510	2.40	0.01
	Plot [Site]	12	49017	0.55	0.88
	Trt*Transect [Site]	12	201359	2.24	0.02
	Trt*Plot [Site]	12	66924	0.75	0.70
	Trt*Site	2	89411	5.98	0.004
Litter Nitrogen Concentration					
	Treatment	1	80.3	10.2	0.002
	Site	2	221	14.1	<0.0001
	Transect [Site]	12	298	3.16	0.001
	Plot [Site]	12	99.2	1.05	0.41
	Trt*Transect [Site]	12	266	2.82	0.003
	Trt*Plot [Site]	12	51.6	0.55	0.88
	Trt*Site	2	15.7	1.00	0.37
Litter Phosphorus Concentration					
	Treatment	1	606802	111	<0.0001
	Site	2	215633	19.7	<0.0001
	Transect [Site]	12	63462	0.97	0.49
	Plot [Site]	12	143380	2.18	0.02
	Trt*Transect [Site]	12	75967	1.16	0.33
	Trt*Plot [Site]	12	135775	2.07	0.03
	Trt*Site	2	24430	2.23	0.11

Table A-13. Full model results for main effects and interactions for litter carbon, nitrogen, and phosphorus storage in Chapter 3. Effects: treatment (pre and post fire), site (non-invaded, herbicide, and biological), transect nested in site (1, 2, 3, 4, and 5), and plot nested in site (1, 2, 3, 4, and 5).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
Litter Carbon Storage					
	Treatment	1	6496	455	<0.0001
	Site	2	2252	78.9	<0.0001
	Transect [Site]	12	633	3.70	0.0002
	Plot [Site]	12	456	2.72	0.005
	Trt*Transect [Site]	12	323	1.89	0.05
	Trt*Plot [Site]	12	323	1.89	0.05
	Trt*Site	2	851	29.8	<0.0001
Litter Nitrogen Storage					
	Treatment	1	108	289	<0.0001
	Site	2	68.2	90.8	<0.0001
	Transect [Site]	12	18.8	4.16	<0.0001
	Plot [Site]	12	11.6	2.57	0.007
	Trt*Transect [Site]	12	6.31	1.40	0.19
	Trt*Plot [Site]	12	7.47	1.66	0.10
	Trt*Site	2	12.2	16.2	<0.0001
Litter Phosphorus Storage					
	Treatment	1	1187	148	<0.0001
	Site	2	1073	66.8	<0.0001
	Transect [Site]	12	410	4.25	<0.0001
	Plot [Site]	12	234	2.43	0.01
	Trt*Transect [Site]	12	115	1.2	0.30
	Trt*Plot [Site]	12	114	1.19	0.31
	Trt*Site	2	63.1	3.93	0.02

Table A-14. Full model results for main effects and interactions for soil % moisture, bulk density, and organic matter in Chapter 3. Effects: treatment (pre and post fire), site (non-invaded, herbicide, and biological), transect nested in site (1, 2, 3, 4, and 5), plot nested in site (1, 2, 3, 4, and 5), and depth (0-5 and 5-15 cm).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
% Soil Moisture					
	Treatment	1	143	520	<0.0001
	Transect [Site]	12	10.2	3.11	0.0004
	Plot [Site]	12	8.17	2.48	0.005
	Site	2	9.96	18.2	<0.0001
	Depth	1	4.07	14.8	0.0002
	Trt*Site	2	0.27	0.49	0.62
	Trt*Depth	1	34.6	126	<0.0001
	Site*Depth	2	2.65	4.83	0.009
	Trt*Transect [Site]	12	3.28	1.00	0.45
	Trt*Plot [Site]	12	3.41	1.04	0.42
	Trt*Site*Depth	2	0.31	0.56	0.57
Bulk Density					
	Treatment	1	0.47	15.5	0.0001
	Transect [Site]	12	0.62	1.70	0.07
	Plot [Site]	12	2.08	5.64	<0.0001
	Site	2	2.05	33.4	<0.0001
	Depth	1	10.5	343	<0.0001
	Trt*Site	2	0.02	0.27	0.76
	Trt*Depth	1	0.47	15.3	0.0001
	Site*Depth	2	1.01	16.4	<0.0001
	Trt*Transect [Site]	12	0.51	1.38	0.18
	Trt*Plot [Site]	12	0.46	1.24	0.25
	Trt*Site*Depth	2	0.003	0.05	0.95
Organic Matter					
	Treatment	1	0.04	2.40	0.12
	Transect [Site]	12	0.41	2.14	0.02
	Plot [Site]	12	0.58	3.01	0.0007
	Site	2	1.20	37.8	<0.0001
	Depth	1	3.12	195	<0.0001
	Trt*Site	2	0.09	2.72	0.07
	Trt*Depth	1	0.08	4.84	0.03
	Site*Depth	2	0.50	15.7	<0.0001
	Trt*Transect [Site]	12	0.21	1.09	0.37
	Trt*Plot [Site]	12	0.09	0.49	0.92
	Trt*Site*Depth	2	0.04	1.25	0.29

Table A-15. Full model results for main effects and interactions for soil carbon, nitrogen, and phosphorus concentration in Chapter 3. Effects: treatment (pre and post fire), site (non-invaded, herbicide, and biological), transect nested in site (1, 2, 3, 4, and 5), plot nested in site (1, 2, 3, 4, and 5), and depth (0-5 and 5-15 cm).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
Soil Carbon Concentration					
	Treatment	1	0.14	2.70	0.10
	Transect [Site]	12	1.18	1.94	0.03
	Plot [Site]	12	2.50	4.10	<0.0001
	Site	2	2.07	20.4	<0.0001
	Depth	1	13.6	266	<0.0001
	Trt*Site	2	0.18	1.79	0.17
	Trt*Depth	1	0.34	6.62	0.01
	Site*Depth	2	0.73	7.14	0.001
	Trt*Transect [Site]	12	0.38	0.63	0.81
	Trt*Plot [Site]	12	0.54	0.89	0.56
	Trt*Site*Depth	2	0.08	0.82	0.44
Soil Nitrogen Concentration					
	Treatment	1	0.007	0.11	0.74
	Transect [Site]	12	1.74	2.45	0.005
	Plot [Site]	12	2.88	4.06	<0.0001
	Site	2	3.15	26.6	<0.0001
	Depth	1	7.41	125	<0.0001
	Trt*Site	2	0.11	0.91	0.40
	Trt*Depth	1	0.06	1.03	0.31
	Site*Depth	2	0.79	6.71	0.002
	Trt*Transect [Site]	12	0.53	0.75	0.70
	Trt*Plot [Site]	12	0.64	0.90	0.55
	Trt*Site*Depth	2	0.03	0.22	0.81
Soil Phosphorus Concentration					
	Treatment	1	5.45	6.88	0.009
	Transect [Site]	12	29.2	3.07	0.0005
	Plot [Site]	12	46.1	4.85	<0.0001
	Site	2	37.5	23.7	<0.0001
	Depth	1	79.5	100	<0.0001
	Trt*Site	2	0.10	0.06	0.94
	Trt*Depth	1	0.46	0.59	0.45
	Site*Depth	2	8.64	5.46	0.005
	Trt*Transect [Site]	12	4.29	0.45	0.94
	Trt*Plot [Site]	12	9.02	0.95	0.50
	Trt*Site*Depth	2	1.03	0.65	0.52

Table A-16. Full model results for main effects and interactions for soil carbon, nitrogen, and phosphorus storage in Chapter 3. Effects: treatment (pre and post fire), site (non-invaded, herbicide, and biological), transect nested in site (1, 2, 3, 4, and 5), plot nested in site (1, 2, 3, 4, and 5), and depth (0-5 and 5-15 cm).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
Soil Carbon Storage					
	Treatment	1	3816	0.06	0.80
	Transect [Site]	12	2640419	3.73	<0.0001
	Plot [Site]	12	2993650	4.23	<0.0001
	Site	2	2021155	17.2	<0.0001
	Depth	1	1178518	20.0	<0.0001
	Trt*Site	2	306693	2.60	0.08
	Trt*Depth	1	415874	7.06	0.009
	Site*Depth	2	455101	3.86	0.02
	Trt*Transect [Site]	12	582541	0.82	0.63
	Trt*Plot [Site]	12	600287	0.85	0.60
	Trt*Site*Depth	2	22031	0.19	0.83
Soil Nitrogen Storage					
	Treatment	1	583	1.54	0.22
	Transect [Site]	12	16472	3.64	<0.0001
	Plot [Site]	12	21589	4.76	<0.0001
	Site	2	24320	32.2	<0.0001
	Depth	1	1.76	0.005	0.95
	Trt*Site	2	668	0.88	0.41
	Trt*Depth	1	522	1.38	0.24
	Site*Depth	2	4019	5.32	0.006
	Trt*Transect [Site]	12	2115	0.47	0.93
	Trt*Plot [Site]	12	3137	0.69	0.76
	Trt*Site*Depth	2	827	1.09	0.34
Soil Phosphorus Storage					
	Treatment	1	4852024	25.2	<0.0001
	Transect [Site]	12	9657604	4.19	<0.0001
	Plot [Site]	12	9617087	4.17	<0.0001
	Site	2	5228600	13.6	<0.0001
	Depth	1	15766435	82.0	<0.0001
	Trt*Site	2	503020	1.31	0.27
	Trt*Depth	1	667172	3.47	0.06
	Site*Depth	2	205794	0.54	0.59
	Trt*Transect [Site]	12	916631	0.40	0.96
	Trt*Plot [Site]	12	1603388	0.69	0.76
	Trt*Site*Depth	2	868325	2.26	0.11

Table A-17. Full model results for main effects and interactions for soil specifically mineralizable nitrogen and specifically mineralizable phosphorus in Chapter 3. Effects: treatment (pre and post fire), site (non-invaded, herbicide, and biological), transect nested in site (1, 2, 3, 4, and 5), plot nested in site (1, 2, 3, 4, and 5), and depth (0-5 and 5-15 cm).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
Specifically Mineralizable Nitrogen					
	Treatment	1	1782	8.37	0.004
	Transect [Site]	12	4675	1.83	0.04
	Plot [Site]	12	3426	1.34	0.20
	Site	2	418	0.98	0.38
	Depth	1	4251	20.0	<0.0001
	Trt*Site	2	202	0.47	0.62
	Trt*Depth	1	1187	5.57	0.02
	Site*Depth	2	182	0.43	0.65
	Trt*Transect [Site]	12	5835	2.28	0.009
	Trt*Plot [Site]	12	1004	0.39	0.97
	Trt*Site*Depth	2	638	1.5	0.23
Specifically Mineralizable Phosphorus					
	Treatment	1	33.5	0.62	0.44
	Site	2	347	3.20	0.05
	Depth	1	197	3.64	0.06
	Trt*Site	2	345	3.18	0.05
	Trt*Depth	1	66.7	1.23	0.27
	Site*Depth	2	563	5.19	0.01
	Trt*Site*Depth	2	120	1.11	0.34

Table A-18. Full model results for main effects and interactions for soil microbial biomass carbon in Chapter 3. Effects: treatment (pre and post fire), site (non-invaded, herbicide, and biological), transect nested in site (1, 2, 3, 4, and 5), plot nested in site (1, 2, 3, 4, and 5), and depth (0-5 and 5-15 cm).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
Microbial Biomass Carbon					
	Treatment	1	12.4	111	<0.0001
	Transect [Site]	12	6.77	5.04	<0.0001
	Plot [Site]	12	3.22	2.40	0.006
	Site	2	1.85	8.28	0.0003
	Depth	1	3.74	33.4	<0.0001
	Trt*Site	2	1.55	6.91	0.001
	Trt*Depth	1	0.16	1.43	0.23
	Site*Depth	2	1.36	6.08	0.003
	Trt*Transect [Site]	12	1.53	1.14	0.33
	Trt*Plot [Site]	12	1.89	1.41	0.16
	Trt*Site*Depth	2	0.93	4.13	0.02

Chapter 4 Model Results

Table A-19. Full model results for main effects and interactions for % mass loss, K value, and turnover time in Chapter 4. Effects: species (*Melaleuca quinquenervia*, *Pinus elliottii*, and *Taxodium distichum*), block (1, 2, and 3), and week (6, 12, 26, and 52).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
% Mass Loss					
	Species	2	11775	564	<0.0001
	Block	3	6728	215	<0.0001
	Week	2	389	18.6	<0.0001
	Species*Block	6	616	9.84	<0.0001
	Species*Week	4	197	4.73	0.002
	Block*Week	6	277	4.43	0.008
	Species*Blk*Wk	12	245	1.95	0.04
K Value					
	Species	2	0.75	65.4	<0.0001
	Block	2	0.09	8.31	0.003
	Species*Block	4	0.004	0.19	0.94
Turnover Time					
	Species	2	9.16	115	<0.0001
	Block	2	1.47	18.5	<0.0001
	Species*Block	4	0.28	1.76	0.18

Table A-20. Full model results for main effects and interactions for carbon, nitrogen, and phosphorus concentration in Chapter 4. Effects: species (*Melaleuca quinquenervia*, *Pinus elliottii*, and *Taxodium distichum*), block (1, 2, and 3), and week (6, 12, 26, and 52).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
Carbon Concentration					
	Species	2	9789	54.4	<0.0001
	Block	2	624	3.47	0.04
	Week	3	767	2.84	0.04
	Species*Block	4	338	0.94	0.45
	Species*Week	6	1827	3.38	0.006
	Block*Week	6	379	0.70	0.65
	Species*Blk*Wk	12	1459	1.35	0.21
Nitrogen Concentration					
	Species	2	827	626	<0.0001
	Block	2	26.9	20.4	<0.0001
	Week	3	79.8	40.2	<0.0001
	Species*Block	4	5.56	2.10	0.09
	Species*Week	6	33.0	8.33	<0.0001
	Block*Week	6	17.6	4.43	0.0007
	Species*Blk*Wk	12	11.9	1.51	0.14
Phosphorus Concentration					
	Species	2	2358060	357	<0.0001
	Block	2	161540	24.4	<0.0001
	Week	3	265121	26.7	<0.0001
	Species*Block	4	70364	5.32	0.0008
	Species*Week	6	53100	2.68	0.02
	Block*Week	6	250597	12.6	<0.0001
	Species*Blk*Wk	12	75048	1.89	0.05

Table A-21. Full model results for main effects and interactions for change in carbon, nitrogen, and phosphorus storage in Chapter 4. Effects: species (*Melaleuca quinquenervia*, *Pinus elliottii*, and *Taxodium distichum*), block (1, 2, and 3), and week (6, 12, 26, and 52).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
Change Carbon Storage					
	Species	2	387	20.3	<0.0001
	Block	2	199	10.5	0.0001
	Week	3	13018	456	<0.0001
	Species*Block	4	81.9	2.15	0.08
	Species*Week	6	14420	252	<0.0001
	Block*Week	6	113	1.97	0.08
	Species*Blk*Wk	12	298	2.61	0.06
Change Nitrogen Storage					
	Species	2	416	1.76	0.18
	Block	2	634	2.68	0.08
	Week	3	6735	19.0	<0.0001
	Species*Block	4	188	0.40	0.81
	Species*Week	6	11458	16.2	<0.0001
	Block*Week	6	1087	1.53	0.18
	Species*Blk*Wk	12	1734	1.22	0.28
Change Phosphorus Storage					
	Species	2	14303	5.26	0.007
	Block	2	35141	12.9	<0.0001
	Week	3	73508	18.0	<0.0001
	Species*Block	4	11054	2.03	0.10
	Species*Week	6	49499	6.07	<0.0001
	Block*Week	6	16327	2.00	0.08
	Species*Blk*Wk	12	74049	4.54	<0.0001

Table A-22. Full model results for main effects and interactions for litter chemical composition in Chapter 4. Effects: species (*Melaleuca quinquenervia*, *Pinus elliottii*, and *Taxodium distichum*), block (1, 2, and 3), and week (6, 12, 26, and 52).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
% Soluble Fiber					
	Species	2	5392	1326	<0.0001
	Block	2	51.0	12.5	<0.0001
	Week	3	1688	277	<0.0001
	Species*Week	6	317	26.0	<0.0001
	Block*Week	6	138	11.3	<0.0001
	Block*Species	4	35.5	4.36	0.003
	Species*Blk*Wk	12	107	4.36	<0.0001
% Lignin					
	Species	2	3454	296	<0.0001
	Block	2	44.0	3.77	0.03
	Week	3	3784	216	<0.0001
	Species*Week	6	572	16.3	<0.0001
	Block*Week	6	141	4.03	0.002
	Block*Species	4	56.8	2.43	0.06
	Species*Blk*Wk	12	85.6	1.22	0.29

Chapter 5 Model Results

Table A-23. Full model results for main effects for non-woody plant species richness and diversity indices in Chapter 5. Effects: site (non-invaded, herbicide, and biological), transect nested in site (1, 2, 3, 4, and 5), and plot nested in site (1, 2, 3, 4, and 5).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
Non-woody Species Richness					
	Site	2	99.9	7.63	0.001
	Transect [Site]	12	71.2	0.91	0.55
	Plot [Site]	12	192	2.45	0.01
Non-woody Shannon Index					
	Site	2	4.08	10.3	0.0002
	Transect [Site]	12	1.46	0.61	0.82
	Plot [Site]	12	1.80	0.75	0.69
Non-woody Simpson Index					
	Site	2	0.75	9.25	0.0004
	Transect [Site]	12	0.54	1.10	0.38
	Plot [Site]	12	0.18	0.38	0.97

Table A-24. Full model results for main effects for *Melaleuca quinquenervia* (MQ) live seedling, *Melaleuca quinquenervia* dead seedling, *Pinus elliottii* (PE) live seedling, and *Taxodium distichum* (TD) live seedling densities in Chapter 5. Effects: site (non-invaded, herbicide, and biological), transect nested in site (1, 2, 3, 4, and 5), and plot nested in site (1, 2, 3, 4, and 5).

Variable	Source	DF	Sums of Squares	F ratio	Prob > F
MQ Live Seedlings					
	Site	2	6434	22.0	<0.0001
	Transect [Site]	12	2136	1.22	0.30
	Plot [Site]	12	3695	2.10	0.04
MQ Dead Seedlings					
	Site	2	2924	7.30	0.002
	Transect [Site]	12	5236	2.18	0.03
	Plot [Site]	12	4368	1.82	0.07
PE Seedlings					
	Site	2	0.33	0.89	0.42
	Transect [Site]	12	3.96	1.75	0.09
	Plot [Site]	12	3.56	1.58	0.13
TD Seedlings					
	Site	2	0.66	4.85	0.01
	Transect [Site]	12	0.00	0.00	1.00
	Plot [Site]	12	0.80	0.98	0.48

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BIOGRAPHICAL SKETCH

Melissa Rosemary Martin was born and raised in South Bend, Indiana where she developed a love of nature at an early age. As an undergraduate at the University of Notre Dame, Melissa participated in research on the plant community structure and biogeochemistry of wetlands. After graduation in 2002, Melissa accepted an internship through the Student Conservation Association at the USDA-ARS Invasive Plant Research Laboratory in Fort Lauderdale, FL. Through this internship, she was introduced to research on the management and control of invasive exotic plants. Melissa continued her studies at the University of Florida, investigating ecosystem-level effects of the invasion of exotic plants in order to develop more effective management and restoration techniques. She received her M.S. degree from the department of Soil and Water Science in May of 2006 and her Ph.D. from the same department in May of 2009. She looks forward to working in a group that uses scientific studies to aid in the active management of natural systems.