BIOGEOCHEMICAL INFLUENCE OF CHINESE PRIVET IN RIPARIAN FORESTS IN WEST GEORGIA AND THE INFLUENCES OF OYSTER HARVESTING IN APALACHICOLA BAY, FLORIDA

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DISSERTATION ABSTRACT

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In the Southeastern U.S., urbanization influences nutrient availability, species composition, and water quality among other ecosystem processes. This study examined the influence of invasive species spread, facilitated by urbanization; and the influence of oyster harvest due to changes in water quality/quantity resulting from urbanization in Apalachicola Bay, FL. First, Chinese privet (*Ligustrum sinense* Lour.) was studied to document biogeochemical changes as it becomes more abundant in riparian forests in Georgia. To determine Chinese privet's influence on biogeochemistry, decomposition rates, litterfall nutrient dynamics, nutrient use efficiency (NUE), nitrogen mineralization rates, and microbial biomass were assessed. Study sites were divided into three different classes (severely invaded>80%, moderately invaded 25-79%, and uninvaded 0%) based on percent of Chinese privet in understory. Two decomposition studies were conducted: one with site specific litter on different microsites and one with predetermined litter bag composition on a single microsite. Both studies indicated Chinese privet increased the rate of decomposition. Chinese privet litter quality was higher than that of native species, because it had lower concentration of the recalcitrant materials lignin and cellulose and high nutrient concentrations. Litterfall had greater mass, carbon content, and N content in moderately invaded sites than in uninvaded or severely invaded sites. Land use had a greater influence on N-NUE than Chinese privet did and urban sites had inefficient N-NUE. N-mineralization was greater in moderately and severely invaded sites for summer collections and microbial biomass tended to be higher in moderately and severely invaded sites. Results from this study indicate that Chinese privet alters nutrient cycling processes in riparian forests.

In the second study, water quality/quantity and economic influence of oyster harvest were examined in relation to land use conversion in Franklin and Gulf counties neighboring Apalachicola Bay, FL. There was a negative relationship between % of the Bay closed and quantity of oysters harvested. There was significant negative relationship between discharge of the Apalachicola River at the Blountstown gauging station and quantity of oysters harvested. Water quality, as measured by fecal coliform abundance, was not significantly influenced by the land use changes in Franklin and Gulf counties from 1995-2005. Closures of <25% harvestable area resulted in an unrealized value >$45,000 per month. Land use change in the entire watershed may have greater influence on discharge and water quality entering the Bay but was not included in this study.

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CHAPTER I

INTRODUCTION

Anthropogenic Changes

Human activities influence the health of terrestrial and aquatic ecosystems (Allan 2004, Chang 2004, Wu and Xu 2006). Anthropogenic changes are responsible for both intentional and unintentional alterations to natural systems. The Southeastern U.S. and its coastal areas have been experiencing explosive population growth in the past decade. Specifically in Florida's Gulf and Franklin counties, which neighbor Apalachicola Bay, there has been 25-75% growth in population from 1980 to 2003 (Crossett et al. 2004). There are some changes frequently associated with urbanization. For example, increased impervious surface extent in urban centers has been associated with altered hydrology, such as lowered groundwater tables and more extreme flow events. When impervious surface cover exceeds 10% of watershed area, runoff increases nitrate, phosphate, heavy metal, and fecal coliform (FC) levels, which greatly affect water quality (Schueler 1995, Booth and Jackson 1997, Bledsoe and Watson 2001, Callender and Rice 2000, Gregory and Frick 2000, Schoonover et al. 2005, 2006).

In addition to alterations from increased impervious surface area, influences of urbanization modify functions of urban vegetation. For instance, green spaces in urban areas are often intensively managed with irrigation and fertilizer, which can contaminate runoff. Landscaping practices are responsible for introducing exotic plants because of their unique appearance and hearty nature. However, these species often have invasive tendencies, and therefore landscaping in urban areas can serve as seed sources (Lowenstein and Lowenstein 2005).

Increasingly, studies are designed to investigate the ecology of urban areas. These studies often examine linkages among human decisions, biogeochemistry, vegetative competition for resources, and water cycling as a complex model of the urban ecosystem (Cadenasso et al. 2008, Pickett et al. 2008). In this dissertation, invasive species are examined to determine their impacts on nutrient dynamics and oyster harvests are examined with respect to their economic impacts. Therefore, these two topics are related with regard to overall anthropogenic influences; exotic species are planted and can become invasive, while declining water quality may cause a loss in profitability for the oyster industry resulting from harvesting closures. Both topics were examined based on impacts of land use conversion and other variables.

Invasive Species

As shifts in human populations occur, plants are intentionally and unintentionally introduced to areas where they otherwise would not occur (Pyšek and Richardson 2008). Over 2,000 plant species in the United States alone have been introduced by humans; nevertheless, only a small number of those are invasive (Vitousek et al. 1997, Langeland and Burkes 1998, Ward 2002). Invasive plants are defined by Cronk and Fuller (1995) as:

> *…an alien plant spreading naturally (without direct assistance of people)*

> *in natural or seminatural habitats, to produce a significant change in terms of composition, structure or ecosystem processes.*

Invasive, non-native plants have few pests and may thrive in new locations as a result of a less stressed existence. Frequently, there is an associated decline in ecosystem services such as habitat loss and reducing the impacts of fire or flooding (Langeland and Burkes 1998). Since invasive species are able to out-compete native species and pose a threat to global biodiversity, they are becoming an increasing concern (Higgins et al. 1999). Not only do invasive plants compromise biodiversity, they are also capable of altering soil properties, carbon and nitrogen availability, and decomposition rates (Kourtev et al. 1998, 2003, Ehrenfeld et al. 2001, Standish et al. 2004). Furthermore, plants with invasive tendencies frequently have increased fecundity, reach reproductive age quickly, or may have different nutrient requirements than co-occurring native species (Ehrenfield 2003). As a result, invasive plants are a threat to the invaded ecosystems, and it is costly to control their population growth and spread. Further research needs to be conducted on invasive species and their impacts on ecosystem processes (Ehrenfeld et al. 2001, Matlack 2002, Ward 2002).

Chinese privet (*Ligustrum sinense* Lour.) is a highly invasive semi-evergreen ornamental shrub introduced to North America from China in 1852 (Dirr 1990, Miller 2003). Chinese privet is a member of the *Oleaceae* family and grows to 9 m in height (Miller 2003). Frequently, trunks occur as multiple, long leafy stems and form thickets (Miller 2003). Leaves are opposite, oval and less than 2-4 cm in length with pubescent midveins (Miller 2003). From April to June it produces small, white flowers forming panicles on short terminal branches (Miller 2003). It has fleshy ovoid fruits 8 mm long that ripen to a dark purple color and persist into winter (Miller 2003).

Its spread was slow prior to the mid 1900s, but by the 1950-70s Chinese privet had become well established and has spread at an exponential rate across the Southeastern and Eastern U.S. (Taylor et al. 1996). The rapid expansion of Chinese privet populations once it is introduced is related to its ability to outcompete native species which may result in alterations of natural succession patterns (Brantley 2008). Chinese privet is introduced to new areas via seed dispersal by birds, especially along fence rows and power line right-of-ways, which provide the species access to forest edges (Montaldo 1993, Langeland and Burks 1998, Merriam and Feil 2002). Chinese privet is most dense in disturbed open areas, such as abandoned pasture land, and it is especially concentrated in low wet places, such as floodplains, which resemble its native habitat in China (Langeland and Burks 1998).

Due to its abundance in the Southeast U.S., Chinese privet is an invasive species of concern, yet knowledge regarding its ecology is lacking (Miller 2003). Previous research on Chinese privet examined invasion patterns, optimal growth conditions, responses to flooding, and invasive properties (Brown and Pezeshki 2000, Matlack 2002, Meriam and Feil 2002, Morris et al. 2002, Ward 2002). Studies of Chinese privet conducted in the same physiographic region as this study have focused on its distribution, reproductive capabilities, and implications in carbon cycling (Lowenstein and Lowenstein 2005, Burton et al. 2005, Burton and Samuelson 2007, Brantley 2008). To date, there have been no reports regarding its influence on nutrient cycling. Therefore, this study was designed to examine how Chinese privet influences decomposition, nutrient dynamics, nitrogen mineralization, and microbial biomass in riparian forests in west Georgia.

Decomposition

Many processes are controlled by rates of decomposition, and alterations can have wide ranging impacts on forest nutrient cycling. Decomposition rates are controlled by three major factors: litter quality, moisture, and temperature (Swift et al. 1982). Furthermore, decomposition rates can be influenced by the differing microsite conditions present in urban areas as opposed to rural areas (Pouyat and Carreiro 2003). Pouyat and Carreiro (2003) attributed the differences in decomposition rates that they observed to the presence of introduced invasive earthworms and warmer temperatures, and did not report whether litter was native vs. exotic in their study. Exotic earthworms are the only earthworms found in areas that were glaciated during the Wisconsinan ice age as a result of slow recolonization rates by native earthworms (James 1995). These exotic earthworms are capable of altering nutrient cycling by increasing rates of decomposition (Scheu and Parkinson 1994, Alban and Berry 1994, Groffman and Bohlen 1999). Multiple factors will be examined in this study in an effort to elucidate influences of both urbanization and invasive species on decomposition.

Litter quality is determined by content and concentration of nutrients and recalcitrant materials. More specifically, comparisons of litter quality among site and species can be made by examining carbon:nitrogen (C:N) ratios, percent of lignin and cellulose, and lignin:N ratios of leaf litter (Fisher and Binkley 2000, Gartner and Cardon 2006, Jolley 2008). Some exotic species have extremely different leaf decomposition rates compared to native species, and alter decomposition rates on a site (Vitousek 1994). Furthermore, a site with an exotic species that has distinctive litter qualities may experience a shift in soil properties and microbial populations, which could alter rates of decomposition (Ehrenfeld 2003). The influence of Chinese privet on decomposition has not been previously examined. As a result of this knowledge gap, I examined Chinese privet's influence on decomposition rates.

Nutrient Cycling

Nutrient availability drives forest productivity and rates of nutrient cycling (Fisher and Binkley 2000). Additionally, it is linked to soil nutrient pools, vegetative nutrient pools, and microbial processes (Fisher and Binkley 2000). Nutrients can be stored in multiple pools, including soil, live plant tissue, and forest floor, and these three pools are tightly integrated. One example of this integration is productivity and decomposition which determine forest floor nutrient composition and mass (Fisher and Binkley 2000). Another example of this integration is nutrient availability for microbes in forest floor material which is determined by litterfall nutrient composition. All of these nutrient pathways are influenced by species composition, and exotic species have the potential to greatly alter nutrient cycling.

Riparian forests provide essential functions such as nutrient conversion and sediment trapping, which may cause them to have increased primary production compared to upland systems. Invasive species can impact nutrient conversion processes during growth, decomposition, and soil formation. In general, the more differences in nutrient requirements and composition between an invasive plant and native species, the greater possibility there is for changes to occur (Ehrenfeld et al. 2001). In this study, the influence of Chinese privet was investigated across a range of understory Chinese privet stem dominance (0-100% Chinese privet) by examining nutrient composition of litterfall and forest floor, microbial biomass C and N, and N-mineralization. Litterfall nutrient composition can provide a variety of information concerning stand nutrient limitations and nutrient dynamics, such as resorption efficiency and proficiency, nutrient use efficiency (NUE), and nutrient budgets.

Resorption efficiency is an estimation of the amount of nutrient uptake from green leaves before abscission (Killingbeck 1996). It has been hypothesized that resorption efficiency indicates nutrient limitations on a site basis; for example, low efficiency would indicate a non-limitation of that nutrient (Aerts 1996, Killingbeck 1996). However, resorption efficiency may provide information about nutrient variations among species or between conifers vs. deciduous trees rather than between sites (Aerts 1996, Killingbeck 1996). Further information on site nutrient dynamics can be gained by making general comparisons of NUE, in which a system can be classified as either efficient or inefficient based on litterfall nutrient composition and primary productivity (Vitousek 1982). The research presented here investigates how nutrient use and internal nutrient cycling change with increasing abundance of Chinese privet and across land uses.

Microbial Biomass and Nitrogen Mineralization

Invasive species are capable of altering soil conditions and thereby impact microbial communities and processes affected by those communities (Kourtev et al. 1998, Ehrenfeld et al. 2001, 2003). Microbial biomass is sensitive to changes in both substrate quality and microsite conditions and therefore is frequently used as an indicator of site conditions (Li et al. 2004). Site conditions can be altered by biotic factors such as the introduction of a new species with different litter chemistry and by abiotic factors such as sedimentation (Ehrenfeld 2003, Jolley 2008). Alterations in site conditions which influence microbial biomass will also influence microbial processes such as decomposition and N-mineralization.

N-mineralization is a process that determines soil N availability and is controlled by microbial populations. Since many forests are limited by N, study of N-mineralization is important in relation to invasive species (Vitousek 1982, 1984). Furthermore, Pouyat and Carriero (2003) have observed modifications of N-mineralization associated with urbanization without accounting for vegetative species composition. Further study is needed to determine if there is an interaction between urbanization and invasive species regarding N cycling. While some invasive species are most common in the urban environment (Lowenstein and Lowenstein 2005), it is possible that there is a shift in rates of N-mineralization in urban areas which occurs without the influence of invasive plants. This study includes both differences in land use and % Chinese privet stems in the understory in its design.

Ecosystem Services

Water quality can be altered by removing vegetation and altering land cover to impervious surfaces. Development along the coast provides an entry point for contaminants such as excess fertilizer, fecal bacteria, and heavy metals to nearby water bodies due to removal of vegetation and increased runoff. In areas that have healthy oyster populations, the impacts of contaminants are frequently shorter lived, since oysters are filter feeders and uptake these contaminates (Henderson and O’Neil 2003). The Chesapeake Bay is as an example where both water quality and oyster populations have declined. The once booming oyster industry of the Chesapeake Bay is no longer thriving and oyster populations can no longer improve water quality in the entire bay. Factors such as overharvesting and high sedimentation levels, have intertwined to cause the decline of oyster populations (Henderson and O’Neil 2003). However, if oyster populations were abundant they would provide an increased value, in terms of ecosystem valuation, to the Chesapeake Bay as a result of improving water quality for boating and recreation purposes (Henderson and O’Neal 2003). Also, intrinsic values such as providing the habitat of oyster reefs would be increased (Henderson and O’Neal 2003). Therefore, Apalachicola Bay residents could use the Chesapeake Bay as an example of the worst case scenario for potential impacts of development and declining water quality in their Bay. Although land use conversion in Apalachicola is not occurring on the same scale of the Chesapeake region, similar conversions from forest to impervious surfaces are occurring.

Apalachicola oysters. Historically, the oyster industry of Apalachicola Bay has contributed 10% to the national harvest and 90% to the Florida harvest (Marchman 2000, Whitfield and Beaumarriage 1977). However, increased development in the Apalachicola/Chattahoochee/Flint watershed threatens the oyster industry by increasing fresh water demands and contamination of the Bay (Kirkland 2006). Oysters are well suited to the long growing season in the Bay and individuals can reach harvestable size in 18 months (Ingle and Dawson 1952, 1953). Their rapid growth rates in the Apalachicola

Bay are attributed to warm water conditions and optimal salinity (Ingle and Dawson 1952, 1953). Nevertheless, as demand for fresh water upstream of the Bay increases, salinity levels will rise due to the decreased input of fresh water and alterations in oyster productivity can be expected. Several studies have indicated that increased salinity has a positive relation to oyster production (Meeter et al. 1979, Wilber 1992, Turner 2006).

Oyster harvesting in Florida is controlled by the Florida Department of Agriculture and Consumer Services Shellfish Environmental Assessment Section (FDACS-SEAS). They regulate which harvesting areas are open for harvesting. Their decisions for opening or closing an area are based on either predicted or measured fecal coliform (FC) concentrations. Decisions to close harvest areas are based on equations that relate discharge or precipitation in the watershed to FC concentration in the Bay, while decisions to re-open harvest areas are made when measured FC is appropriate. Therefore, changes in water quantity and quality will have an influence on the quantity of oysters harvested in the Apalachicola Bay and the percentage of the Bay that is open to harvest.

Objectives

Although there is a large body of knowledge concerning the repercussions of urbanization and its associated effects on natural systems, there is still a vast amount of knowledge to be gained regarding invasive species and water quality. This research was designed to provide information on the biogeochemical impacts of the invasive Chinese privet and the economic influence of changing demands for natural resources in Apalachicola Bay. Specific study objectives were: 1) to assess how Chinese privet alters decomposition rates, by testing whether Chinese privet increases decomposition rates in direct proportion to its contribution to litter and by comparing the litter quality of Chinese privet to that of other native species; 2) to investigate and describe the influence of Chinese privet on nutrient cycling in forest floor, litterfall, retranslocation, NUE, N-mineralization, and microbial biomass in riparian forests; and 3) to investigate changes in oyster harvests associated with alterations in water quantity, quality, and land use.

Chapter 2 examines decomposition rates with a focus on the influence of Chinese privet. Two distinct decomposition studies are reported in this chapter. One, a field study, examined changes in decomposition rates by utilizing local litter mixtures on their respective sites. The other was a controlled study in which selected proportions of Chinese privet litter were mixed with native litter and placed at a single site to reduce the influence of microsite variation. Chapter 2 also discusses comparisons between the litter quality of Chinese privet and four native species, yellow poplar (*Liriodendron tulipifera*), sweetgum (*Liquidambar styraciflua*), elm (*Ulmus* sp.), and water oak (*Quercus nigra*).

Chapter 3 explores nutrient dynamics across sites with varying percentages of Chinese privet in the understory. These nutrient dynamics include litterfall nutrient content and concentration, forest floor mass and nutrient composition, NUE, resorption efficiency and proficiency, microbial biomass, and N-mineralization rates. NUE was conducted on a site basis for N, phosphorus (P), magnesium (Mg), calcium (Ca), and potassium (K). Resorption efficiency was determined for each species, while resorption proficiency was determined by site and species. Comparisons made were made between three invasion classes: uninvaded sites which had no Chinese privet in the understory, moderately invaded sites which had 25 to 80 percent Chinese privet in the understory, and severely invaded sites which had more than 80 percent Chinese privet in the understory. This chapter provides insight into how different intensities of invasion influence the overall nutrient regimes of riparian forests in west Georgia.

An examination of the linkages between river discharge, FC concentrations and quantity and value of oyster harvests in Apalachicola Bay, FL is presented in Chapter 4. The time period of 1994-2006 was examined for relationships between changes in land use in Gulf and Franklin counties, which neighbor the Apalachicola Bay, and closures of harvest areas. This chapter also provides a synthesis of previous research on the Apalachicola Bay's oyster industry, as well as an examination of how the economy of the Apalachicola Bay area has been influenced by closures of the Bay in response to deleterious water quality.

Chapter 5 presents major conclusions and findings of the preceding chapters with an emphasis on the potential implications. There is also integration and discussion of some of the overarching themes presented in this research.

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CHAPTER II

INFLUENCE OF CHINESE PRIVET (*LIGUSTRUM SINENSE* LOUR.) ON DECOMPOSITION IN RIPARIAN FORESTS

ABSTRACT

Decomposition in forest ecosystems is one process that determines nutrient availability. It is a complex process influenced by many factors, one of which is leaf litter composition. Invasive species are becoming increasingly abundant in forests and thus may influence forest nutrient cycles. Two studies were conducted to determine the influence of Chinese privet (*Ligustrum sinense* Lour.) on decomposition in riparian forests. One used site specific leaf litter (composed of 20 g of litter with representative proportions of the five dominant species) and is called the west Georgia study. The other study utilized a single site with 0, 10, 20, 30, 40, and 50% Chinese privet contributing to the 20 g in litter bags and is called the controlled study. In the controlled study, the remainder of the leaf mass was evenly distributed between sweetgum (*Liquidambar styraciflua* L.), yellow poplar (*Liriodendron tulipifera* L.), oak (*Quercus* sp.), and elm (*Ulmus* sp.). The controlled study was conducted at a single riparian site to provide minimal microsite differences across treatments, allowing the influence of Chinese privet on decomposition to be isolated. Individual species litter quality was also examined to compare the four native species to Chinese privet. For both approaches, initial litter samples and time lapse samples were analyzed for C, N, and P concentration. Percent lignin and cellulose were determined for t=0. Both studies showed a positive regression between percent Chinese privet in decomposition bag and k-rates. Analysis of individual species litter indicated that Chinese privet leaf litter is easier to decompose, with lower % lignin and % cellulose, higher N concentration, low lignin:N, and balanced C:N ratios than the native species. The positive relationship between k-rates and Chinese privet's contribution to decomposition indicates that Chinese privet could impact decomposition rates in forests as it becomes more abundant. Carbon and mass turnover rates may increase and a new forest floor steady state would be established.

INTRODUCTION

Riparian forests are a vital component of healthy watersheds. Intact riparian forests provide several functions including sediment trapping, nutrient uptake, buffering flood velocity, and stream bank stabilization (Mistch and Gosselink 1993). Many studies have investigated nutrient cycling in riparian forests and some have focused on decomposition, which may be viewed as a controlling process in nutrient cycles (Brinson 1977, Lockaby et al. 1996, Schilling and Lockaby 2005). This chapter examines the influence of an invasive species, Chinese privet (*Ligustrum sinense* Lour.), on decomposition rates in riparian forests in west Georgia. Other studies have observed decomposition rates increasing as invasive species become more abundant in forest ecosystems (Ehrenfeld 2003). Other studies on Chinese privet have not focused on the nutrient cycling implications of its invasion.

Decomposition

Decomposition is a driving factor of forest productivity because it regulates nutrient availability and can be defined as microorganisms, fungi, and macroinvertebrates mechanically and chemically converting plant material into soil organic matter (SOM). Nutrients are converted from organic to inorganic forms that micro-organisms, soil fauna, and vegetation can assimilate. Three major factors influence decomposition rates: soil physiochemical properties (temperature, soil pH, and moisture regime), litter quality, and microbial populations (Swift et al. 1979). Many studies have investigated how each of these factors influences decomposition (Brinson 1977, Conn and Dighton 2000, Ayres et al. 2006, Schilling and Lockaby 2006, Fioretto et al. 2007).

Three phases are used to describe the changing slopes associated with decomposition mass loss curves and the processes in decomposition (Berg and McClaugherty 2003). In the first phase, soluble nutrients such as N and P are removed from leaf litter, and mass loss is very rapid with a steep slope (Berg and McClaugherty 2003). In the second phase, lignin and cellulose are degraded, mass loss slows, and the slope of the curve to decrease (Berg and McClaugherty 2003). Finally, only recalcitrant portions of leaves remain and mass loss remains constant through time (Berg and McClaugherty 2003). These three phases yield the curvilinear shape typical of mass loss curves.

Numerous studies have investigated the relationship between decomposition and the intensity and frequency of flooding. For example, Lockaby et al. (1996) found that intermittent flooding and drying pulses coincide with more rapid decomposition rates than in absence of flooding. Prolonged exposure of leaves to moist soil provides ideal microsite conditions to microbial and fungal populations which may promote more rapid decomposition rates (Yates and Day 1983). However, prolonged flooding may create anaerobic conditions that reduce decomposer activity and slow decomposition.

Although it is possible to quantitatively compare flooding duration across studies, few decomposition studies measure soil moisture. Using a simple site classification such as flooded or not flooded may indicate the presence of standing water, but gives no indication of flooding depth or duration (Battle and Golladay 2007). Therefore, a quantitative measure of soil or litter layer moisture would be beneficial in decomposition studies conducted on sites influenced by high groundwater tables.

Mass loss rates are strongly driven by litter quality, and several factors unite to determine litter quality (Day 1982). These factors include nutrient content, nutrient concentration, nutrient ratios, and recalcitrant constituents (Swift et al. 1979). High nutrient content of leaf litter typically results in rapid mass loss, enabling decomposing organisms to quickly convert leaf litter into biologically available nutrients. Elevated N levels can slow decomposition in phase two of decomposition since high N interferes with lignin breakdown (Lockaby et al. 1996, Hobbie 2008).

Frequently, litter quality is used to predict decomposition rates. There are typically differences in litter quality among species; however, depending on the growing season or site, litter quality may vary considerably within a species (Gartner and Cardon 2006, Jolley 2008). Despite site and seasonal differences, some species have unique, identifiable litter quality (Gartner and Cardon 2006). Interestingly, there are often detectable differences in litter quality not only between species but also between individuals of the same species. For example Madritch et al. (2006) was able to discern differences in leaf quality among clones of quaking aspen (*Populus tremuloides* Michx.). These discernable genetic differences may also be important for Chinese privet which, like aspen, has clonal growth (Miller 2003).

Precipitation patterns during a growing season influence litter quality but are frequently neglected in discussions of litter quality (Wood et al. 2005, Battle and Golladay 2007, Jolley 2008). Not only is it important to observe precipitation patterns during decomposition studies, it is also important to be aware of precipitation patterns of a prior season, when leaves were actively growing. During drought conditions, litter quality (*i.e.*, nutrient composition) may be altered, which can greatly influence decomposition rates (Battle and Golladay 2007).

Many studies have found that decomposition is impacted by species composition (Hector et al. 2000, Zimmer 2002, Hoorens et al. 2003, Ashton et al. 2005, Madritch and Cardinale 2007). Frequently, decomposition studies in the Southeastern U.S. have been conducted on intact native riparian forests dominated by oaks (*Quercus* sp.), elms (*Ulmus* sp.), sweetgum (*Liquidambar styraciflua* L.), and yellow poplar (*Liriodendron tulipifera* L.) (Lockaby et al. 1996, Schilling and Lockaby 2006, Ozalp et al. 2007). Studies that examine multiple species will include greater natural variability in litter quality and decomposition rates but also will more accurately represent natural forest floor conditions.

Indicators most frequently used to quantify litter quality are carbon:nitrogen (C:N) ratio, nitrogen:phosphorus (N:P) ratio, and lignin:N ratio. These ratios of nutrients play an important role in determining the rate of decomposition because decomposers require an optimum nutrient balance to efficiently decompose plant material (Swift et al.

1977). The lignin:N ratio is described as optimal around 35 (Fisher and Binkley 2000). If it is wider than this, N-mineralization halts and the system becomes N deficient. Optimal ratios for microbial populations are 10 for N:P ratios (Alexander and Fairley 1983) and 30:1 for C:N (Tate 2000). If ratios become imbalanced, decomposers must obtain nutrients from other sources, such as the soil, through a process known as immobilization (Tate 2000, Alexander and Fairley 1983).

Another factor determining litter quality is the concentration of recalcitrant materials, such as lignin, cellulose, and hemicellulose, which are frequently the last components of leaves to decompose (Swift et al. 1979). Therefore, their contribution to leaf mass will determine the amount of mass remaining in the final stages of decomposition. Long-term mass loss rates are dependent on the presence of organisms capable of breaking down these recalcitrant materials.

Site-specific microbial activity also influences mass loss rates. It has been hypothesized that some plant species alter soil quality by altering soil pH, which promotes specifically-adapted soil biota to decompose their litter material (Ayres et al. 2006, Madritch and Cardinale 2007). Ayres et al. (2006) tested this hypothesis but found no such relationship. Similarly, Madritch and Cardinale (2007) conducted a decomposition study using mixed-species litter, consisting of one, two, four, and six species for one year. They found decreased mass loss with increased species richness, suggesting that decomposers favored single species litter. In contrast, Hu et al. (2006) observed decomposition bags containing mixed species leaf litter promoted increased microbial activity and more rapid decomposition rates in comparison to bags containing a single species of leaf litter.

Decomposition studies frequently quantify decomposition rates based on mass loss rates, and corresponding predictive models have been developed. Mass loss rates are determined by the following equation:

$$\% \text{ original remaining} = e^{-kt}$$

where k= litter specific decomposition rate change, and
t= time in days.

The average decomposition k-rate in temperate floodplain forests is 1.01 (Lockaby and Walbridge 1998). This rate, however, will change depending on flooding and export of decomposed material (Lockaby and Walbridge 1998). Therefore, rates change from year to year and from site to site. Decay rates in Southeastern U.S. studies ranged from 0.055 to 1.77 (Lockaby et al. 1995, Lockaby et al. 1996, Baker et al. 2001, Schilling and Lockaby 2005, Battle and Golladay 2007).

Recent studies have scrutinized the applicability of predicted decay rates because of the limited number of observations in decomposition studies that typically only last a year (Prescott 2005). Prescott (2005) suggested that better predictions of decomposition rates can be made by using ecosystem-level approaches. Such an approach would incorporate plant life and soil faunal attributes in order to predict decay rates rather than, correlations of specific litter quality and decomposition rates.

Land use changes. Urbanization promotes the spread of non-native species through increased incidence of disturbance events. Greater frequency, cover, and richness of invasive plant species occur along roadsides and near urban areas (Lungren et al. 2004). Edges created when land is cleared provide a foothold for invasive species to establish and invade neighboring forests. There is also an increased abundance of propagules from invasive plants used in landscaping. Numbers of invasive species and individuals typically outnumber native species and individuals in urban areas (Loewenstein and Loewenstein 2005).

Decreased biodiversity is often associated with urbanization, and urban systems are further degraded by increasing populations of invasive species (McKinney 2002). Burton et al. (2005) observed decreased native diversity and regeneration near an urban center. King and Buckney (2000), on the other hand, concluded that number and abundance of native species were similar in urban and non-urban areas but the particular native species differed between urban and non-urban areas. Therefore, it is possible that community composition prior to development and species hardiness may influence which plant species survive in the new urban ecosystem.

Non-native Invasive Plant Species

Chinese privet. Recently, non-native invasive plant species have been recognized as a threat to native ecosystems. Invasive species have been shown to alter timing and quantity of nutrient availability in forest systems because of altered litter chemistry and senescence compared to native species (Ehrenfeld 2003). Chinese privet is an invasive species of concern in the Southeastern U.S. (Miller 2003).

Chinese privet is a member of the *Oleaceae* family. It was introduced into the U.S. in 1852 (Dirr 1990, Miller 2003). Since the early 1900s, Chinese privet was planted around homes and outhouses due to its fragrant flowers (Dirr 1990). It is very hardy and thrives in many conditions; therefore, it is frequently used in landscaping and is capable of reproducing both sexually and vegetatively by root sprouting (Morris et al. 2002). Frequently, Chinese privet is found along fence rows and power line right-of-ways as a result of bird seed dispersal and occurs most densely in disturbed open areas, such as abandoned pasture land and low wet places, such as floodplains (Langeland and Burks 1998). Langeland and Burks (1998) suggested floodplains are most susceptible to Chinese privet invasion because they resemble its native habitat in China. Direct repercussions of the invasion of Chinese privet have been observed in Florida, where Chinese privet is preventing regeneration of the federally endangered miccosukee gooseberry (*Ribes echinellum* [Coville] Rehder) (Langeland and Burks 1998).

Few studies have investigated the influence of Chinese privet on floodplain ecosystem processes (Brown and Pezeshki 2000, Ward 2002). Previous research on Chinese privet examined invasion patterns, optimal growth conditions, responses to flooding, and invasive properties (Brown and Pezeshki 2000, Matlack 2002, Merriam and Feil 2002, Morris et al. 2002, Ward 2002). However, no studies to date have evaluated its effects on biogeochemical processes.

Nutrients. Differences between native and non-native species' leaf litter quality and quantity may alter decomposition processes and explain differences in soil C and N dynamics (Finzi et al. 1998). Therefore, the introduction of a new species into an ecosystem may alter overall nutrient fluxes (Swift et al. 1979, Vitousek et al. 1994, Zimmer 2002, Sariyildix and Anderson 2003). More rapid decomposition rates occur for litter of certain non-native species (Ashton et al. 2005, Allison and Vitousek 2004). If the leaf litter of an invasive species has high N content and concentration relative to a native species, then N may be mineralized more rapidly, altering nutrient cycling patterns. Invasive species have been found to alter local biogeochemistry by changing the rates of litter decomposition processes and N cycling (Vitousek and Walker 1989). While invasive species can influence decomposition by changing the rate of mass loss (Ehrenfeld et al. 2001, Standish et al. 2004), the influence of Chinese privet on decomposition rates has not been examined.

Invasive plants can increase nitrification rates and alter soil properties such as pH, thus serving to increase rates of invasion by providing favorable soil conditions for invasive species which may alter decomposition rates (Ehrenfeld et al. 2001). For example, Japanese barberry (*Berberis thunbergii* DC.), an invasive shrub, and Japanese stiltgrass (*Microstegium vimineum* [Trin.] A. Camus), an invasive grass, significantly increase soil pH in both field and laboratory studies (Kourtev et al. 1998, Ehrenfeld et al. 2001, Kortev et al. 2003). Japanese stiltgrass has been reported to change pH from 4.75 to 6.5 (Ehrenfeld et al. 2001). Changes in soil pH influence decomposition rates by altering physical and chemical properties of soil while altering microflora and microfauna communities (Ehrenfeld et al. 2001).

Study Objectives

The objective of this study was to assess how Chinese privet alters decomposition rates, which could significantly impact nutrient cycling at the community level. Hypotheses are : 1) leaf litter of Chinese privet is of high quality (litter will have narrow litter quality ratios for C:N, N:P, and N:lignin) in comparison to native litter; and 2)

Chinese privet will increase decomposition rates in proportion to the magnitude of Chinese privet contribution to litter.

METHODS

Field and Laboratory Procedures

Decomposition. Decomposition rates were determined using the litterbag technique of Swift et al. (1979). Senesced leaves were collected in the fall from 16 sites in west Georgia that ranged from 0-100% understory stem abundance of Chinese privet. Leaf collection utilized tarps suspended above the forest floor to prevent inoculation of leaves by soil microbes. After delivery to the laboratory, leaves were separated by species and site, and then air dried for two weeks. Nylon litterbags with 6 mm and 1 mm openings on the top and bottom, respectively, were used to estimate mass loss rates and nutrient dynamics of leaf litter (Swift et al. 1979). This study used two approaches: 1) 16 floodplain sites where leaf litter for decomposition bags was collected on a “plot specific” basis (west Georgia study); and 2) litterbags with pre-determined proportions of Chinese privet litter placed on a single field site (controlled study). See each section for details on litter bag composition and collection schedules.

In the laboratory, leaves were cleaned of roots, macroinvertebrates, and soil. Samples were oven dried at 70^{o}C for 72 hours, and then ground to pass a number 20-mesh screen. Analysis of leaf C and N used a Perkin Elmer Series II CHNS/O Analyzer 2400 (Perkin Elmer Corp., Norwalk, CT). Total P determination utilized dry-ashing and extraction with acid digestion, using the vanadomolybdate procedure (Jackson 1958) before analyzing the samples spectrophotometrically. Ash-free dry mass (AFDM) determination utilized pre- and post-ashing masses. Samples were ashed at 500^{o}C for at least 8 hours. The mass loss rate constant, k, was calculated using the exponential decay formula, -*k*=ln (X/X$_0$)/t (where X$_0$= initial dry weight and X= final dry weight and t=time) (Swift et al.1979).

Moisture, temperature, and light intensity were monitored on all sites. Moisture monitoring utilized a specially-created sensor consisting of a nylon litterbag wrapped in wires which monitored changes in voltage resulting from variations of moisture in the litter layer (inventor: Robert Price, Auburn, AL). Voltage data were recorded every 15 minutes with a Hobo RH Temp 2xExternal logger made by Onset Computer Corporation (Pocasset, MA). Moisture level classifications were based on voltage readings and moisture calibrations of the logger under controlled conditions. Four classifications were used: dry (voltage >2 volts), damp (voltage between 1.5 to 2 volts), wet (voltage between 0.6 to 1.5 volts), and flooded (voltage <0.6 volts). Moisture logger installation occurred on 21 July 2005 and loggers were removed with the last litterbag collection on 14 September 2006. Loggers were not weather proof and did not work consistently on all sites.

Two StowAway TidbiT Temp Data Loggers© by Onset Computer Corporation monitored temperature on each site (Pocasset, MA); one was buried 15 cm below the soil surface (Brantley 2008) and one was placed in the litter layer near the decomposition bags. Horizontal distance between loggers ranged from 3 to 10 meters. Installation of temperature loggers occurred on 29 April 2005 and they remained until August 2007, with measurements recorded hourly. A single HOBO Light Intensity Data Logger©

(Pocasset, MA) in the center of each plot at a height of 1.5 meters (m) from the ground recorded data every 35 minutes for the entire study duration.

Leaf litter lignin and cellulose for time = 0 samples were determined with acid detergent fiber (ADF) and neutral detergent fiber (NDF) methods which utilize proximate carbon fractionation analyses (Goering and Van Soest 1970). The lignin-cellulose index (LCI) was determined from the equation: LCI= lignin/(lignin+cellulose) (Melillo et al. 1982).

West Georgia Study

Description of study sites. The study sites lie along a continuum of Chinese privet invasion across a range of land uses. Land use categories include urban, developing, rural, and pasture sites in Muscogee and Harris counties, near Columbus, GA. Sites were classified by dominant land use and impervious surface according to Crim (2007) (Figure 1). These counties occur in the Piedmont physiographic province which has annual temperatures mean that range from 0^{o}C to 38^{o}C, annual mean precipitation of 127 cm, and mean growing season length of 220 days (USFS 2005). Soils in the area are dominated by Ultisols, which have clayey or loamy subsoil and a kaolinitic or mixed mineralogy (USFS 2005). More specifically, soil series on sites was either Chewacla (fine-loamy, mixed, active, thermic Fluvaquentic Dystrudepts), Vance (sandy-clay-loam, fine, mixed, semiactive, thermic Typic Hapludults), or Toccoa (coarse-loamy, mixed active, nonacid, thermic Typic Udifluvents series).

Sites were classified based on the percent stems of Chinese privet in the understory and divided into classes based on the following criteria. Each class had similar structure and vegetation layers, indicating relevance of these divisions. The overstory vegetative layer was defined as anything taller than 20 m, the midstory layer was defined as vegetation between 4-7 m tall, the understory consisted of woody plants less than 1.3 m tall and the regeneration layer was all woody plants with a root collar diameter less than 4 cm. Uninvaded sites had 0% Chinese privet, moderately invaded sites were between 25 and 79% understory stems of Chinese privet, and severely invaded sites exhibited greater than 80% Chinese privet stems in the understory. Invasion classes were also unified by several other characteristics. Uninvaded sites all had a closed canopy, with an overstory of mature native trees including sweetgum (*Liquidambar styraciflua* L.), yellow poplar (*Liriodendron tulipifera* L.), red maple (*Acer rubrum* L.), and elm (*Ulmus* sp.), with a relatively high basal area (mean of 36.4 m^2/ha measured with a 10 BAF prism), a midstory composed of dogwood (*Cornus florida* L.), and an open understory. Moderately invaded sites had a mean basal area of 19.0 m^2/ha, an overstory composed of mature native trees such as sweetgum, water oak, and yellow poplar, with Chinese privet and muscle wood (*Carpinus caroliniana* Walter) occurring in the midstory. Severely invaded sites had a few mature, overstory, native trees such as water oak and sweetgum, coupled with a Chinese privet dominated sub-canopy and only Chinese privet found in the understory, with a mean basal area of 20.9 m^2/ha.

Sampling scheme. A total of 16 circular 0.04 hectare plots were located in riparian forests within 6 watersheds, with 2 to 3 sites located in each watershed, all with closed canopy. Leaf collection began in October 2004 and ended in May 2007.

Soil analysis. Soil nutrients were collected at the beginning (January 2005) and end of the study (August 2007). Surface soils were sampled to a depth of 20 cm, sieved, and then analyzed for nutrients. Soil samples were sent to the Auburn University Soil Testing Laboratory for analysis. Soil samples were analyzed for pH, extractable P, and exchangeable potassium (K), magnesium (Mg), and calcium (Ca), and analyzed with methods specified in Johnson et al. (1984) and Auburn University Soil Testing Laboratory (1986). Analysis of exchangeable K, Ca, and Mg used an atomic absorption (AA) spectrophotometer, while other cations and extractable-P in samples were determined using inductively coupled argon plasma spectrophotometry (ICAP).

Nitrogen mineralization. Nitrogen mineralization measurement utilized the *in situ* method of Hart et al. (1994). Sample collection occurred at approximately 2-month intervals between November 2005 and April 2007. At each collection time, two arbitrarily placed soil cores were taken to a depth of approximately 7.5 cm within the same quadrant of each plot. After removal of coarse roots (defined as diameter >1 mm and length >1 cm), soil from each core was divided between two polyethylene bags (about 150 ml of soil in each bag). One bag was sealed and buried to a depth of approximately 7.5 cm and incubated for 30 days, and one served as a pre-incubation sample. Pre-incubation and post-incubation samples were transported on ice to the laboratory at Auburn University for processing. After sieving soils to remove organic matter, soil moisture content was measured gravimetrically for each sample using a 10 g sub-sample which was dried at 105° C for 48 hours and placed in a desiccator until a constant weight was reached. A second 10 g sub-sample was shaken for 1 hour with 100 mL 2 M potassium chloride (KCl), filtered, and then frozen. Thawing of samples took place prior to N analysis. Extracts were evaluated for NH_4-N and NO_3-N using a BIO-RAD Model 450 microplate reader. Mineralized N estimation involved calculating the difference in total N (sum of NH_4-N and NO_3-N) between pre- and post-incubation samples. Soil bulk density was determined for each site in order to convert mineralized N values to a per hectare basis. Bulk density was determined for 3 samples taken from each site using a 5 cm diameter double-cylinder push probe (0-7.5 cm depth). Samples were dried to a constant mass at 105^oC to quantify bulk density (Blake and Hartge 1986, Brantley 2008).

West Georgia study litter bag composition. The five dominant species from each plot, and their relative contribution to litterfall mass, determined litterbag sample composition. Litterbags had 20 grams (g) of leaf litter of appropriate species composition. Dominant species in litterfall consisted of sweetgum, hickory (*Carya* sp.), red maple (*Acer rubrum* L.), elm, yellow poplar, hophornbeam (*Ostrya virginiana* Mill. K. Koch), oak species (*Quercus* sp.), sycamore (*Platanus occidentalis* L.), black walnut (*Juglans nigra* L.), black cherry (*Prunus serotina* Ehrh.), and Chinese privet. Bag installation on plots occurred in April 2005. At each collection time (0, 1, 2, 4, 8, 12, 24, 36, 48, 60, and 72 weeks), two bags from each site were collected. Bags were transported individually on ice in labeled re-sealable plastic bags. Two sets of 11 bags per site were placed in close proximity to one another on top of the current forest floor and stabilized with pin flags at each corner of the bags. Handling loss and moisture content estimation utilized bags transported to each site and collected at t=0.

Controlled Study

Site description. The controlled study was conducted in a riparian forest in north Auburn, AL. Site selection was based on its proximity to the laboratory and its resemblance to streams in the west Georgia study sites, including having a closed canopy of native hardwood trees. Bag placement mimicked conditions in west Georgia, where bags had been placed flat on the current forest floor in close proximity both to a stream and to one another.

Controlled study leaf litter bag composition. The controlled study allowed influences of litter quality to be separated from site microclimate influences by holding site conditions constant, and thus better isolating causal factors. Composition of the 20 grams of litter was assigned according to the following treatments: 0%, 10%, 20%, 30%, 40%, and 50% Chinese privet. The remnant mass in each bag had equal proportions of sweetgum, yellow poplar, water oak, and elm: these species were chosen because of their frequent occurrence on west Georgia sites. Leaves used were from west Georgia leaf collections. Installation of bags occurred in June 2005, and two bags from each treatment were collected at 0, 1, 2, 3, 6, 9, 15, 20, 30, and 42 weeks. Bags were transported individually on ice in labeled re-sealable plastic bags. Two sets of 11 bags per site were placed in close proximity to one another and stabilized with pin flags at each corner of the bags. Handling loss and moisture content estimation utilized bags collected at t=0.

Statistical Analysis

Soil data were analyzed with a one-way analysis of variance (ANOVA). Decomposition relationships were described using nonlinear regression analysis in order to determine k-rates. Linear regression was also used to test for relationships between treatments, litter quality, and k-rates. For comparisons, a one-way ANOVA was conducted using 3 classes (uninvaded: 0% Chinese privet, moderately invaded: 25-79% Chinese privet and severely invaded: > 80% Chinese privet) based on percent of Chinese privet stems in the understory (Table 11) (PROC GLM, SAS Institute 2002-2003). Classes were divided based on shifts in structure among sites. If significant, a Tukey's post hoc mean separation test was performed. Data analysis used SAS version 9.1 (SAS-Institute, 2002-2003). Statistical significance was set at $\alpha=0.05$; however, all p-values <0.1 are presented for informational purposes.

RESULTS

West Georgia Study

Soil nutrient data. There were significant differences across classes of understory Chinese privet for pH, and for exchangeable Ca, K, and Mg (Table 1, Figure 2). Uninvaded sites had soils with higher pH and K in comparison to moderately invaded or severely invaded classes. Exchangeable soil Ca was higher for the severely invaded class compared to the moderately invaded class. Soil Mg was lower in the moderately invaded class compared to uninvaded and severely invaded classes. Soil P lacked significant differences across classes. In addition, severely invaded sites had lower bulk density than uninvaded and moderately invaded sites (Table 2).

Soil temperature data. No differences were observed between mean forest floor temperatures among sites (Figure 3, Table 2). There were significant differences among classes for mean soil temperatures 5 cm below the soil surface level (Table 2). The range of those values was less than 1.6^{o} C.

Microsite moisture variation. The data loggers frequently malfunctioned resulting in a smaller than desired data set for moisture data on microsite conditions. However, data were analyzed to try to quantify moisture variation differences among sites and moisture classifications (flooded, wet, damp, and dry). No differences were observed in percent of time each class was classified as dry or wet (Figure 4). There was a significant difference between microsite conditions among classes for the damp moisture classification (Table 3, Figure 4). Uninvaded sites were classified as damp for a greater percent of the time compared to severely or moderately invaded sites (Figure 4).

Litter Quality

West Georgia litter quality at t=0. Litter quality was characterized in terms of mean C:N, N:P, C:P, lignin:N ratios and percent lignin for t=0 (Table 4). Contribution of Chinese privet to decomposition bags ranged from 0-17.7 %. Individual samples had a range of C:N ratios from 29.7 to 76.1, N:P ratios from 4.0 to 8.6, C:P ratios from 182.8 to 411.0, and lignin:N ratios from 8.2 to 21.7. Percent lignin of individual samples ranged from 12.5 to 19.2. A significant negative linear regression relationship existed between LCI and percent Chinese privet in litterbags (F=5.80, p=0.022, Figure 5). As the percent of Chinese privet in decomposition bags increased, the LCI at t=0 decreased.

Final litter quality. Mean nutrient content, mass remaining, and k-rates for all sites after 72 weeks of field residence were compared (Table 5). Percent mass remaining at 72 weeks for all sites ranged from 2.5 to 39.8%. Differences in N:P ratios were significant between understory Chinese privet classes at 72 weeks, with a significantly wider ratio for the moderately invaded and severely invaded classes compared to the uninvaded class ANOVA: (F=5.13, p=0.012, df=2, 45, Table 5). A significant positive linear regression relationship existed between k-values and final N:P ratios (F=4.41, p=0.044, Figure 6).

Decomposition rates. Mass loss curves for all sites had the traditional curvilinear shape associated with decomposition (Figure 7); however, each site had unique slopes and these indicated that their rates of decomposition differed. Similarly, % N remaining was greatly influenced by rates of mass loss for some sites and therefore had graphs of similar shapes (Figure 8a). However, on most sites, graphs of % N remaining across time showed initial immobilization peaks indicating low N availability (Figure 8). Yet, these peaks over the 100% line were not present for % P remaining across time (Figure 9).

Values of k ranged from 0.186 to 0.432 across all sites. A significant negative regression relationship was present between % lignin and k-value (F= 4.53, p=0.042, Figure 10). However, there was a significant positive regression between percent Chinese privet in litterbags and k-values (F= 4.75, p= 0.037, Figure 11). Yet, there was no significant linear relationship observed between % lignin and % Chinese privet in litterbags (F= 0.45, p=0.51, data not shown). A significant linear regression was observed between k-values and mean N-mineralization across sites (F=5.49, p=0.026,

Figure 12). Furthermore, a significant negative regression relationship occurred between litter layer temperature and k-values, (F=9.3, p=0.005, Figure 13).

Controlled Study

Individual species litter quality. Comparison of senesced leaf litter revealed significant variation in litter quality among species (Table 6). Percent cellulose was significantly lower for Chinese privet than all other species (Figure 14). Percent cellulose in leaf litter had the following order: yellow poplar (21%)>water oak>elm>sweetgum>Chinese privet (9.6%) (Figure 14). The range of % lignin was 9.5 to 16.5%. Percent lignin differed significantly among species with Chinese privet having significantly less lignin than any of the other species (Figure 15). Significant differences also occurred among species for the variable LCI, with a range of 0.4 to 0.6 (Figure 16), and Lignin:N (Figure 17). The highest lignin:N ratio occurred for water oak, followed by elm and sweetgum, and yellow poplar while Chinese privet had the lowest lignin:N ratio (Figure 17). Initial C and N concentration in each species differed significantly among species (Table 5, Figures 18, 19). Furthermore, a significant difference among species in terms of C:N ratio was observed, ranging from 33.3 for Chinese privet to 74.9 for water oak (Figure 20).

Initial litter quality at t=0. As in the field study, initial litter quality was characterized in terms of C:N, N:P, C:P, lignin:N ratios and % lignin (Table 7). There were significant differences in C:N ratios between bags containing different % Chinese privet litter (Table 8, Figure 21). There was also a significant regression showing narrowing C:N ratio, as the percent of Chinese privet in decomposition bags increased (F= 11.4, p=0.007, Figure 22). N:P ratios were not different among treatments (Table 8, Figure 23).

Final litter quality. Differences in % mass, % C, % P, % N remaining among the treatments were significant (Table 9, Figures 24, 25, 26, and 27). Litter quality after week 42 in the field is presented in Table 10. A significant quadratic regression described the relationship between % C remaining at week 42 and % Chinese privet in bags (F= 22.8 p= 0.0005, Figure 28) and the relationship between % mass remaining at week 42 and % Chinese privet in bags (F=20.4, p=0.0007, Figure 29).

Rates of decomposition. Values of k ranged from 0.14 to 0.39. A significant positive linear regression between k-values and the % Chinese privet in bags existed (F= 160.8, p<0.0001, Figure 30). There were also significant differences in k-values among the treatments (F=40.8, p=0.0001, df=5, 12, Figure 31). Furthermore, the negative linear regression for k-values and C:N ratio at time=0 was also significant (F=15.6, p=0.003, Figure 32).

DISCUSSION

West Georgia Study

Temperature and moisture regime. In this study, moisture and temperature did not explain the variation in decomposition rates. Interestingly, the negative relationship found between temperature and decomposition rate (Figure 13) indicated that moisture requirements were limiting. Hot, dry summer conditions decreased soil moisture, reduced microbial populations and thereby slowed decomposition rates (Figure 33). Although there was a significant negative regression relationship between forest floor temperature and decomposition rate (Figure 13), there were no significant differences in forest floor temperature across treatments (Table 2). These results indicate that high temperatures, which coincided with dry periods in year 2 (Figure 33), slowed decomposition rates.

Microsite variation in moisture regimes did not have a detectable influence on decomposition rates. It is possible that little effect was observed since there was little variation in moisture regimes across sites. In the present study, flooding (defined as standing water above the soil surface) was minimal and brief. Similar flooding conditions across all sites may have reduced my ability to detect the influence of moisture regime on decomposition rates. Although there were only slight differences in duration of standing water among sites (Figure 4), there were significant differences among sites with regard to moisture classifications (Table 3). Uninvaded sites were classified as damp for a greater percentage of the time (Figure 4), which may have increased decomposition rates since damp conditions favor microbial activity more than wet or dry conditions. Lockaby et al. (1996) found that a single three month flooding and drying event increased decomposition rates, while repeated episodes of flooding and drying slowed decomposition. Therefore, the ability of Chinese privet to increase decomposition rates in invaded sites may have been masked by moisture conditions in uninvaded sites which were more conducive to decomposition.

Soil nutrients. Soil pH of the study sites was acidic, as expected in the Piedmont physiographic region. While there was significantly lower soil pH in moderate and severely invaded classes (Figure 2), further studies are needed to determine if Chinese privet has a greater base cation demand and thereby lowered pH by depleting bases from the soil. However, Ehrenfeld et al. (2001) suggested that changes in pH due to invasive plants can be attributed to high rates of nitrification, increased rates of ammonification, or changes in litter composition.

Soil Ca and Mg levels were significantly lower for the moderately invaded class versus uninvaded and severely invaded classes (Figure 2). A possible reason that uninvaded soils were higher in Ca was the abundance of flowering dogwoods on those sites. These have been termed Ca "pumps" (Jenkins et al. 2007) which means that they make Ca more abundant in the litter layer because their leaves have a high Ca concentration. The inverse u-shape of mean soil Ca and Mg across the continuum of increasing Chinese privet (Figure 2) may be explained by depletion of soil Ca and Mg if it occurs with the establishment of Chinese privet or it may be due to site differences.

Soil K was significantly lower for moderately and severely invaded classes (Figure 2). It is possible that Chinese privet has high K requirements and depletes K from soil when it is established. For a more in-depth explanation of litterfall nutrient requirements and nutrient cycling through litterfall see Chapter 3.

Initial litter quality. Decomposition rates were influenced by litter quality measured by lignin and LCI. As expected, decomposition slowed as initial (t=0) lignin concentration increased across sites (Figure 10). Lignin is a recalcitrant material which is difficult for many decomposer organisms to degrade (Fisher and Binkley 2000). Although it was hypothesized and supported in this study that Chinese privet would have lower percent lignin than native species (Figure 15) and therefore decompose rapidly, there was not a significant linear regression between percent lignin and percent Chinese privet in the litter bags for the west Georgia study.

Another indicator of litter quality that had a significant relationship with decomposition was LCI. Typically, LCI is utilized to determine when litter reaches the humus stage, which has been suggested to occur at LCI of 0.7 (Melillo et al. 1982). There was a significant negative relationship between LCI at t=0 and % Chinese privet in litterbags (Figure 5). A larger LCI generally means material is more recalcitrant, therefore the hypothesis that Chinese privet decomposes more rapidly than native species was supported, because Chinese privet had lower LCI.

Final litter quality. Final litter quality was related to decomposition rates. Final N:P ratios had a positive linear relationship with k-values (Figure 6). More rapid k-values occurred on sites with N:P ratios around 12-14 which is the ideal ratio and, as the ratio narrowed, becoming N-limited, decomposition slowed. Fluctuations in N and P have often been explained by the processes of mineralization/immobilization, when a system becomes limited in a nutrient, immobilization rates are increased (Fisher and Binkley 2000).

The relationship between mean N-mineralization and k-values relate the influence of microbial activity on decomposition in this study (Figure 12). Decomposition was more rapid on plots that had lower N-mineralization rates, possibly because most of the N was immobilized. However, strong initial N-immobilization peaks (Figure 8) for most sites support the hypothesis of N limitation in these systems thereby promoting faster decomposition and release of nutrients. Similarly, Brinson (1977) observed strong mineralization/ immobilization peaks on low nutrient sites. However, there does not appear to be P limitation on the west Georgia sites because strong mineralization/ immobilization peaks are not evident (Figure 9).

Decomposition rates. There was a significant linear regression between percent Chinese privet in litterbags and k-values. Values of k increased as contribution of Chinese privet increased (Figure 11). However, rates of decomposition are closely related to N-mineralization rates (Figure 12) which has a positive relationship with the amount of Chinese privet on sites (Chapter 3). This suggests that the rate of C turnover increased with increased Chinese privet which had more rapid decomposition. Similarly, a study by Allison and Vitousek (2004) found that exotic species increased the rate of decomposition in comparison to native species, while Ashton et al. (2005) showed similar results in hardwood forests. Therefore, Chinese privet was similar to other non-native species that sped up decomposition rates.

Controlled Study

Individual species litter quality. There were measurable differences between litter quality of native species compared to Chinese privet. Chinese privet had a significantly lower percentage of the recalcitrant leaf components cellulose and lignin (Figures 14 and 15), which supports the hypothesis that Chinese privet would have litter that is easier for microorganisms to decompose. Low lignin:N ratios have been associated with rapid decomposition rates in some studies (Melillo et al. 1982). Chinese privet had a significantly lower lignin:N ratio compared to the other species in this study (Figure 17), indicating it would have more rapid decomposition. Furthermore, there was significantly greater N concentration in Chinese privet leaves (Figure 19), which is an advantage for microbial degradation of leaves in N limited systems. Since Chinese privet had a low C concentration (Figure 18) and high N concentration (Figure 19), the C:N ratio was closer to 30 (Figure 20), indicating the litter had balanced nutrient ratios favoring rapid microbial decomposition (Tate 2000).

Litter quality at t=0. The objective of this study was to maintain a mixture of native species while increasing Chinese privet contribution to decomposition bags in order to mimic natural systems as they become dominated by Chinese privet. Litter quality across different proportions of Chinese privet in decomposition bags reflected the expected trends of contributing individual species litter chemistry (Figures 14-21 and 23).

Initial litter quality differed significantly among proportions of Chinese privet in bags. There was a significantly lower C:N ratio for the 40% Chinese privet bags compared to the 0% Chinese privet bags (Figure 21). All the treatments had very wide C:N ratios (Figure 21) while N:P ratios were narrow for all treatments ranging from 6 to 7.5 (Figure 23), indicating microbial processes could be N limited. This is an instance of litter quality, especially N:P ratios, not being a good predictor of decomposition rates.

Despite the narrow C:N ratio for Chinese privet, there was a significant linear regression between C:N ratio and % Chinese privet in litterbags (Figure 22), indicating that C:N ratios narrow as more Chinese privet enters the system. Narrower ratios suggest that decomposition should, in turn, increase with increasing Chinese privet. Furthermore, this was supported by the negative regression of k-values and C:N ratios (Figure 32). This is an example of C:N ratios being a good predictor of decomposition rates.

Final litter quality. After 42 weeks in the field, there were significant differences in % of original mass remaining in relation to % Chinese privet in bags (Figure 24). There appears to be a threshold or inflection point near 30% Chinese privet in decomposition bags where the relationship between % original C (Figure 28) and mass remaining (Figure 29) flattens at 42 weeks. This threshold may represent the amount of Chinese privet required to significantly alter nutrient regimes and increase C turnover rates. Table 11 shows that the leaf litter in the forest floor of a site with a 100% Chinese privet understory composition will have a composition similar to controlled study treatment with 30% Chinese privet composition. Therefore, sites with 100% Chinese privet in the understory can be predicted to have decomposition rates similar to the control study treatment of 30% Chinese privet. The site with 100% Chinese privet in the understory had a yearly average of 24% Chinese privet in leaf litterfall (Table 11). Therefore, sites with greater than 30% Chinese privet in litterfall would likely have a more dense subcanopy of Chinese privet than in this study, with only a few mature overstory native trees contributing to the litterfall. Regeneration would be dominated by Chinese privet (Brantley 2008) and decomposition processes would be altered.

Rates of decomposition. There was a strong (R^2=0.94) positive linear regression relationship among k-values and % Chinese privet in litterbags (Figure 30). Decomposition rates were also significantly different between the different proportions of

Chinese privet in litterbags (Figure 31). Chinese privet increased decomposition rates in comparison to the bags with only native litter (Figure 31). These results complement those of Hobbie (2000), who also observed faster decomposition and accelerated N- and C- cycling in low lignin invasive plants. Therefore, the low lignin of the Chinese privet leaves and rapid decomposition support the findings of more rapid cycling of C and N in Hobbie (2000). It is also important to note that Chinese privet leaves have different physical properties and are very tender compared to native leaves (personal observation), which may promote their rapid physical breakdown. Dascanio et al. (1994) observed similar increases in decomposition rates as glossy privet (*Ligustrum lucidum*) increased in abundance in Argentina.

Turnover rates can be estimated by taking the reciprocal of the k-value. For this study, turnover rates ranged from 6.8 years for bags with 0% Chinese privet to 2.59 years for bags with 50% Chinese privet. Implications for more rapid litter turnover reflect a decline in a riparian forest’s ability to sequester C.

CONCLUSION

Chinese privet has the potential to alter decomposition in native ecosystems across the Southeastern U.S. In this research, Chinese privet influenced decomposition processes in two field studies with increased rates of decomposition for bags with increased percentage of Chinese privet. There is the possibility Chinese privet may have a greater influence as the number of Chinese privet stems increase and overstory species die. However, data from the controlled study indicated Chinese privet litterfall of approximately 30% of total litterfall would increase C turnover rates in comparison to uninvaded sites. Increased frequency of damp conditions in uninvaded sites compared to moderately or severely invaded sites (Figure 4) had increased decomposition rates and masked the influence Chinese privet in the west Georgia study. Therefore, Chinese privet has the capability to further increase decomposition rates if it becomes present in these damp, uninvaded sites. Also, Chinese privet leaves are senesced in late winter and early spring rather than in the fall, which provides microsite conditions different that those experienced by the native species with peak litterfall in autumn.

If observed turnover time (1/k) changes from 6.8 years for sites with 0% Chinese privet in the controlled study to 3.14 years for 30% Chinese privet in bags, then forest floor dynamics change. For example, the mean standing forest floor mass for the uninvaded sites was 567 g m^{-2} and C content is 248 g m^{-2} (Chapter 3). As Chinese privet increases its contribution to the forest floor, it exerts a greater influence on the turnover rate and the steady state floor would likely decrease in both mass and C content.

The hypothesis that Chinese privet will increase decomposition rates was accepted for both the west Georgia study (Figure 11) and controlled study (Figure 30). The controlled study had greater mass of Chinese privet in bags and consequently had more rapid decomposition rates, especially for 50% Chinese privet treatment compared to 0% Chinese privet. Greater than 30% Chinese privet in decomposition bags represent a site with 100% Chinese privet in the midstory and few native overstory species. The hypothesis that Chinese privet would have higher litter quality than coexisting native species was accepted. Chinese privet had lower % lignin, narrower lignin:N, C:N, and higher N concentrations compared to the native species studied. It is possible that the lower % lignin and tender leaves of Chinese privet drive their rapid breakdown and decomposition. Therefore, litter quality may improve as Chinese privet becomes more dominant and increase nutrient cycling rates.

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Table 1. One-way ANOVA results for soil characteristics compared between all sites, F, p-values, and degrees of freedom (df) listed.

Variable	F	p	df
pH	20.7	<0.0001	2, 61
K (kg/ ha)	9.10	0.0003	2, 61
Ca (kg/ ha)	4.52	0.015	2, 61
Mg (kg/ha)	6.16	0.0037	2, 61

Table 2. Bulk density, mean forest floor temperature and soil temperature for classes of Chinese privet in west Georgia. Means presented with standard error in parentheses. Letters represent significant differences at p<0.05 by Tukey's post hoc test.

variable	Chinese privet class			F	df
	uninvaded	moderately Invaded	severely invaded		
bulk density (Mg/m^3)	1.14 (0.02)^a	1.10 (0.007)^a	1.0 (0.01)^b	34	2, 30
forest floor temperature (^{o}C)	16.5 (0.14)	16.8 (0.12)	16.6 (0.14)	1.6	2, 14
soil temperature (^{o}C)	16.4 (0.12)^b	16.8 (0.10)^a	16.8 (0.07)^a	0.03	2, 14

Table 3. One-way ANOVA results for moisture classification compared among Chinese privet classes, F, p-values, and degrees of freedom (df) listed.

moisture class	F	p	df
dry	1.18	0.36	2, 7
damp	10.7	0.007	2, 7
wet	0.79	0.49	2, 7
flooded	0.39	0.69	2, 7

Table 4. Initial quality of litter in litterbags utilized in the west Georgia study. Means (n=2) are presented with standard error in parentheses.

Class	Percent privet in decomposition bag	C:N	N:P	C:P	Lignin:N	% lignin
uninvaded	0	49.4 (0.2)	6.4 (0.3)	318.4 (12.4)	15.0 (0.2)	14.0 (0.001)
uninvaded	0	46.4 (0.7)	4.6 (0.6)	212.5 (29.7)	13.7 (0.9)	13.3 (0.9)
uninvaded	0	53.7 (4.7)	4.2 (0.3)	226.2 (29.7)	18.1 (0.6)	15.8 (1.0)
moderately invaded	2.7	46.3 (2.5)	6.4 (0.1)	298.8 (17.8)	16.5 (0.9)	15.8 (0.2)
severely invaded	3.56	42.4 (3.0)	6.7 (0.7)	280.9 (7.9)	15.7 (0.01)	17.0 (0.8)
severely invaded	3.7	52.3 (2.5)	5.7 (0.3)	299.3 (1.0)	18.0 (1.4)	16.2 (0.4)
moderately invaded	4.7	68.3 (0.03)	5.7 (0.5)	403.9 (6.1)	19.2 (0.3)	13.5 (0.4)
moderately invaded	5.65	40.5 (1.7)	6.4 (0.2)	260.8 (5.1)	15.4 (0.1)	18.2 (1.0)
severely invaded	5.9	47.8 (0.1)	5.5 (0.3)	262.8 (14.6)	15.0 (0.01)	14.6 (0.2)
severely invaded	6.05	50.7 (4.9)	7.3 (1.1)	364.6 (19.5)	18.2 (1.5)	16.9 (0.1)
moderately invaded	6.35	48.2 (3.6)	5.6 (0.5)	266.1 (1.3)	15.6 (0.8)	15.4 (0.5)
severely invaded	8.05	64.3 (0.03)	5.7 (0.5)	365.8 (32.46)	19.2 (0.3)	13.5 (0.4)
severely invaded	8.3	72.6 (3.5)	5.2 (0.2)	377.0 (34.0)	12.0 (0.7)	13.1 (0.1)
severely invaded	10.85	50.5 (0.7)	6.4 (0.2)	321.2 (4.2)	16.1 (1.0)	14.6 (1.2
severely invaded	13.7	43.0 (1.6)	7.6 (0.4)	326.1 (5.6)	13.8 (1.4)	15.1 (1.0)
severely invaded	17.1	36.9 (7.2)	7.8 (0.8)	280.6 (26.3)	15.6 (0.8)	15.4 (0.8)

Table 5. Final % mass, C, N, P remaining at 72 weeks. C:N, N:P ratios displayed by percent of Chinese privet in litterbag. Means (n=2) presented with standard error in parentheses.

Class	Percent privet in litterbag	Mass	C	N	P	C:N	N:P	C:P	k
		--------------------------------%---------------------------							
uninvaded	0	16.7 (4.7)	59.5 (23.5)	64.8 (20.6)	62.2 (22.0)	31.7 (0.25)	7.7 (0.03)	243 (2.9	0.26 (0.005)
uninvaded	0	6.93 (3.7)	53.5 (26.8)	55.1 (26.0)	53.3 (27.0)	33.2 (2.0)	6.4 (0.30)	212 (2.9	0.36 (0.025)
uninvaded	0	18.2 (4.4)	60.1 (23.8)	67.0 (19.2)	60.8 (22.8)	30.8 (0.80)	6.9 (0.63)	211 (14)	0.32 (0.0005)
moderately invaded	2.7	37.1 (2.7)	70.0 (17.5)	77.6 (16.7)	77.6 (16.2	28.8 (1.5)	7.5 (0.47)	216 (25)	0.19 (0.0003)
severely invaded	3.56	22.3 (2.4)	59.9 (23.3)	63.7 (19.2)	65.9 (19.8)	30.5 (0.65)	5.8 (1.1)	176 (28)	0.26 (0.003)
severely invaded	3.7	11.1 (2.3)	55.9 (25.5)	60.2 (23.1)	56.8 (25.0)	31.2 (2.9	8.5 (0.07)	266 (27)	0.36 (0.007)
moderately invaded	4.7	6.9 (0.08)	53.4 (26.9)	56.5 (25.1)	55.4 (25.8)	36.5 (2.1)	7.0 (0.09)	256 (11)	0.33 (0.006)
moderately invaded	5.65	16.9 (4.0)	59.9 (23.5)	66.0 (20.3)	59.1 (23.7)	26.2 (4.1)	10.9 (2.3)	277 (14)	0.34 (0.005)

class	Percent privet in litterbag	Mass	C	N	P	C:N	N:P	C:P	k
		-------------------------------%---------------------------							
severely invaded	5.9	24.8 (1.1)	64.5 (20.6)	70.5 (17.1)	66.4 (19.4)	33.7 (0.83)	6.8 (0.15)	230 (0.76)	0.31 (0.0008)
severely invaded	6.05	23.6 (2.4)	62.8 (21.4)	70.9 (17.0)	62.3 (21.8)	31.4 (0.77)	12.2 (0.84)	384 (36)	0.34 (0.005)
moderately invaded	6.35	14.2 (2.8)	57.8 (24.3)	70.0 (17.3)	58.7 (23.8)	19.0 (1.9)	12.9 (1.9)	241 13)	0.33 (0.007)
severely invaded	8.05	12.3 (4.5)	56.9 (24.9)	66.9 (19.6)	60.9 (23.0)	25.8 (2.4)	9.7 (2.5)	245 (42)	0.26 (0.015)
severely invaded	8.3	16.8 (14.4)	59.0 (24.5)	70.4 (22.3)	64.2 (23.2)	33.0 (0.15)	9.0 (1.4)	296 (46)	0.30 (0.025)
severely invaded	10.85	10.5 (2.0)	55.6 (25.6)	58.9 (23.8)	55.6 (25.6)	32.4 (0.51)	9.9 (1.6)	319 (46)	0.43 (0.007)
severely invaded	13.7	25.5 (3.8)	64.2 (20.8)	71.7 (16.8)	66.5 (19.6)	28.5 (0.47)	10 (0.48)	284 (18)	0.30 (0.009)
severely invaded	17.1	14.7 (0.68)	58. 5 (24.1)	64.1 (21.1)	58.3 (24.1)	25.4 (2.7)	11.5 (1.3)	286 (1.2)	0.38 (0.012)

Table 6. One-way ANOVA results for litter quality of species used in the controlled study, F, p-values, and degrees of freedom (df) listed.

Variable	F	p	df
Carbon (mg/kg)	49.43	<0.0001	5, 18
Nitrogen (mg/kg)	117.7	<0.0001	5, 18
% Cellulose	389.3	<0.0001	5, 18
% Lignin	113.4	<0.0001	5, 18
LCI	32.24	0.0001	5, 18
C:N	337.1	<0.0001	5, 18
Lignin:N	94.62	<0.0001	5, 18

Table 7. Initial leaf litter quality for controlled study with different percent Chinese privet in litterbags. Means (n=2) presented with standard error in parentheses.

Percent privet in litterbag	C:N	N:P	LCI	Lignin:N	% lignin	k
0	55.8 (3.4)	6.3 (0.4)	0.5 (0.001)	17.6 (0.2)	14.7 (0.8)	0.14 (0.009)
10	49.7 (0.3)	5.9 (0.5)	0.5 (0.02)	17.1 (1.3)	15.6 (1.2)	0.22 (0.023)
20	50.7 (1.3)	6.4 (0.2)	0.5 (0.008)	15.4 (0.2)	14.2 (0.1)	0.27 (0.019)
30	46.0 (2.8)	7.2 (0.1)	0.5 (0.02)	14.1 (2.1)	14.0 (1.0)	0.32 (0.013)
40	42.9 (0.5)	7.4 (0.4)	0.5 (0.03)	13.7 (1.8)	14.9 (2.2)	0.33 (0.001)
50	47.4 (1.0)	6.6 (0.3)	0.5 (0.001)	12.8 (0.04)	12.3 (0.4)	0.39 (0.003)

Table 8. One-way ANOVA results for treatments of litter quality at t=0 for controlled study, F, p-values, and degrees of freedom (df) listed.

Variable	F	p	df
C:N	5.31	0.03	5, 11
N:P	2.65	0.13	5, 11

Table 9. One-way ANOVA results between treatment for litter quality at time 42 weeks for controlled study, F, p-values, and degrees of freedom (df) listed.

Variable	F	p	df
% C remaining	12.7	0.007	5, 10
% P remaining	16.1	0.004	5, 10
% N remaining	7.6	0.02	5, 10
% mass remaining	11.5	0.009	5, 10

Table 10. Percent of original mass, carbon, nitrogen and phosphorus remaining at week 42 for controlled study. C:N and N:P ratios also given. Means (n=2) presented with standard error in parentheses.

Percent privet in litterbag	Mass	C	N	P	C:N	N:P
	-------------------------------%	--				
0*	61.8 (.)	61.3 (.)	99.8 (.)	69.2 (.)	34.2 (.)	9.13 (.)
10	41.1 (3.2)	42.2 (2.7)	61.1 (6.7)	36.6 (2.2)	34.5 (1.6)	9.85 (0.5)
20	38.0 (1.1)	38.5 (0.3)	63.3 (0.8)	40.2 (0.8)	31.0 (0.7)	10.0 (0.1)
30	26.9 (5.4)	28.6 (5.2)	39.7 (8.9)	26.3 (6.0)	33.3 (1.5)	10.9 (0.04)
40	30.5 (2.9)	31.8 (2.3)	47.1 (7.3)	30.5 (0.7)	29.3 (2.4)	11.4 (1.5)
50	25.8 (1.2)	26.9 (1.3)	43.6 (4.6)	27.7 (2.3)	29.4 (1.7)	10.4 (0.2)

*- indicates only one bag was remaining for this treatment and so no standard error was calculated

Table 11. The mean % that Chinese privet contributed to leaf litter across all sites in west Georgia across a range of Chinese privet stems in the understory and the classes.

% Chinese privet in understory	Chinese privet class	mean % contribution of Chinese privet to litterfall
0	Uninvaded	0 (0)
0	Uninvaded	0 (0)
0	Uninvaded	0 (0)
29	Moderately invaded	3.6 (1.1)
35	Moderately invaded	3.7 (0.8)
48	Moderately invaded	16.4 (2.6)
65	Moderately invaded	13.1 (2.1)
76	Moderately invaded	15.0 (2.2)
82	Severely invaded	9.2 (1.2)
86	Severely invaded	15.9 (2.5)
88	Severely invaded	15.5 (2.3)
91	Severely invaded	7.8 (1.6)
92	Severely invaded	18.9 (1.2)
98	Severely invaded	29.9 (2.1)
99	Severely invaded	17.3 (1.9)
100	Severely invaded	23.9 (2.5)

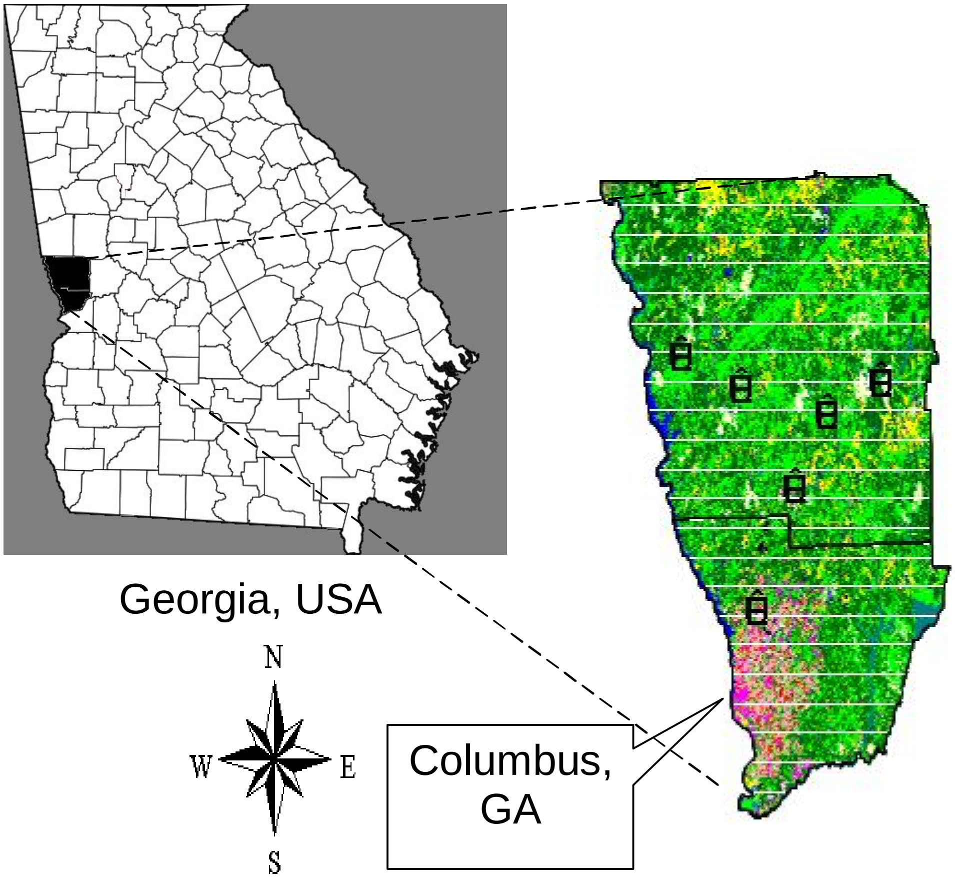


Figure 1. Map showing the location of the six study site watersheds in Muscogee and Harris counties, west Georgia. Chinese privet in understory ranged from 0 for uninvaded sites to 100% for severely invaded sites

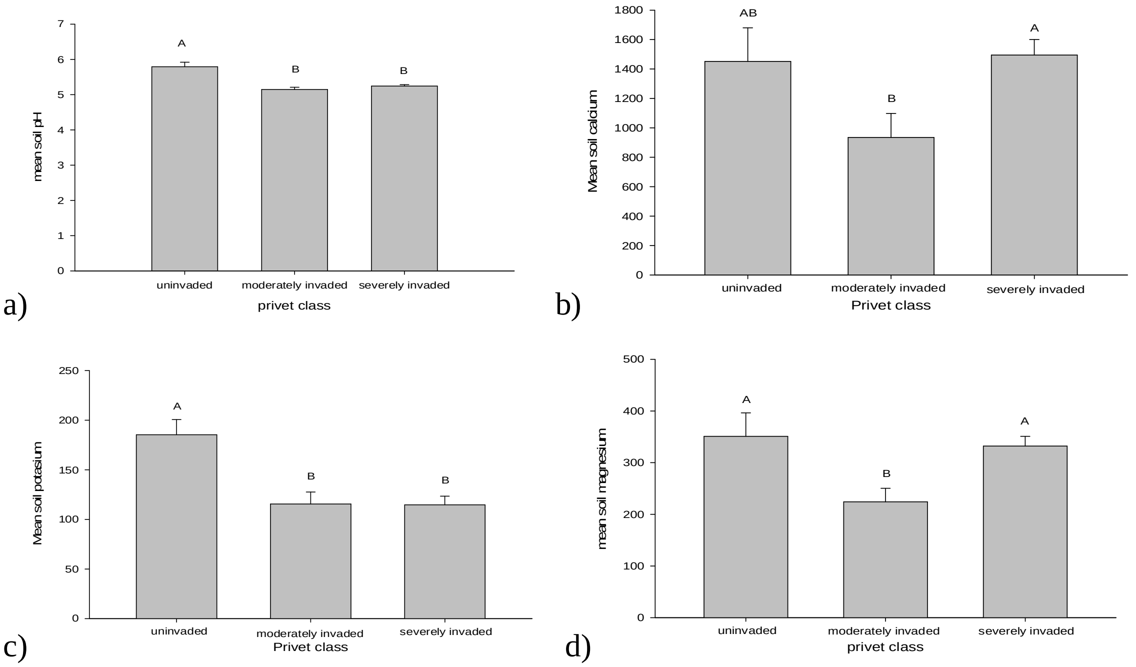


Figure 2. Mean soil a) pH, b) mean exchangeable soil calcium (kg/ha) c) mean exchangeable soil potassium (kg/ha), and d) mean exchangeable soil magnesium (kg/ha) separated by privet categories for sites in west Georgia floodplains. Error bars represent standard error. Letters represent significant differences at $p<0.05$ by Tukey's post hoc test.

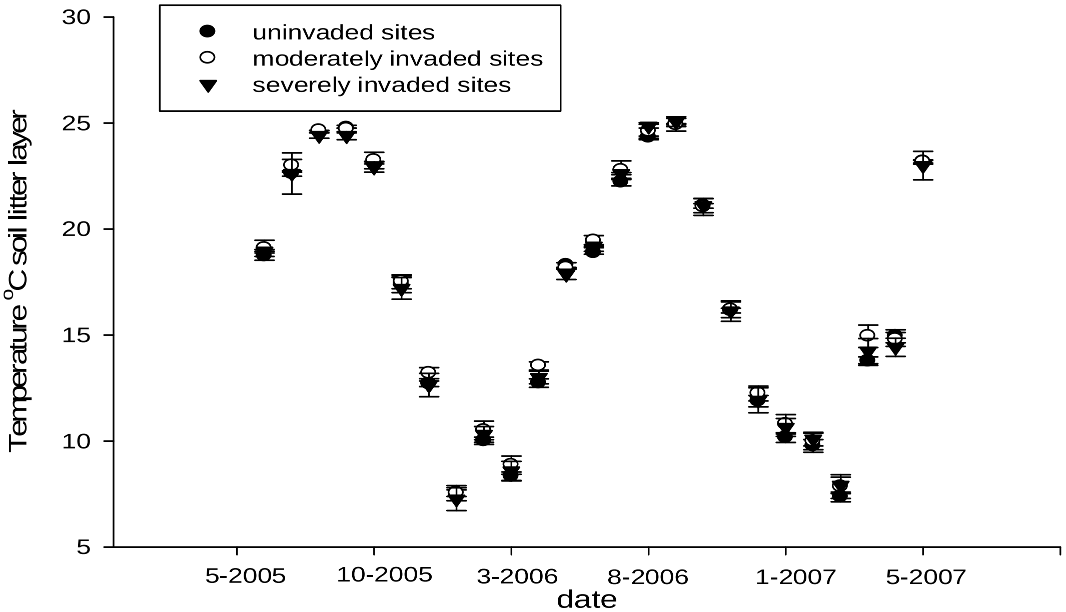


Figure 3. Mean monthly temperatures (°C) in the litter layer for each class in west Georgia. There were no significant differences among classes.

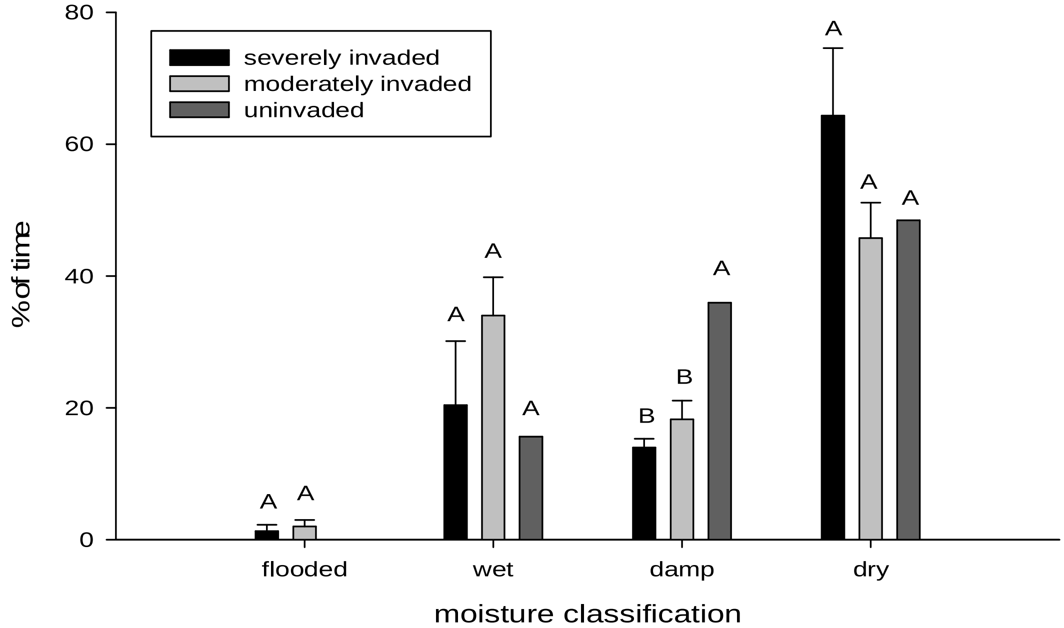


Figure 4. Mean percent of readings in each moisture classification for Chinese privet classes in west Georgia. Error bars represent standard error. Letters represent significant differences at p<0.05 by Tukey's post hoc test.

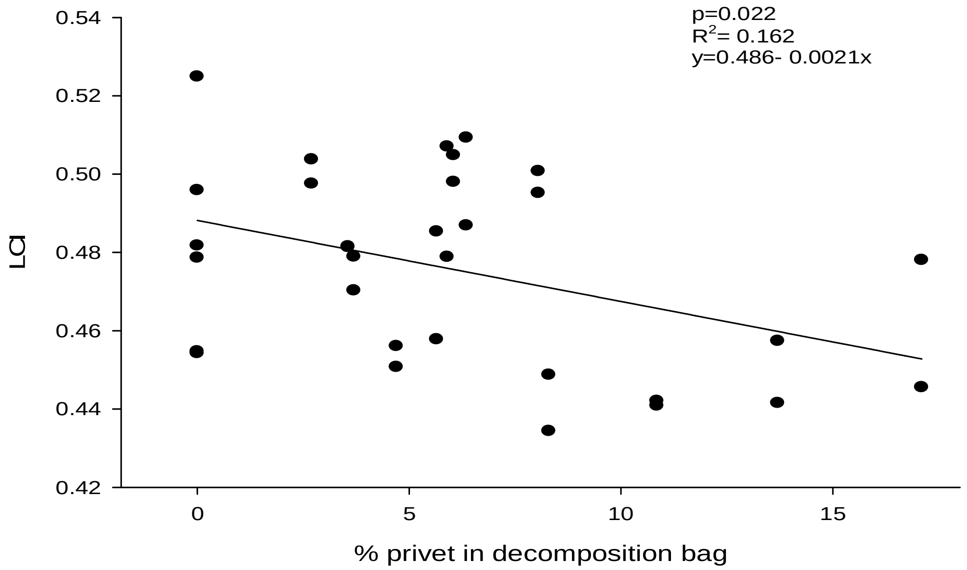


Figure 5. Linear regression relationship at time= 0 between lignin cellulose index (LCI) and % Chinese privet composition in decomposition bags across sites in west Georgia.

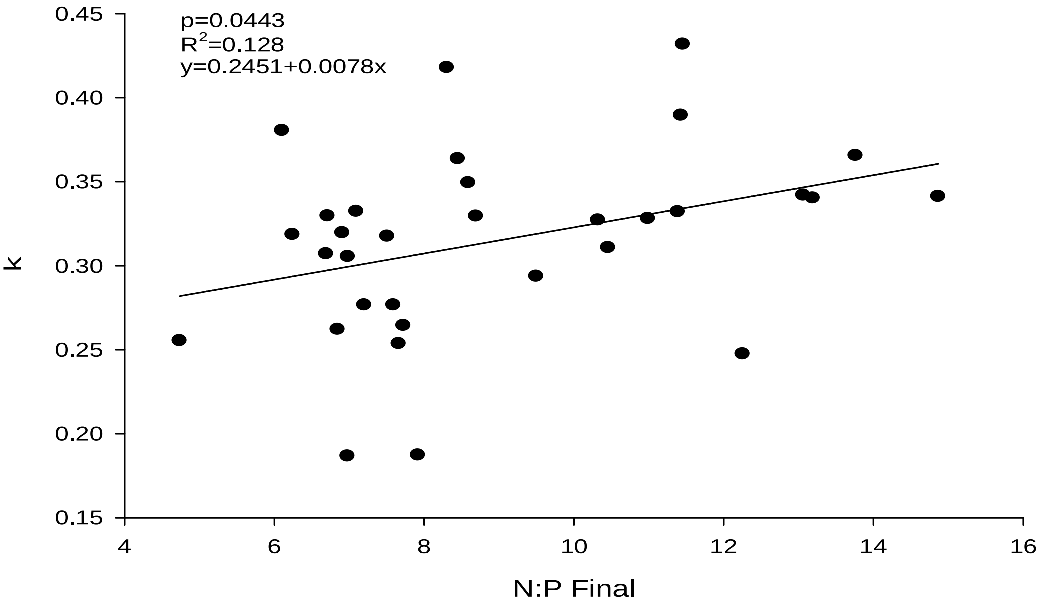


Figure 6. Linear regression relationship between decomposition rates (k) and N:P ratios at week 72, the final collection, for sites in west Georgia with different levels of Chinese privet invasion.

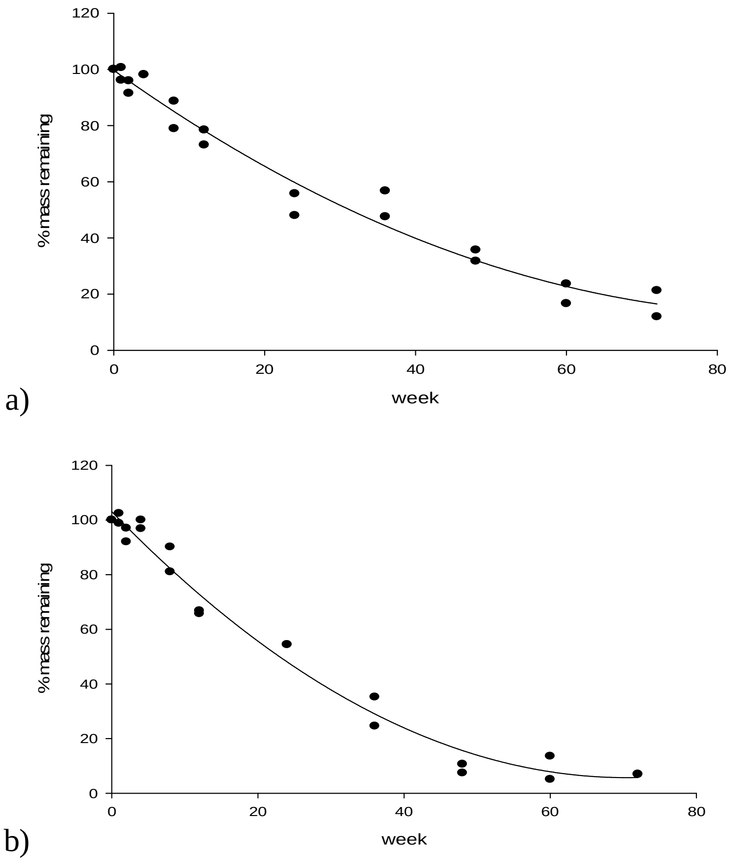


Figure 7. Representative graph of mass loss curve over time for sites in west Georgia across a range of Chinese privet in the understory. This graph depicts data from a) one of the uninvaded plots with 0% Chinese privet in decomposition bag and b) 4.7% Chinese privet in decomposition bag. Each dot represents a decomposition bag.

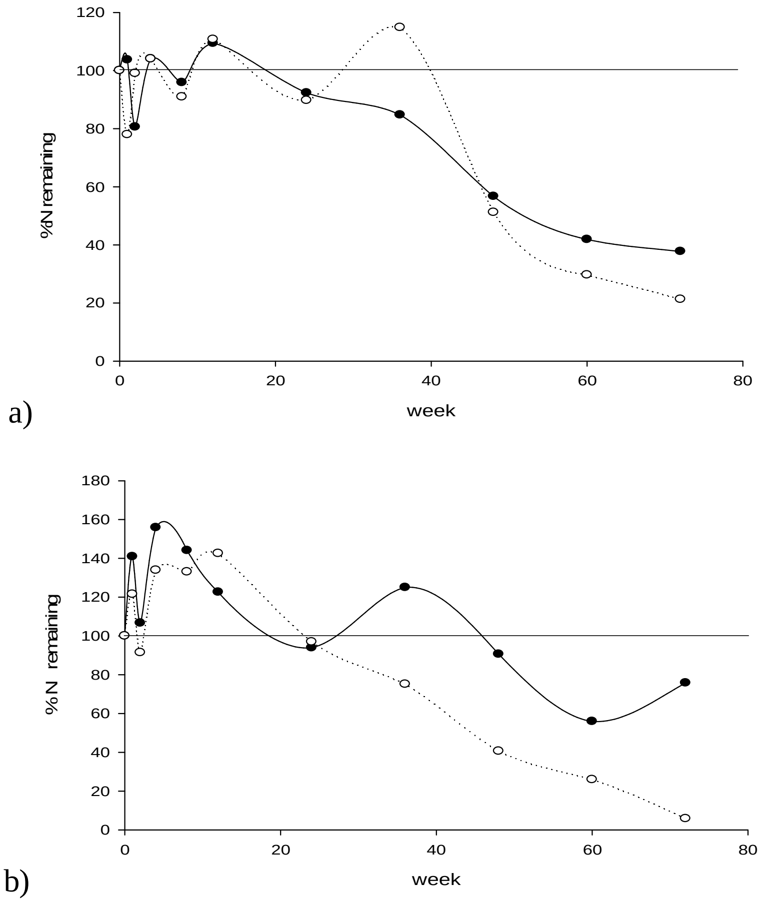


Figure 8. Representative graph of % N remaining over time for a site in west Georgia. Each line represents a set of decomposition bags from a) one of the uninvaded plots with 0% Chinese privet in decomposition bag and b) a severely invaded site with 8.3% Chinese privet in decomposition bag.

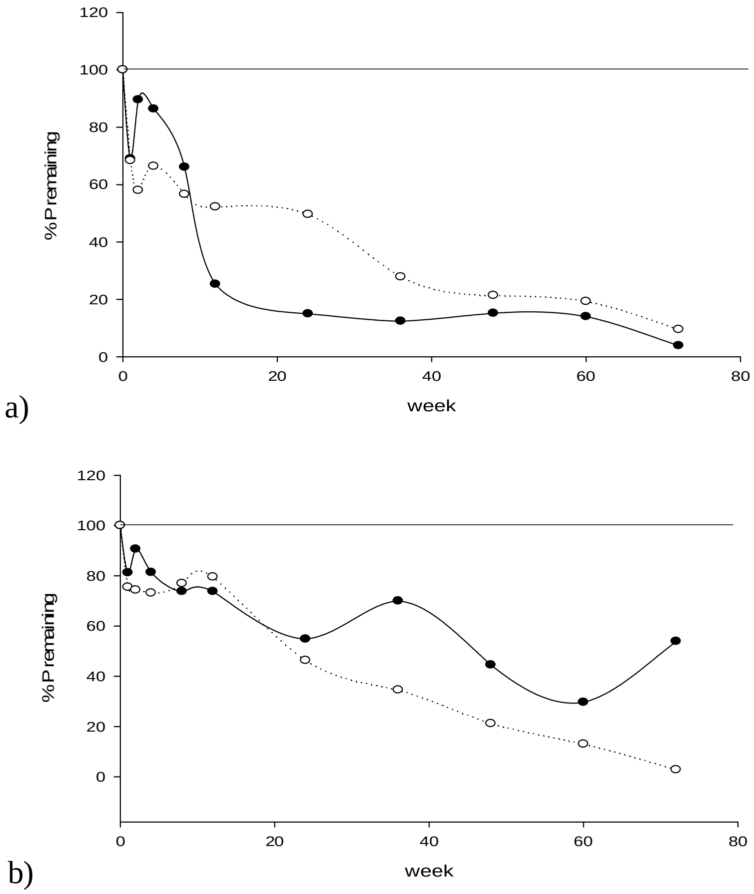


Figure 9. Representative graph of % P remaining over time for a sites in west Georgia. Each line represents a group of decomposition bags from a) one of the uninvaded plots with 0% Chinese privet in decomposition bag and b) a severely invaded site with 8.3% Chinese privet in decomposition bag.

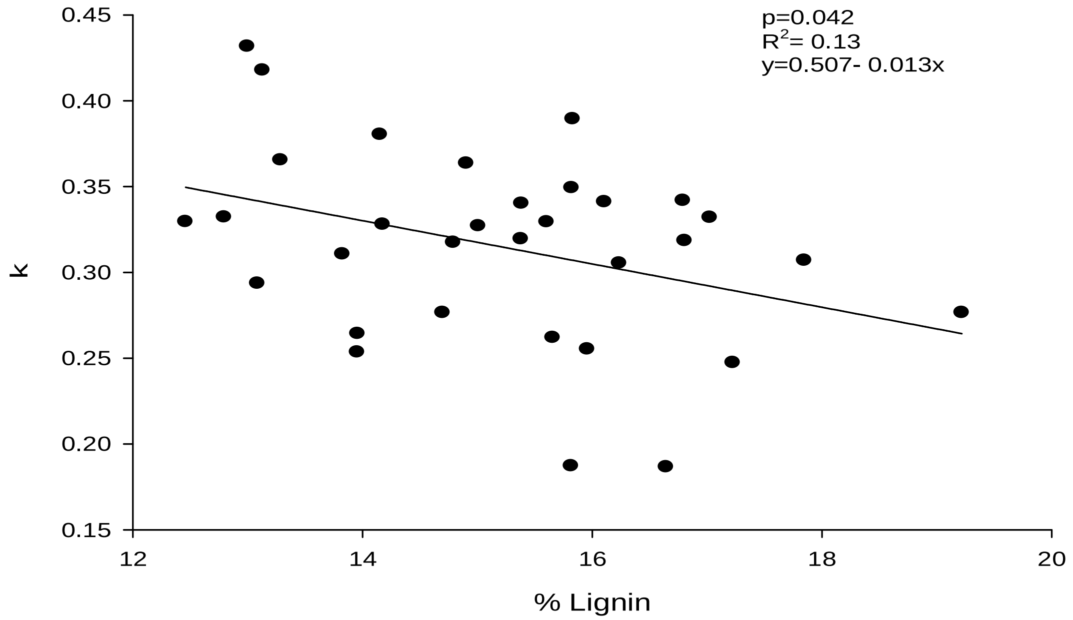


Figure 10. Linear regression between decomposition rates (k) and % lignin at time=0 for sites in west Georgia.

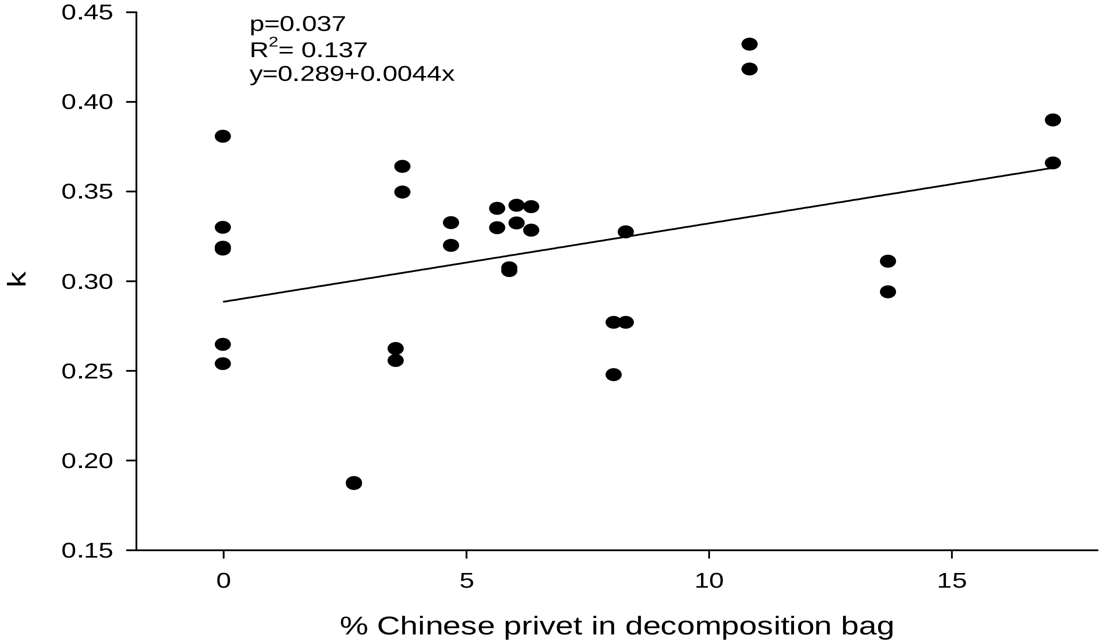


Figure 11. Linear regression between decomposition rates (k) and % Chinese privet in decomposition bag composition for sites in west Georgia.

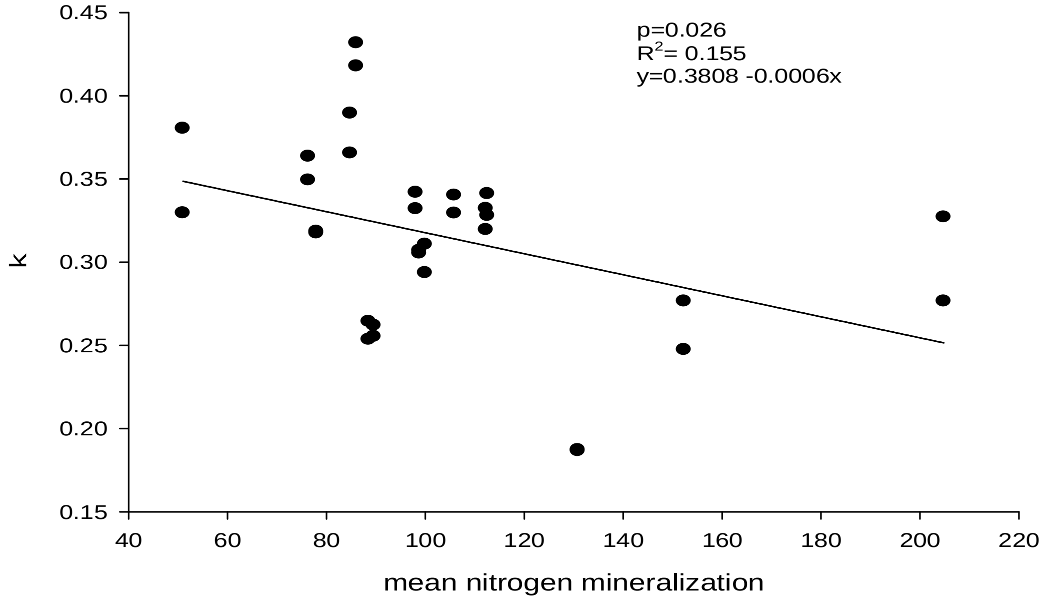


Figure 12. Linear regression between decomposition rates (k) and mean nitrogen mineralized for sites in west Georgia.

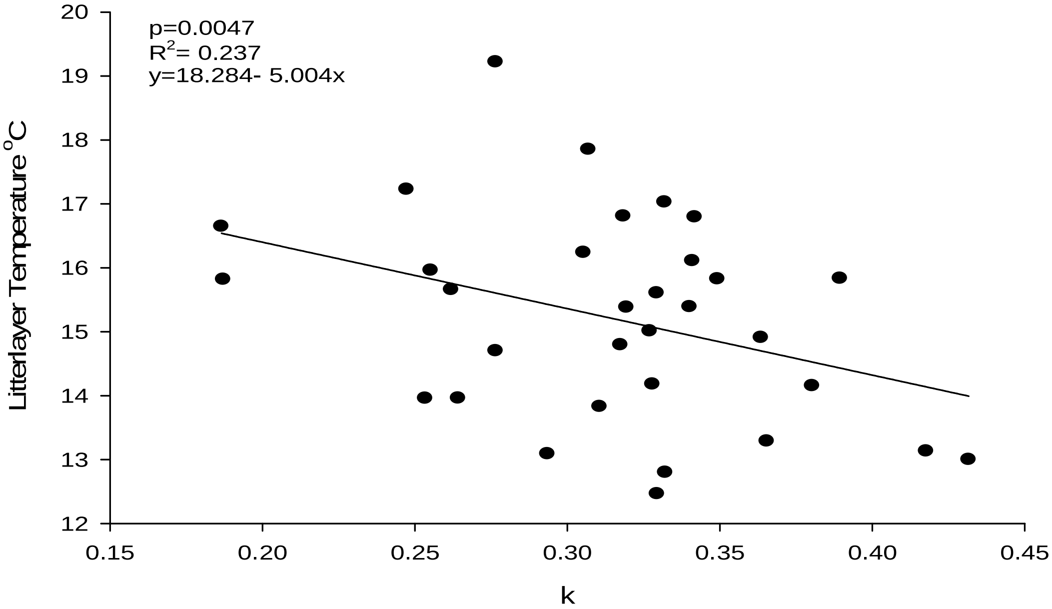


Figure 13. Linear regression relationship between mean litter layer temperature (^{o}C) and decomposition rates (k) across privet sites in west Georgia.

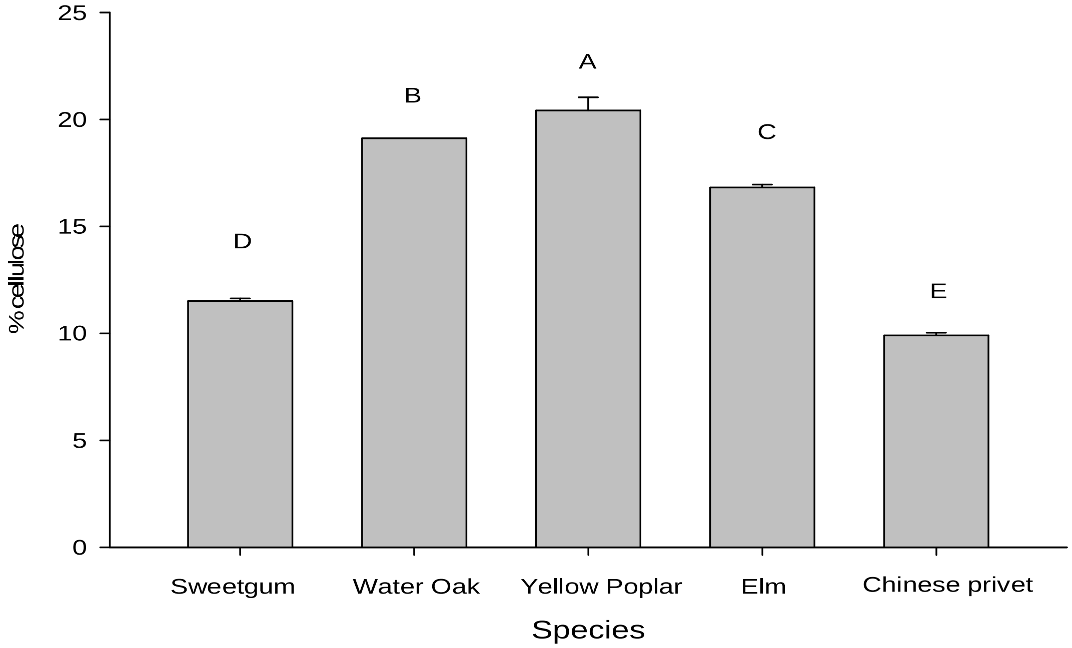


Figure 14. Percent cellulose contained in the five species used in the controlled study. Error bars represent standard error. Letters represent significant differences at p<0.05 by Tukey's post hoc test.

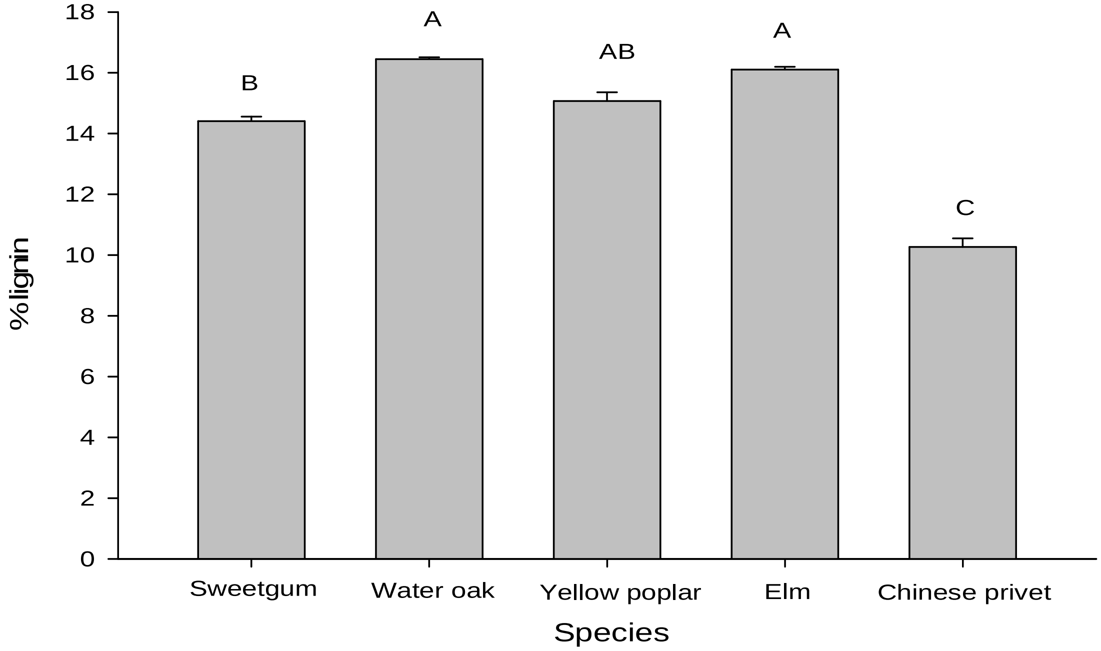


Figure 15. Percent lignin contained in the five species used in the controlled study. Error bars represent standard error. Letters represent significant differences at p<0.05 by Tukey's post hoc test.

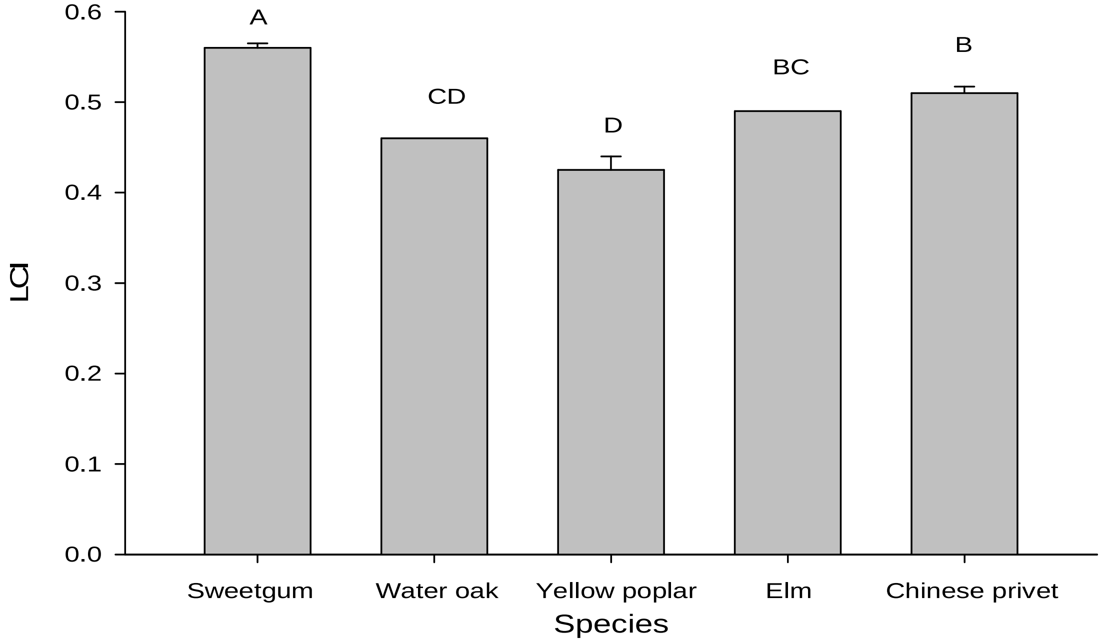


Figure 16. Lignin cellulose index (LCI) for the five species used in the controlled study. Error bars represent standard error. Letters represent significant differences at p<0.05 by Tukey's post hoc test.

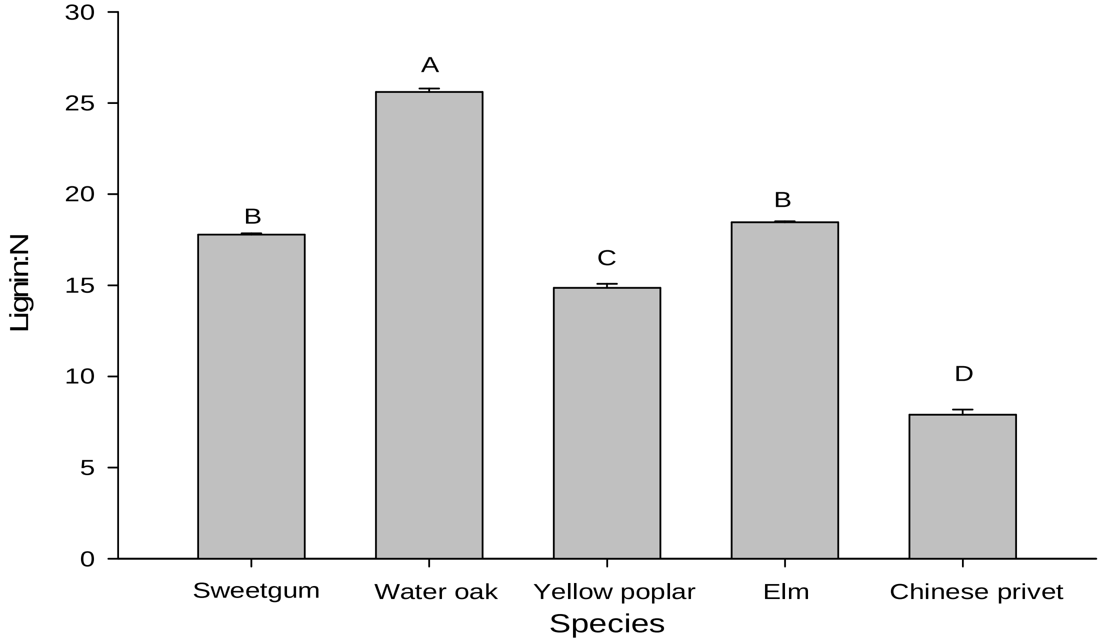


Figure 17. Lignin:N ratio for time= 0 leaves of the five species used in the controlled study. Error bars represent standard error. Letters represent significant differences at p<0.05 by Tukey's post hoc test.

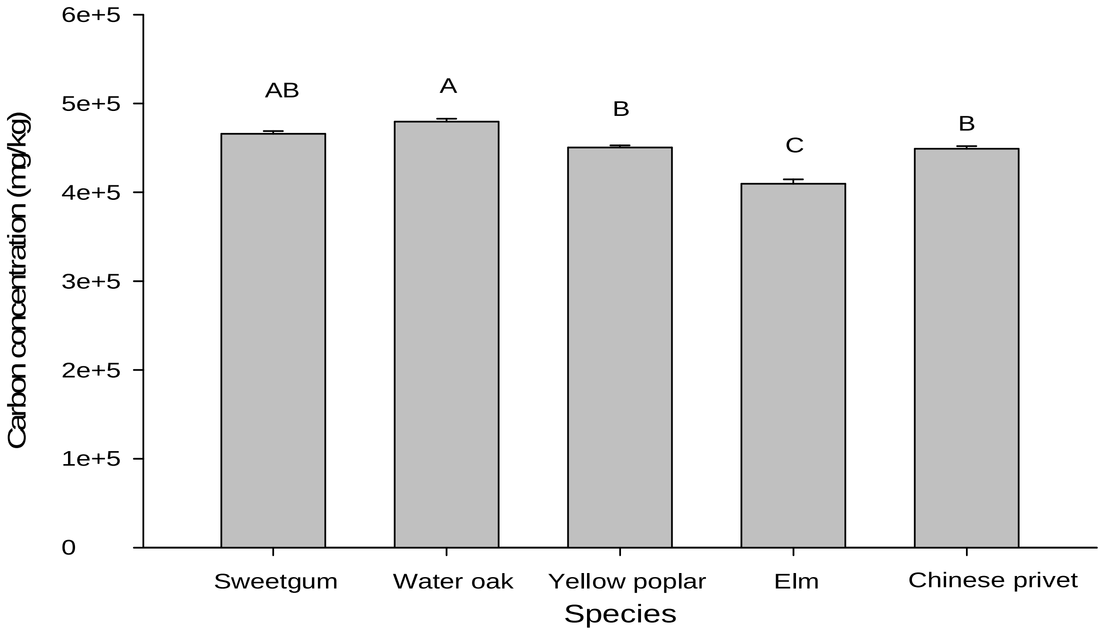


Figure 18. Carbon concentration in the five species used in the controlled study. Error bars represent standard error. Letters represent significant differences at $p<0.05$ by Tukey's post hoc test.

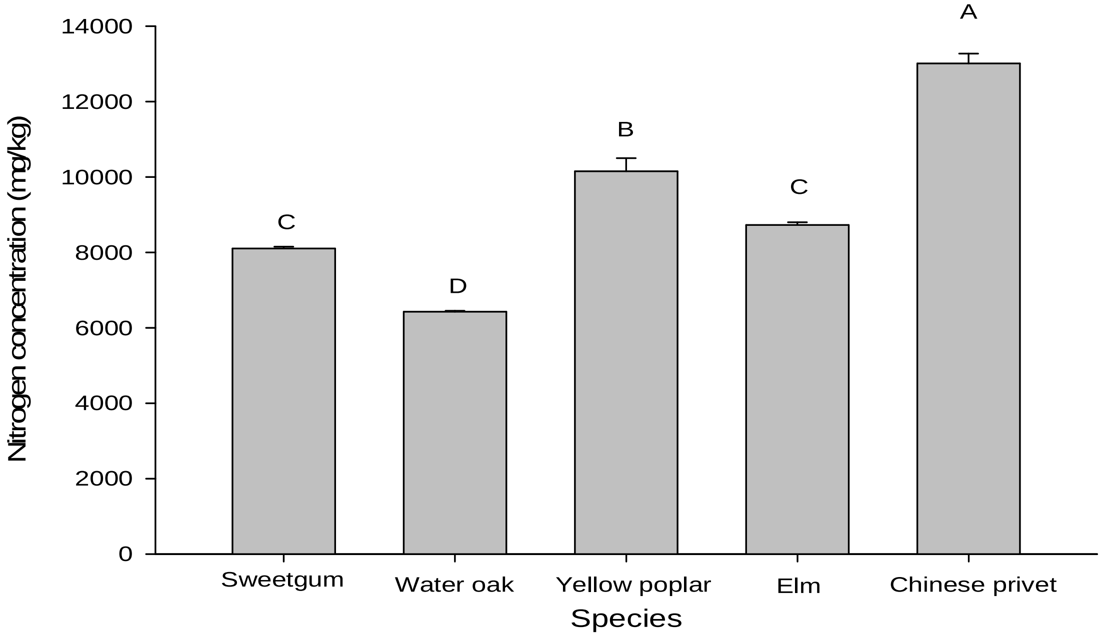


Figure 19. Nitrogen concentration in the five species used in the controlled study. Error bars represent standard error. Letters represent significant differences at $p<0.05$ by Tukey's post hoc test.

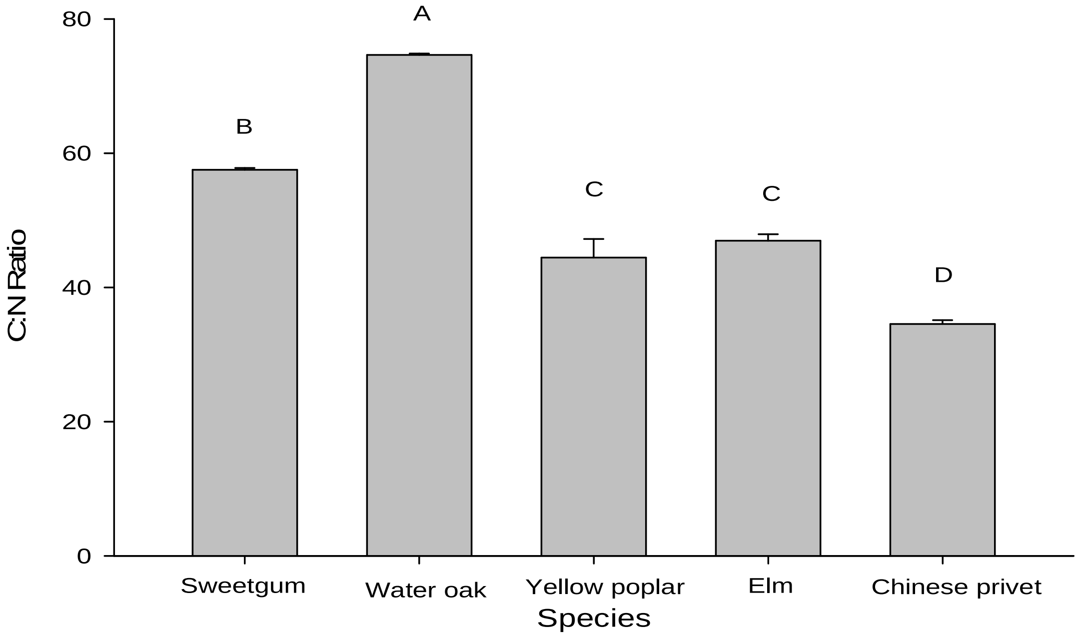


Figure 20. C:N ratio for time= 0 leaf composition in the five species used in the controlled study. Error bars represent standard error. Letters represent significant differences at p<0.05 by Tukey's post hoc test.

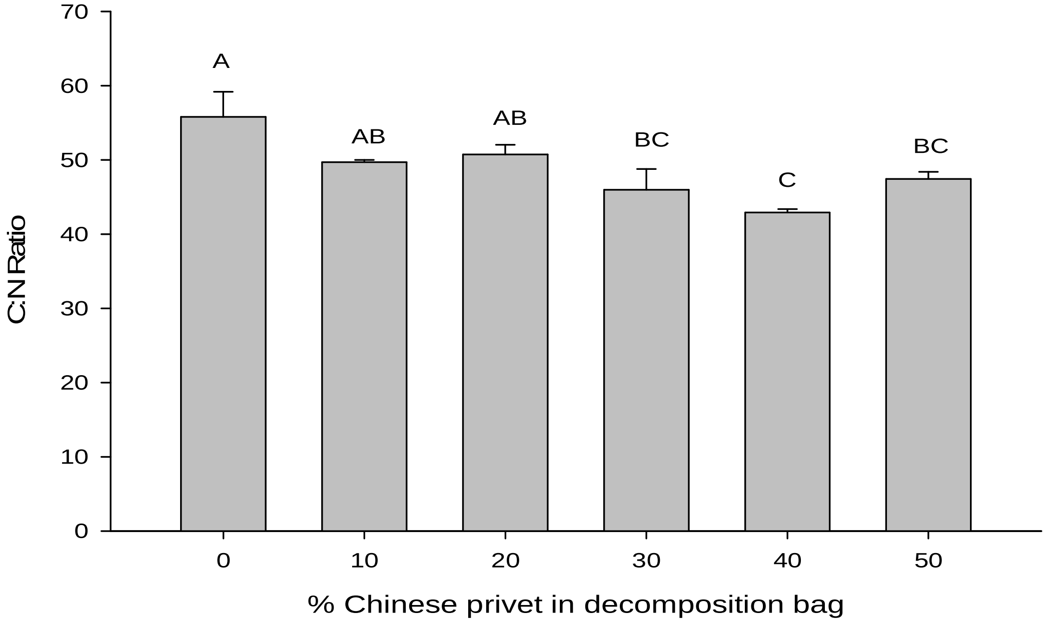


Figure 21. C:N ratio for time= 0 decomposition bags in the controlled study. Error bars represent standard error. Letters represent significant differences at p<0.05 by Tukey's post hoc test.

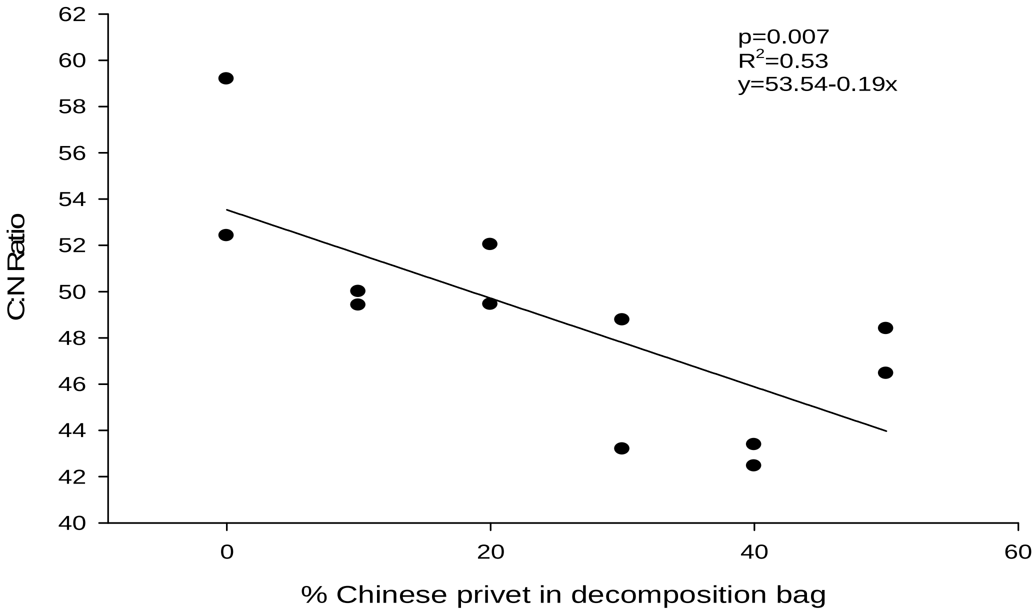


Figure 22. Significant linear regression between C:N ratio and % Chinese privet at time= 0 in decomposition bags in the controlled study.

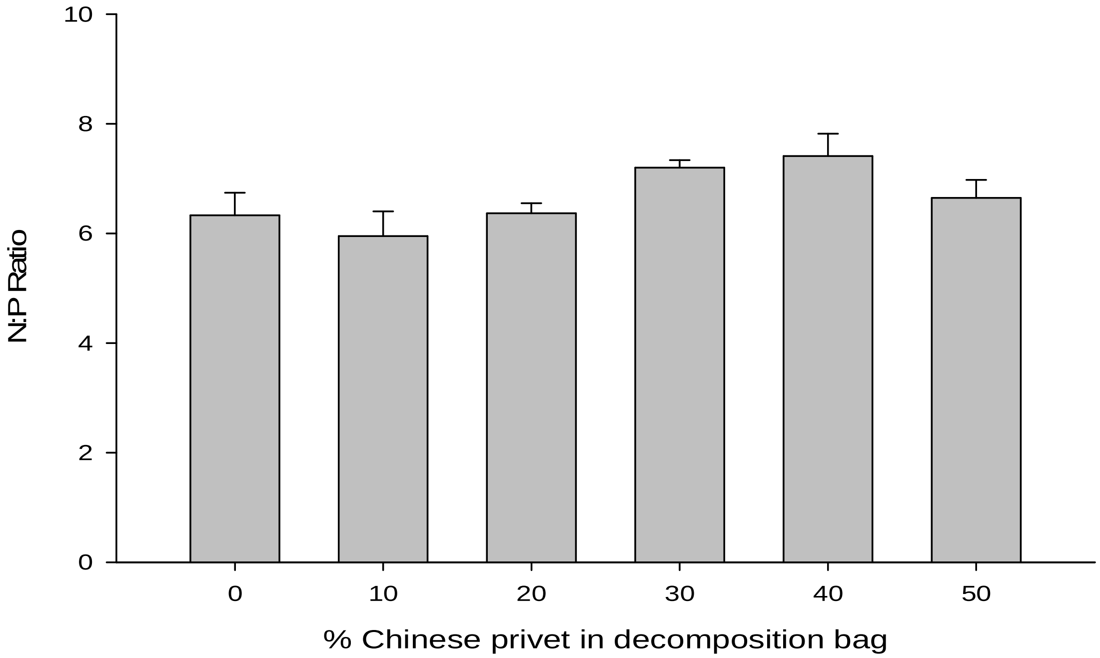


Figure 23. N:P ratio for time= 0 decomposition bags in the controlled study. Error bars represent standard error.

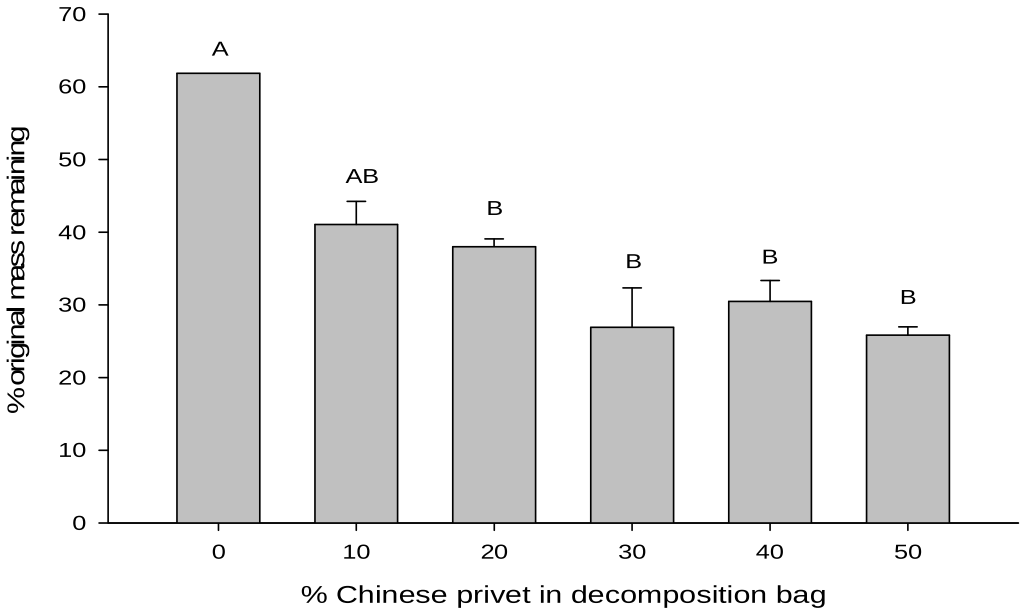


Figure 24. Percent of original mass remaining at week 42 for decomposition bags in the controlled study. Error bars represent standard error. Letters represent significant differences at p<0.05 by Tukey's post hoc test.

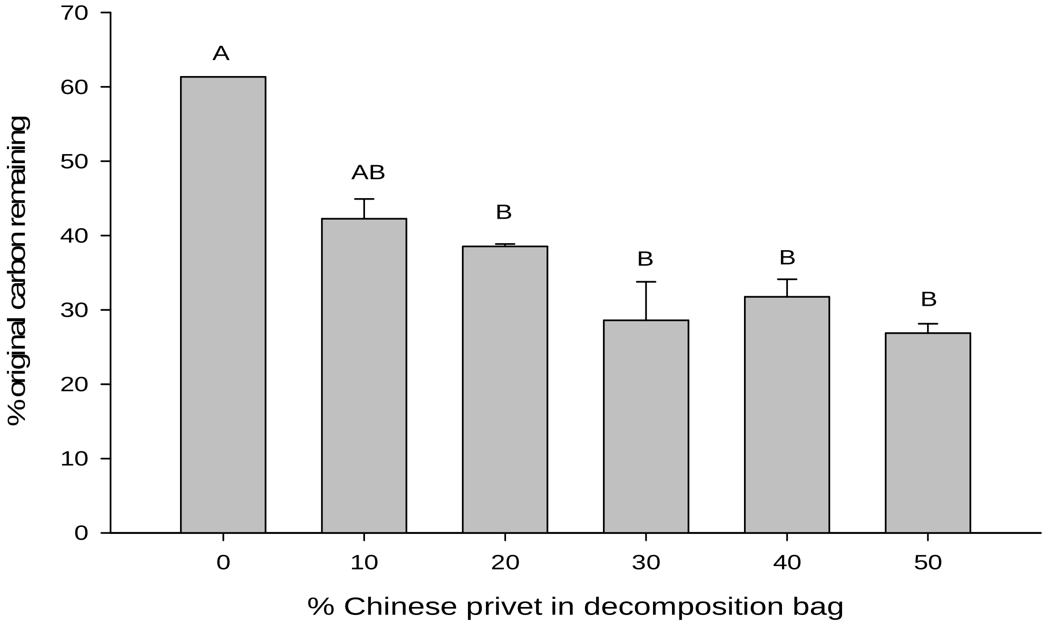


Figure 25. Percent of original carbon remaining at week 42 for decomposition bags in the controlled study. Error bars represent standard error. Letters represent significant differences at p<0.05 by Tukey's post hoc test.

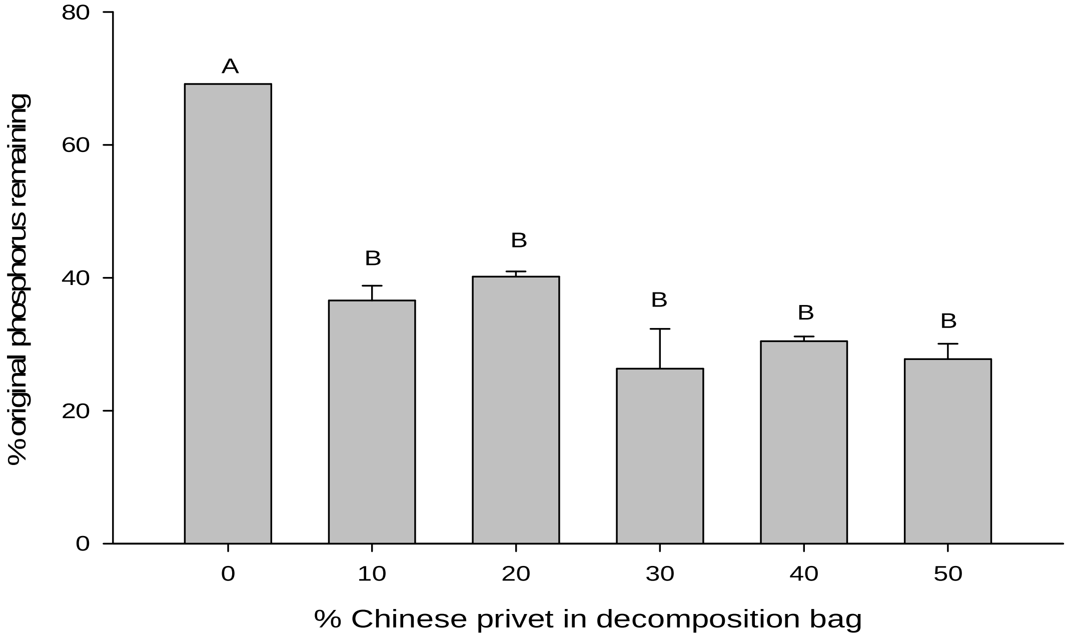


Figure 26. Percent of original phosphorus remaining at week 42 for decomposition bags of different % Chinese privet composition in the controlled study. Error bars represent standard error. Letters represent significant differences at p<0.05 by Tukey's post hoc test.

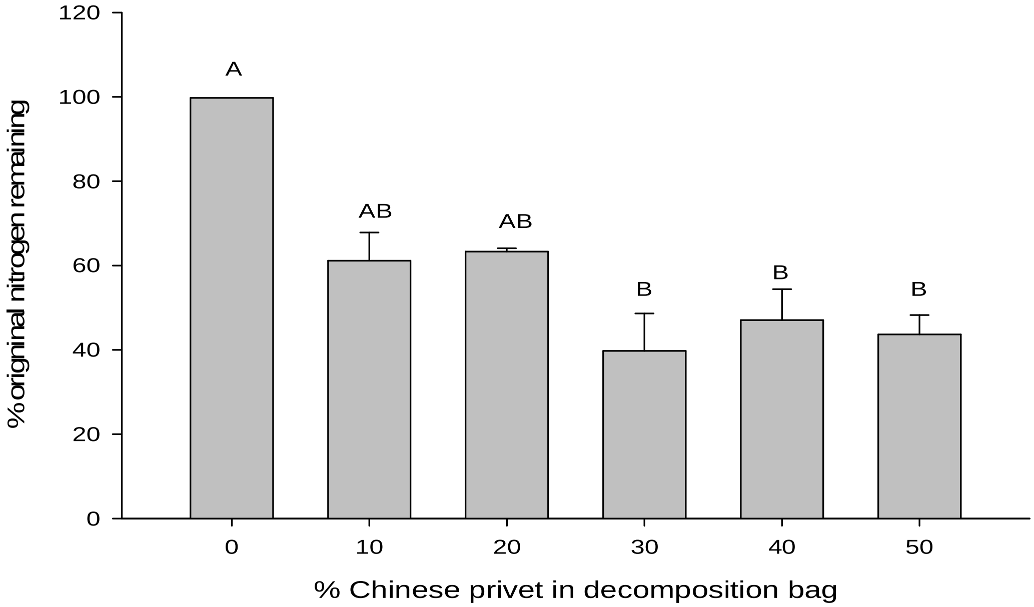


Figure 27. Percent of original nitrogen remaining at week 42 for decomposition bags of different % Chinese privet composition in the controlled study. Error bars represent standard error. Letters represent significant differences at p<0.05 by Tukey's post hoc test.

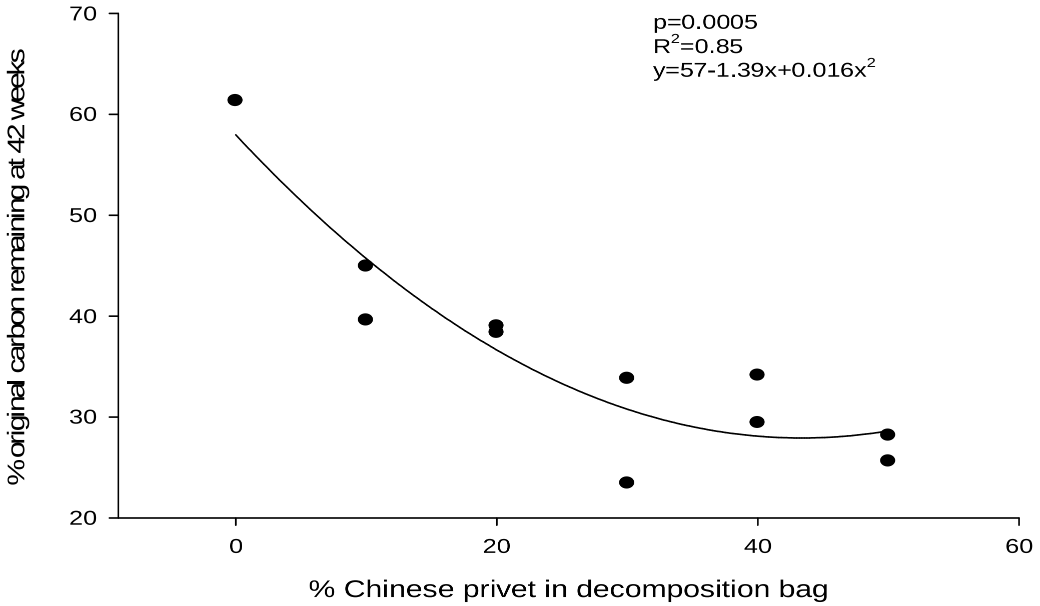
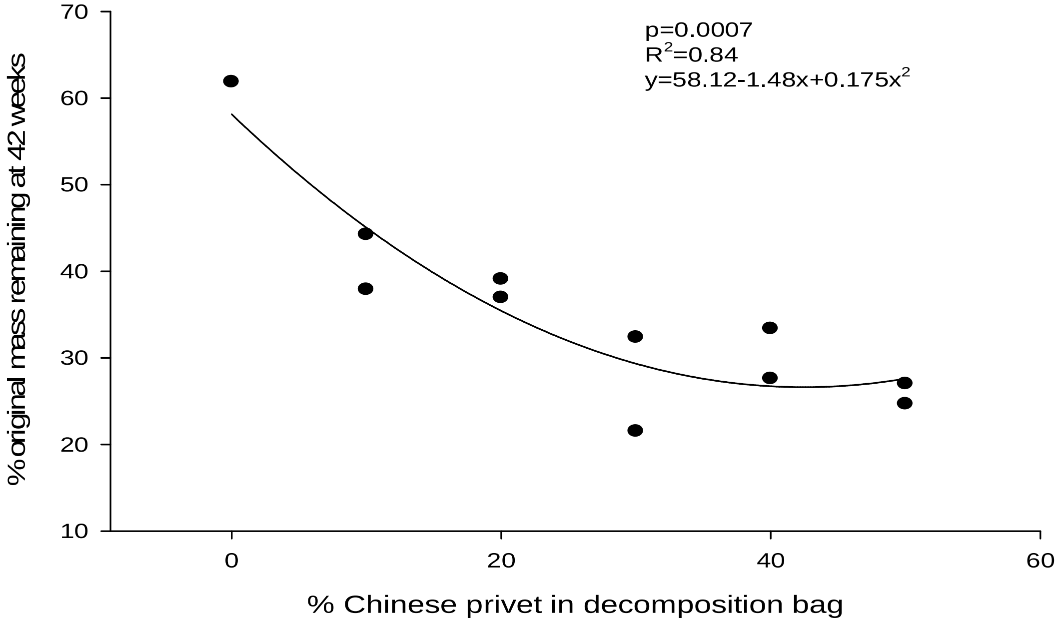


Figure 28. Significant curvilinear regression between percent of original carbon remaining at week 42 and percent Chinese privet in decomposition bag in controlled study.



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igure 29. Significant curvilinear regression between percent of original mass remaining at week 42 and percent Chinese privet in decomposition bag in controlled study.

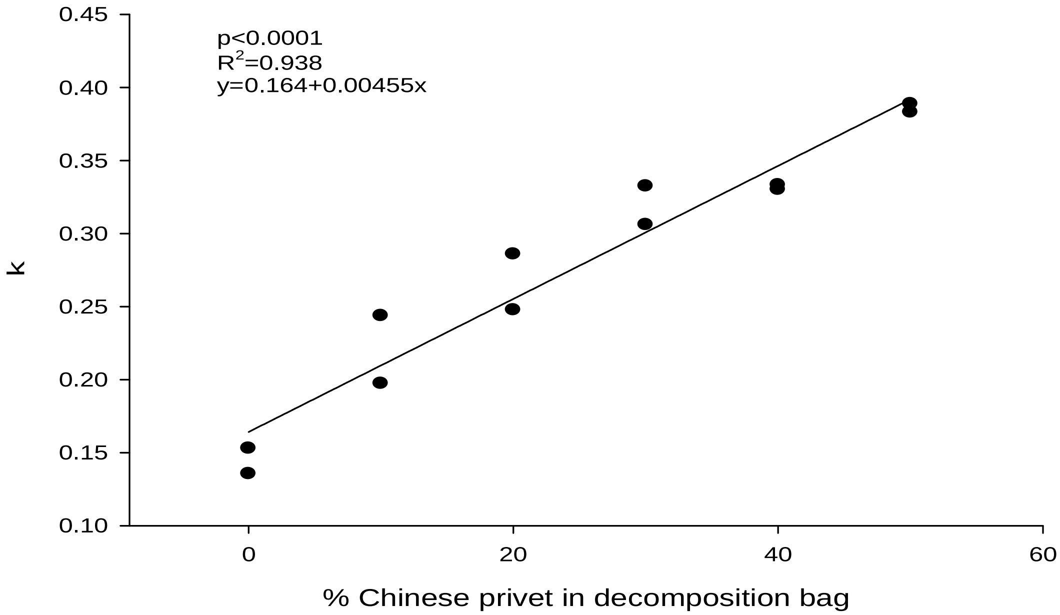

Figure 30. Significant linear regression between decomposition rates (k) and % Chinese privet composition in decomposition bags in the controlled study.

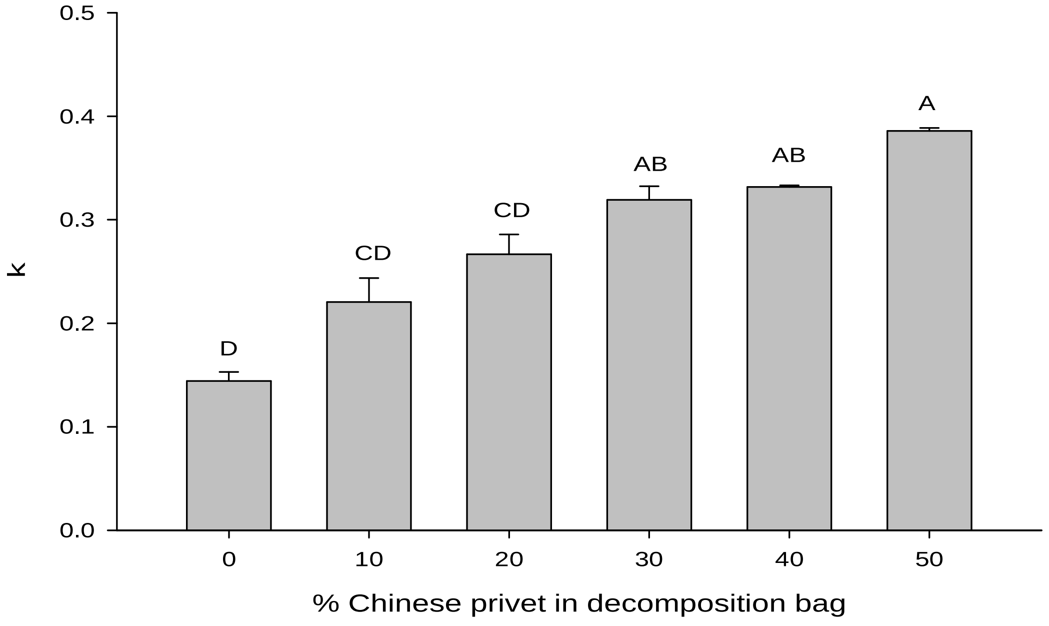

Figure 31. Decomposition rates (k) for decomposition bags in the controlled study. Error bars represent standard error. Letters represent significant differences at $p<0.05$ by Tukey's post hoc test.

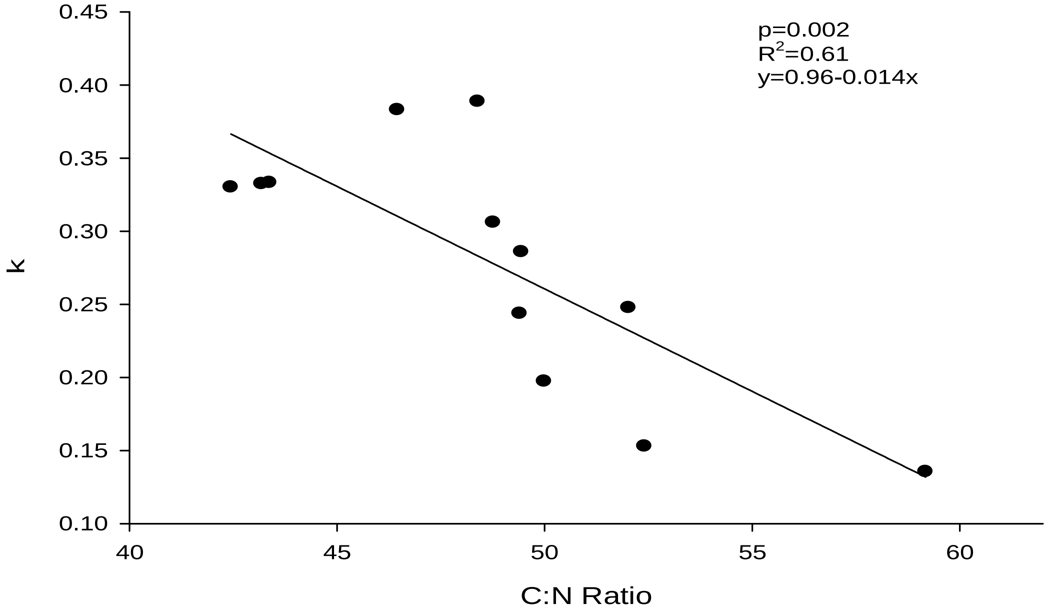

Figure 32. Significant linear regression between decomposition values (k) and C:N ratio for the controlled study.

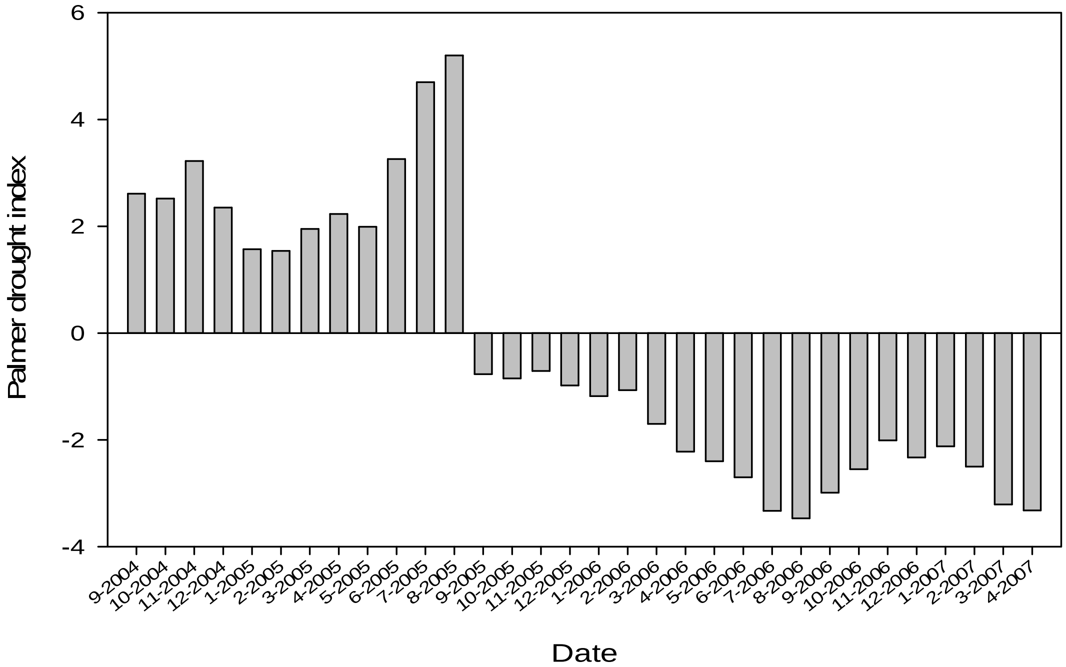

Figure 33. Monthly Palmer drought severity indices for September 2004 – April 2007. Positive bars indicate excess moisture, negative bars indicate drought.

CHAPTER III

INFLUENCE OF CHINESE PRIVET (*LIGUSTRUM SINENSE* LOUR.) ON NUTRIENT CYCLING IN RIPARIAN FORESTS IN WEST GEORGIA

ABSTRACT

Nutrient dynamics can be greatly influenced as invasive species become more abundant in riparian forests. Forest productivity is dependent on nutrient availability and therefore can be altered by changes in nutrient cycling. In this study, the influence of Chinese privet (*Ligustrum sinense* Lour.), an invasive shrub, on nutrient dynamics was examined by measuring nutrient concentration and content in forest floor and litterfall, nutrient use efficiency (NUE), resorption efficiency and proficiency, nitrogen mineralization and microbial biomass. The study was conducted in Muscogee and Harris counties (west Georgia) across a continuum of Chinese privet abundance and four land use classifications. In order to assess the influence of Chinese privet on nutrient dynamics, comparisons were made on a site basis (based on % Chinese privet in the understory) and directly between Chinese privet and native species. Chinese privet had higher resorption proficiency and lower resorption efficiency than sweetgum (*Liquidambar styraciflua* L.), a native species. Nitrogen availability limited productivity on most sites but N-NUE was related to land use rather than the abundance of Chinese privet. Urban sites had inefficient N-NUE that may have resulted from high levels of nitrate in streams. However, there were differences among levels of Chinese privet with respect to Ca- and Mg-NUE, with uninvaded sites having less efficient Mg-use, and severely invaded sites having less efficient Ca-use. Furthermore, seasonal trends were detectable for microbial biomass and N-mineralization among levels of Chinese privet. There was a trend of increased microbial biomass in the summer for both moderately and severely invaded sites. N-mineralization was significantly higher in the summer for moderately and severely invaded sites in comparison to the uninvaded sites, but there were no differences in other seasons. Chinese privet influenced nutrient cycling because of its unique litter quality. These changes influenced nutrient composition of litterfall, NUE, and resorption efficiency and proficiency across levels of Chinese privet.

INTRODUCTION

Recently, invasive plant species have been noted as an important agent of change in natural systems (Erhenfeld 2003). The impacts of these species include alterations in vegetation composition, altered nutrient dynamics, and altered water availability (Erhenfeld 2003). Chinese privet (*Ligustrum sinense* Lour.) is an invasive shrub in the Southeastern U.S. yet little is known about its ecology (Ward 2002). Furthermore, there are no published studies investigating the impacts of Chinese privet on nutrient cycles. This study investigated the influence of Chinese privet on nutrient dynamics in litterfall and forest floor nutrient pools. The influence of Chinese privet on nutrient dynamics was further studied by measuring N-mineralization rates and microbial biomass across a continuum of Chinese privet.

Worldwide, and particularly in the Southeastern U.S., plant growth is limited primarily by nitrogen (N) and secondarily by phosphorus (P), or by a combination of the two (Vitousek and Howarth 1991). Other nutrients can be limiting as well. Nutrient limitations can be examined by investigating ratios of nutrients found in vegetation and soil. N:P ratios of plant material are often used as an indicator of biogeochemical limitations in a system (Lockaby and Conner 1999). Nutrient ratios in foliage have been studied with fertilizer diagnostics in some systems to determine which nutrients are limiting productivity and therefore could be added to increase productivity. Benchmark ratios have been determined that indicate a system in balance respect to with nutrient composition and fertilization, such ratios are included in the Diagnosis and Recommendation Integrated System (DRIS, Coleman et al. 2003).

Information on site N and P limitations can be examined by investigating N:P in leaf litter. In a compilation of information about N:P balance, Vogt et al. (1986) found worldwide litterfall N:P ratios range from approximately 9 to 27 and suggested that as leaf litter differs from a ratio of 10, it becomes less palatable to decomposers. Lockaby et al. (1996) observed P-immobilization and N-mineralization with forest floor ratios slightly higher than 10, indicating P limitations in the Ogeechee River floodplain, and nutrient imbalance. Another study by Lockaby and Conner (1999) suggested that litterfall N:P ratios were considered balanced at 12 for forested wetlands. System nutrient requirements vary by region, ecosystem, and plant species, and nutrient ratios can also serve as guidelines for determining which nutrients are limited. In the present study, there were comparisons of the nutrient composition of native species to those of

Chinese privet. There were also comparisons of the site variation of nutrients in litterfall and forest floor as the percent of Chinese privet increased in riparian systems.

Invasive Exotics

It is generally accepted that invasive plants possess traits which create conditions favorable to alterations in species composition, by influencing decomposition and nutrient cycling rates in invaded communities (Ehrenfeld 2003, Allison and Vitousek 2004). Some examples of these traits are rapid growth and reproduction, high specific leaf area, and increased concentration of nutrients in leaves, which allow invasive species to spread quickly (Allison and Vitousek 2004). Other differences between invasive and native species physiological traits, include higher photosynthetic rates and lower costs for leaf construction which may lead to rapid growth rates (Lambers and Poorter 1992, Reich et al. 1997, Baruch and Goldstein 1999). Allison and Vitousek (2004) suggest that invasive species in Hawaii can cause a fertilization effect and possibly a positive feedback loop of nutrient enrichment in soil, because invasive plants tend to have a higher nutrient concentration and decompose rapidly. In their study, the fertilization effect created conditions favorable to the invasive species allowing them to out-compete native plants (Allison and Vitousek 2004). Invasive plants present in the Southeastern U.S. may have a similar influence.

Invasive plants have the potential to alter soil properties through a variety of mechanisms (Ehrenfeld 2003). Since invasive species can alter rates of nutrient cycling, composition of soil microbial communities and physical conditions of the soil may also be altered (Ehernfeld et al. 2001, Kourtev et al. 2002, Ehrenfeld 2003, Kourtev et al.

2003, Callaway et al. 2004, Hawkes et al. 2005). Invasive plants altered soil conditions both in field and greenhouse studies (Ehernfeld et al. 2001, Kourtev et al. 2002). However, the majority of these studies have been conducted with either invasive grasses or herbaceous plants, and there are no published data regarding the effects of Chinese privet on soil conditions and nutrient dynamics within its associated ecosystems.

Land Use

Anthropogenic changes in land use can alter rates of nutrient cycling. These alterations range from the use of invasive species in landscaping and altered disturbance regimes, physiologic stresses (such as air pollution), and landscape structure (McDonnell and Pickett 1990, Lowenstein and Lowenstein 2005). The abundance of invasive species and patterns of nutrient cycling have been also been influenced by changes in land use patterns (Lowenstein and Lowenstein 2005, Groffman et al. 2006). Groffman et al. (2006) observed different plant species composition in forests across varying degrees of urbanization. Another alteration was observed in urban riparian forests of Georgia that had increased productivity which might be caused by elevated N loads in associated urban streams (Brantley 2008).

Urbanization can also impact forests by reducing litter quality and inducing slower decomposition rates (Carreiro et al. 1999, Pouyat and Carreiro 2003, Pavao-Zuckerman and Coleman 2005). However, when rural leaf litter was placed in both urban and rural sites in Baltimore, Maryland there was more rapid nutrient turnover in urban sites and this was attributed to warmer microsite conditions (heat island effect) (Pouyat and Carreiro 2003). Similarly, the heat island effect caused net N-mineralization to increase, albeit with no change in net nitrification rates in North Carolina (Pavao-Zuckerman and Coleman 2005). In contrast, net nitrification rates in New York City were 5 times greater than on rural sites, while N-mineralization did not vary significantly between land use (Baxter et al. 2002).

Urban environments frequently produce a variety of conditions, since they provide both warmer and drier conditions which have different influences on nutrient cycling processes. Therefore, the influence of urbanization on nutrient cycling can both increase and decrease rates of specific nutrient conversion, but many of these interactions are not well understood, especially for Chinese privet. Urban areas are also associated with increased nutrients because of sediment deposition, which in excess can suffocate roots, possibly increasing productivity of leaves with lower litter quality (Pouyat and Carreiro 2003, Noe and Hupp 2005)

Forest Floor

The forest floor, in this study, was defined as the organic layer atop the mineral soil which includes litterfall, and partially decomposed organic material. Since nutrient cycling in the forest floor is not adequately described in either decomposition or litterfall studies alone, forest floor dynamics should be examined directly. Furthermore, the forest floor represents an important nutrient pool for soil micro- and macro-organisms. The nutrient composition and mass of forest floor are two important factors in determining the importance of this nutrient pool for an ecosystem. In areas that do not have overland flow capable of transporting litter, the mass of the forest floor is determined by decomposition and litterfall rates (Fisher and Binkley 2000). Forest floor in a steady state, can give a crude estimate of decomposition rates by comparing differences in the annual maximum and minimum masses (Fisher and Binkley 2000).

Litterfall

Nutrients in leaves on plants have three possible fates; leaching during precipitation, retranslocation prior to senescence, or retention in litterfall (Lugo et al. 1990). Timing of leaf senescence determines the temperature and moisture condition influencing litterfall decomposition and nutrient transformations. Since seasonal cues for leaf senescence vary by species, it is important to observe phenology for all species on a site to know what conditions of moisture and temperature occur for litterfall. For example, Conner and Day (1992) observed that water tupelo (*Nyssa aquatica*) foliage senesced earlier than baldcypress (*Taxodium distichum*) occurring on a common site and was therefore introduced to a different microclimate, due to seasonal temperature variations. In addition, Lockaby and Walbridge (1998) indicate that different wetland communities have different species which exhibit temporal variation of leaf senescence. Atypical senescence occurring during late summer or late winter in the northern hemisphere would provide leaves contact with a microclimate that is warmer and possibly wetter than the microclimate experienced by litter that is senesced in fall, which would stimulate decomposition for the atypical litter (Swift et al. 1979).

Invasive plants may have very different phenology and litter chemistry than native species and, as a result, may impact an ecosystem in direct relationship to their differences from the native species (Ehrenfeld 2003). The phenology of Chinese privet is greatly different than native deciduous trees found in the riparian forests of west Georgia

(Brantley 2008). Chinese privet is a semi-evergreen shrub with peak senescence in early spring but drops leaves year round (Brantley 2008). Therefore, it is not likely that Chinese privet becomes dormant for overwintering as the native trees do and it remains photosynthetically active.

Nutrient Use Efficiency

Many studies have investigated the relationship between nutrient use efficiency (NUE) and nutrient availability (Vitousek 1982, Shilling and Lockaby 2006). NUE can be calculated using a variety of methods in order to determine ecosystem limitations (Shaver and Melillo 1984, Birk and Vitousek 1986, Knops et al. 1997). NUE is typically defined as production or C fixation per unit of nutrient (Gerloff 1976, Shaver and Melillo 1984). Efficient nutrient circulation in forests is represented by large amounts of C fixed per unit nutrient assimilated (Vitousek 1982). A system with efficient circulation may be more limited in nutrient availability than systems with inefficient circulation patterns (Vitousek 1982, 1984, 1997), and consequently plants in low nutrient ecosystems would benefit from conserving nutrients in tissue and re-allocating those nutrients when needed. Vitousek (1982) suggested that since variations in NUE occur with nutrient availability and nutrient circulation in litterfall, NUE is a good indicator of nutrient availability of a site. As an example, Schilling and Lockaby (2006) were able to use NUE and N:P ratios in red- and black-water floodplain systems in Georgia to make distinctions between the two systems based on their different limitations to N and base cations.

Retranslocation

Retranslocation occurs with mobile nutrients such as N and P and may be measured by determining resorption proficiency and efficiency (Aerts 1996, Killingbeck 1996). Resorption proficiency is the concentration of nutrients in senesced foliage and can be calculated for an individual tree or for a stand (Aerts 1996, Killingbeck 1996). Resorption efficiency is the ratio of the difference in nutrient content in green foliage and abscised leaves divided by green leaf content (Aerts 1996, Killingbeck 1996). It has been hypothesized that to retain nutrients prior to leaf senescence, trees on nutrient poor sites will lower leaf nutrient content to a greater extent than trees on fertile sites (Aerts 1996, Killingbeck 1996). However, others suggest this is not the case (Knops et al. 1997, Kobe et al. 2005). Since nutrient needs vary by species, species may differ in regard to species specific nutrient limitations among species on the same site. This makes it difficult to decipher whether site conditions or differences in species' requirements determine variations in resorption efficiencies and proficiencies when examining a single species.

Killingbeck (1996) suggested that both resorption proficiency and efficiency are important measures of nutrient availability and, when used correctly, both can give useful information regarding nutrient cycling. Resorption efficiency indicates the proportion of nutrients from green foliage that are reabsorbed into the woody material before senescence thus reducing the requirement for plant uptake of those nutrients from the soil nutrient pool at a later time (Switzer and Nelson 1972, Killingbeck 1996). On the other hand, proficiency is the concentration of nutrients in foliage after senescence. Therefore, it is frequently used to compare a single species across sites to compare their nutrient conservation and gain information on which nutrients are limiting (Killingbeck 1996). The more nutrients a plant retains, the less that it may require from the soil.

Several studies have been conducted to investigate the links between nutrient limitation and resorption efficiency and proficiency (Aerts 1996, Reich et al. 1997). Resorption efficiency and proficiency have had contrasting results, yet some repeatable trends have been observed (Aerts 1996, Reich et al. 1997). Among these repeatable trends is that deciduous trees have higher resorption efficiencies than evergreen species (Aerts 1996). Therefore, Aerts (1996) suggests that leaf retention may be a more effective mechanism for maintaining nutrients than resorption of nutrients. Reich et al. (1997) found that deciduous leaves with a shorter lifespan have greater resorption proficiency compared to the longer-lived foliage of evergreens. It is possible that the semi-evergreen nature of Chinese privet may influence its nutrient resorption proficiency and efficiency. However, some species have high nutrient concentrations in green leaves which can influence resorption efficiency (Kobe et al. 2005). In general, Kobe et al. (2005) observed that species with high N and P content in their green leaves had lower resorption efficiencies in comparison to species with lower initial nutrient contents.

N-Mineralization and Microbial Biomass

Nitrogen mineralization is the conversion of organic N to inorganic plant-available N. Since most forest systems are N-limited, a positive relationship has been noted for N-mineralization and net primary production (NPP) in forests (Reich et al. 1997, Newman 2006). Newman (2006) observed that aboveground net primary productivity (ANPP) in a 90-year old, second growth, mixed hardwood forest was strongly correlated to soil N availability, while belowground net primary productivity (BNPP) was related to water availability. Furthermore, rates of N-mineralization are controlled by moisture availability in soils and C availability in organic matter (Groffman and Crawford 2003). However, C:N ratios in the soil, among other things, determine whether N is immobilized or mineralized. It is proposed that when the C:N ratio of the mineral soil drops below the range of 20-25, N-mineralization occurs (Waksman 1952, Morris and Campbell 1991).

Microbial biomass is an indicator of change in substrate quality and quantity that can occur after invasive species are established (Li et al. 2004). Changes in vegetational species composition and substrate quality will impact microbial biomass since microbes and vegetation compete for available N (Zak et al. 1994, Badalucco and Kuikan 2001). However, Ehrenfeld et al. (2001) stated that patterns of changes in soil properties resulted from the presence of invasive plants are similar to those that occur due to natural succession. Change in microbial composition after the invasion of exotic plants such as Japanese barberry (*Berberis thunbergii* DC.), Japanese stilt grass (*Microstegium vimineum* (Trin.) A. Camus), and firetree (*Myrica faya* (Aiton) Wilbur)(Vitousek et al. 1994, Ehrenfeld 2003) have also been observed. Altered microbial populations, could result in different rates of biochemical reactions, such as N-mineralization, which may further change system function and composition on both microbial and vegetation scales.

Study Objectives

The objectives of this study were to investigate and describe the influence of Chinese privet and land use on nutrient cycling processes and microbial biomass in riparian forests. Sites had a range of percent understory stems of Chinese privet of 0 to 100% in order to study the biogeochemical influence of this invasive shrub. Five hypotheses were tested in order to ascertain the influence of Chinese privet; 1) the forest floor will have less mass at annual maximum leaf fall on sites that have a high abundance of Chinese privet, and turnover time will be faster for those sites, 2) sites with high Chinese privet abundance will have greater amounts of N and P in litterfall compared to sites with only native species, 3) Chinese privet will display lower resorption efficiency and proficiency because of its semi-evergreen nature, 4) NUE of essential elements will be more efficient for uninvaded sites (0 % Chinese privet) compared to moderately (25-79% Chinese privet in understory) and severely (>80% Chinese privet stems in understory) invaded sites due to the wide range of foliar nutrients in leaves after abscission (see Chapter 2 species comparison), and 5) sites with a high percentage of Chinese privet in the understory will have faster rates of N-mineralization and larger microbial biomass, resulting from the high N inputs in litterfall.

METHODS

Description of Study Sites

The study began in October 2004 and was completed in May 2007. Study sites were along a continuum of Chinese privet growth across a range of land uses. Land use categories include urban, developing, and rural sites in Muscogee and Harris counties, near Columbus, GA (Figure 1). These counties are in the Piedmont physiographic province where mean daily temperatures range from 0^{o}C to above 32 ^{o}C, annual mean precipitation is 127 cm, and mean growing season length is 220 days (USFS 2005). Soils in the area are dominated by Ultisols which have clayey or loamy subsoil and a kaolinitic or mixed mineralogy (USFS 2005). More specifically, soil series were either Chewacla (fine-loamy, mixed, active, thermic Fluvaquentic Dystrudepts), Vance (sandy-clay-loam, fine, mixed, semiactive, thermic Typic Hapludults), or Toccoa (coarse-loamy, mixed active, nonacid, thermic Typic Udifluvents). A total of 16 circular sites had an area of 0.04 hectare and were located in riparian forests on six watersheds.

Sites were classified into 3 classes based on the percent stems of Chinese privet in the understory based on the following criteria. Uninvaded sites had 0% Chinese privet, moderately invaded sites had a range of 25 to 79% understory stems of Chinese privet, and severely invaded sites exhibited greater than 80% Chinese privet stems in the understory (Chapter 2, Table 11). Classes had several other characteristics in common. Uninvaded sites all had a closed canopy, with an overstory of mature native trees including sweetgum (*Liquidambar styraciflua* L.), yellow poplar (*Liriodendron tulipifera* L.), red maple (*Acer rubrum* L.), and elm (*Ulmus* sp.), with a relatively high basal area (mean of 36.4 m^2/ha measured with a 10 BAF prism), a midstory composed of dogwood (*Cornus florida* L.), and an open understory. Moderately invaded sites had a mean basal area of 19.0 m^2/ha, an overstory composed of mature native trees such as sweetgum, water oak, and yellow poplar, with Chinese privet and muscle wood (*Carpinus caroliniana* Walter) occurring in the midstory. Severely invaded sites had a few mature, overstory, native trees such as water oak and sweetgum with a mean basal area of 20.9 m^2/ha, coupled with a Chinese privet dominated midstory and only Chinese privet found in the understory.

Forest Floor

The minimum forest floor sample was collected in August 2006 and the maximum was collected in February 2007 because all trees would have senesced their leaves and decomposition would be minimal. Four $0.1m^2$ samples from each plot were collected at each time from areas selected systematically. Samples were collected by using a metal form and scoring the outline of it with a knife to obtain organic matter on top of mineral soil layer. Differences in average maximum and minimum sample masses were used to determine a crude estimate of annual decomposition rates. N, C, and P concentration and content were determined for each sample. Nutrient comparisons were conducted on content at minimum and maximum collections and percent change between the two.

Litterfall

Litterfall collection occurred from December 2004 until June of 2007. In November 2004, three $0.25m^2$ square litterfall traps were systematically installed at each plot. Traps were made of treated lumber and the bottom was covered with 2-mm nylon mesh. Each trap was staked approximately 30 cm above the ground to avoid flooding. Contents in each trap were collected monthly. After oven drying samples for 72 hours at 70 ^{o}C, contents were sorted into 5 categories (native species leaves, Chinese privet leaves, twigs, reproductive parts, and miscellaneous) and then weighed. A subsample from each trap was ground and then analyzed for N, P, and C concentrations. The three samples were averaged for statistical analysis.

Resorption Efficiency and Proficiency

Resorption efficiency was determined for sweetgum and Chinese privet, on co-occurring sites, by comparing nutrients in green leaves and senesced leaves in order to observe variability among different species and across classes (Clawson et al. 2001). Collection of green leaves from the mid-canopy, approximately 4 m high and canopy 8-12 m, occurred in June 2006. Senesced leaves were collected from litterfall traps in November and December 2006. Leaf area index (LAI), air dried weights, oven dried weights, and N, C, and P concentrations were determined for green and senesced leaves. Leaf area was measured using Delta T video imaging system (Delta-T Devices LTD, Burwell, Cambridge, England), and then site LAI was calculated by multiplying annual foliar litterfall production by sampled leaf area. The percentage of each nutrient not reabsorbed before abscission was determined by subtracting nutrient content in senesced litterfall from that in green foliage and then dividing by green nutrient content (i.e. resorption efficiency) (Killingbeck 1996). Resportion proficiency was based on the concentration of N and P remaining in senesced leaves collected in November and December 2006 on a species basis. Comparisons for mean nutrient concentrations were conducted among Chinese privet classes for sweetgum and Chinese privet.

Plant Tissue Nutrients

Nitrogen (N), carbon (C), and phosphorus (P) concentration and content were determined for litterfall, green foliage, and forest floor samples. All samples were oven dried for 72 hours at 70 ^{o}C and ground to pass through a 20-mesh screen in a Wiley mill. Total C and N concentrations were determined using a Perkin Elmer Series II CHNS/O

Analyzer (Perkin Elmer Corp., Norwalk, CT). Total P was determined by dry-ashing, acid digestion using the vanadomolybdate procedure (Jackson 1958), followed by spectrophotometrical analysis.

Nitrogen Mineralization and Microbial Biomass

N-mineralization estimation utilized the *in situ* method described by Hart et al. (1994). Sample collection occurred at 60 day intervals between November 2005 and April 2007. At each collection, two systematically placed soil cores were taken to a depth of approximately 7.5 cm within the same quadrant (approximately 0.01 ha) of each plot. After removal of coarse roots, the soil from each core was divided between two polyethylene bags (about 150 ml of soil in each bag). One bag was buried to a depth of 7.5 cm and incubated for approximately 30 days. The second bag served as a pre-incubation soil. Pre-incubation and post-incubation samples were transported on ice to the laboratory at Auburn University for processing. After sieving samples to remove organic matter, soil moisture content was measured gravimetrically for each sample using a 10-g subsample which was dried at 105° C for 48 hours. A second 10-g subsample was shaken for 1 hour with 100 mL of 2 M potassium chloride (KCl), filtered, and then frozen. Thawing of samples took place prior to analysis. Extracts were evaluated for NH_4-N and NO_3-N using a BIO-RAD Model 450 microplate reader for NH_4-N and NO_3-N. Mineralized N estimation involved calculating the difference in total N (sum of NH_4-N and NO_3-N) between pre- and post-incubation samples. Conversion of N values to a N mass per unit area basis was done using soil bulk density for each site.

Microbial biomass sampling followed the same sampling schedule used for N-mineralization. This analysis was conducted using the chloroform-fumigation method of Vance et al. (1987). Soil used for microbial biomass analysis was a subsample of the pre-incubation soil samples collected for N-mineralization measurement. Both a fumigated and unfumigated sub-sample of 18.5g field moist soil was analyzed. Fumigated samples were placed in a vacuum desiccator with chloroform ($CHCl_3$) for 24 hours then extracted with 125 mL of 0.5 M potassium sulfate (K_2SO_4). Unfumigated samples were extracted with the same technique within 2 days of collection. To extract microbial biomass C and N, fumigated and unfumigated samples were individually combined with K_2SO_4 and shaken for 1 hour and then filtered. Samples were then frozen for at least 48 hours and thawed for analysis. Microbial biomass C and N were estimated as the difference between the measurements of organic C and N between fumigated and unfumigated samples. Organic C and N were measured using a Shimadzu TOC-V and (Shimadzu Scientific Instruments, Columbia, MD) and total N (TN) was measured with a Apollo 9000 combustion total organic carbon (TOC) analyzer with TN module (Teledyne Tekmar Instruments, Mason, OH).

Statistical Analyses

SAS software version 9.1 was used for all statistical analyses (SAS Institute, Cary, NC). One-way analysis of variance (ANOVA) (PROC GLM, SAS Institute 2002-2003) was used to examine differences in each variable among privet classes and among land use classifications. If significant differences were found, a Tukey's HSD post-hoc test was utilized to compare Chinese privet classes. Statistical significance was set at

α=0.05, however all p-values <0.1 are presented for informational purposes. Linear regressions (PROC Reg, SAS Institute 2002-2003) were conducted using percent Chinese privet in the understory as the independent variable.

RESULTS

Forest Floor

The difference between minimum and maximum biomass was examined for forest floor across class of understory Chinese privet and dominant land-use. Mean minimum collection ranged from 355.8±89.9 g m^{-2} to 526.5±89.3 g m^{-2} and mean maximum collection varied between 687.6±66.9 g m^{-2} and 860.1±112.3 g m^{-2}. When sites were grouped by class of Chinese privet, there were no differences between classes for dry weight, C, N, or P content for minimum, maximum sampling periods, or percent change (Table 1). However, when sites were grouped by dominant land use in the watersheds, there was a significant difference between classifications (Table 2). Dry weight and C content in maximum samples were higher for urban sites in comparison to developing, forested, or sites (Table 2). However, there were no significant differences among Chinese privet classes for the change in nutrients or mass. There was a significantly narrower N:P ratio of 4.5 observed for the maximum collections in the uninvaded sites compared to the mean ratios of 6.7 and 6.4 for moderately invaded and severely invaded sites, respectively (Figure 2, F=10.4, df=2,61, p<0.0001). No differences were detected among Chinese privet classes for C:N or C:P ratios for either maximum or minimum samples or for N:P ratios in minimum samples.

Litterfall

Differences among classes. Nutrient composition of litterfall was examined among classes of Chinese privet for year 1, year 2, and both years combined (Table 3). There was a significant curvilinear relationship between percent Chinese privet in the understory and N content, which peaked in mid-ranges of understory Chinese privet (Figure 3). There were also differences between N content among classes of Chinese privet in year 1 (Figure 4). Trends had similar relationships of greater N content in litterfall in the moderately invaded sites compared to other classes for year 1, year 2, and both years combined (Figure 4).

Mass of litterfall was not significantly different among classes but was numerically lower in uninvaded sites in comparison to other Chinese privet classes for year 1 and year 2 (Figure 5, Table 4). Mass of litterfall ranged from 565±6.6g m^{-2} to 849±49.0g m^{-2} across all sampling periods. Carbon content varied between classes in year 2, when the uninvaded sites had significantly less C content (262.8±4.6g m^{-2}) than the moderately invaded class (329.4±15g m^{-2}) or the severely invaded class (312.4± 11.9 g m^{-2}) (Figure 6, Table 4). In year 2, C content had a curvilinear relationship with percent Chinese privet in understory (Figure 7) which was similar to the curvilinear relationship of N content and Chinese privet in the understory (Figure 3). The curvilinear observation is influenced by elevated litterfall mass in the moderately invaded sites and lower C concentration in severely invaded sites (Figure 8). P content, however, did not follow a detectable pattern and no differences were found among classes (Table 4).

There were significant differences in N concentration of litterfall among sites with moderately invaded sites having a higher concentration of N than other classes of

Chinese privet (Figure 9). For all N content and concentration comparisons productivity was greater for moderately invaded sites than severely invaded and uninvaded sites (Figures 3, 4, 5, and 9).

Seasonal trends for N concentration: In comparisons for year 1, year 2, and years 1 and 2 combined, classes varied in terms of highest N concentration across seasons (Table 5, Figure 10). The greatest seasonal difference among classes occurred in the summer when both moderately and severely invaded sites had significantly higher N concentration than uninvaded sites (Table 5, Figure 10). In the spring, moderately invaded sites had more N concentration in comparison to uninvaded and severely invaded sites for all years (Table 5, Figure 10). N concentration was higher in year 1 compared to the dry conditions of year 2. However, N concentration in the fall and winter did not exhibit a consistent trend and there were no observed differences among classes (Figure 10).

Seasonal comparisons of P concentration: Although there were no observed differences among classes for P content, there were significant differences for P concentration among classes (Table 5, Figure 11). Uninvaded sites consistently had the greatest P concentration, followed by moderately invaded then severely invaded sites for year 1, year 2, and both years combined in winter, fall, and spring (Table 5, Figure 11). In the summer of year 1, moderately invaded sites had significantly higher concentration of P than severely invaded sites (Table 5, Figure 11). There was an increase of P concentration for all classes in the spring of all time periods in comparison to the other seasons (Figure 11).

Seasonal comparisons of C:N and N:P. There was little annual variation in C:N among classes and seasonal trends were similar across year 1, 2, and both years combined (Table 5, Figure 12). In the spring and summer, mean C:N ratios were typically significantly wider in uninvaded sites than in moderately and severely invaded sites (Table 5, Figure 12). There were no significant differences in C:N ratio among classes for the fall (Table 5, Figure 12). There were annual differences in the ranges of C:N ratios where year 2 had wider ratios than year 1 (Figure 12). For all comparisons mean N:P ratios were significantly narrower in uninvaded sites compared to severely and moderately invaded sites (Table 5, Figure 13). There were few significant differences in seasonal variation of N:P ratios (Figure 13).

Nutrient Use Efficiency

Nitrogen and phosphorus. For all sample periods (Figure 14), urban sites had less efficient use of N than other sites since they occurred together toward the upper right corner of the graph. In year 2, urban sites followed the same trends of rural, pasture and developing sites of N-NUE. The uninvaded sites clustered to the left in an area which suggests more efficient nutrient use (Figure 14). Phosphorus NUE had no noticeable trends among Chinese privet classes (Figure 15).

Magnesium, calcium, potassium. Uninvaded sites had lower Mg-NUE than the moderately and severely invaded sites (Figure 16a). However, there were no visible trends for K-NUE by Chinese privet class or land use classification (Figure 16b).

Severely invaded sites clustered together with low Ca-NUE compared to uninvaded and moderately invaded sites (Figure 16c).

Resorption Efficiency/ Proficiency

Species differences had a greater influence than site differences on nutrient resorption efficiency or proficiency. Although there were no differences among Chinese privet classes for site resorption proficiency, Chinese privet had lower resorption proficiency than sweetgum in the moderately and severely invaded sites (Figure 17, $F_{1,6}$=6.9, p=0.04, $F_{1,10}$=1100, p<0.0001, respectively). Chinese privet N resorption proficiency ranged from 6700 to 14700 with a mean of 9900± 1010 mg kg^{-1}. The range for sweetgum N resorption proficiency was from 1900 to 5500 with a mean of 4500± 590 mg kg^{-1}. P resorption proficiency for Chinese privet ranged from 0.08 to 0.21 with a mean of 0.13±0.01 mg kg^{-1}, while sweetgum was more proficient with P resorption ranging from 0.07 to 0.41 mg kg^{-1} with a mean of 0.15±0.02 mg kg^{-1}. However, there was not a significant difference between Chinese privet and sweetgum for P resorption proficiency (p>0.1, data not shown).

N resorption efficiency for Chinese privet ranged from 43 to 67% with a mean of 55±3.8%. Sweetgum resorption efficiencies ranged from 27 to 85% with a mean of 72±4.7%. There were significant differences between Chinese privet and sweetgum N resorption in the severely invaded class but not the moderately invaded class (Figure 18, $F_{1,10}$=12.4, p=0.005). There were no differences between the two species for P resorption efficiencies (p>0.1, data not shown).

There were no significant differences in resorption efficiencies between classes for all species combined (p>0.1, data not shown). Box elder (*Acer negundo* L.) had different N resorption efficiency than the other species examined except for two-winged silverbell (Figure 19). However, sample size was small and some species had only one sample, consequently within species variation was not observed for all species.

Nutrient concentration was one of the variables used to calculate resorption efficiency; therefore, it was also examined. Chinese privet had significantly higher N concentrations in live foliage than sweetgum (Table 6, Figure 20a). Similarly, N concentrations were higher in senesced leaves of Chinese privet than in those of sweetgum or water oak (*Quercus nigra* L.) (Table 6, Figure 20a). Chinese privet had significantly greater P concentrations in green foliage than water oak (Table 6, Figure 20b).

Nitrogen Mineralization and Microbial Biomass

The amount of N mineralized during each collection ranged from 0 to 819 g ha^{-1} d^{-1} (Figure 21). The range of N-mineralization rates was greater as the percent understory Chinese privet increased (Figure 21). In the summer, the mean rate of N-mineralization was significantly greater for the severely invaded class compared to the uninvaded sites (Figure 22, Table 7). Among classes, means of total N mineralized for spring, winter, and fall were not significantly different (Figure 22, Table 7). No differences were observed among classes for total N mineralized (Figure 23, p=0.2, $F_{2,13}$=1.7). Not all sites had data in the summer season, so summer collections were omitted from the total N mineralized (Figure 23).

Microbial N ranged from 9 to 219 $\mu g\ g^{-1}$ and microbial C ranged from 37 to 1824 $\mu g\ g^{-1}$ (Figure 24). Significantly higher microbial biomass N occurred in summer on severely invaded sites compared to the other classes (Table 7, Figure 25b). However, severely invaded sites had higher microbial N and C in winter and spring compared to moderately invaded sites (Table 7, Figure 25b). The greatest seasonal microbial N occurred in the fall for both uninvaded and severely invaded sites (Table 7, Figure 25). In the winter, microbial N was significantly greater in the severely invaded class compared to moderately invaded class (Table 7, Figure 25a). Both C content and litterfall mass had positive linear regressions with net N-mineralization (Figures 26 and 27). N-mineralization was only measured during year 2 and, therefore, comparisons utilized year 2 litterfall data.

DISCUSSION

Forest Floor

Differences in mass and nutrients of the forest floor layer were linked to the dominant land use in the watershed than to the percent Chinese privet in the understory (Tables 1 and 2). One possible explanation for differences in forest floor mass could be due to land use could be increased productivity in the urban sites possibly related to higher stream N availability (Brantley 2008) or increased photoperiod with urban lights (Chaney 2002). When compared to ephemeral streams in the coastal plain of Georgia (Jolley 2008), forests in west Georgia had greater mass for both minimum and maximum sampling periods suggesting either increased productivity or slower decomposition. Productivity data (Table 4) suggested that the riparian forests of west Georgia had a greater litterfall contribution and there was increased forest floor mass in comparison to the coastal plain sites studied by Jolley (2008). Chinese privet leaves may have had little influence on maximum forest floor mass because its senescence peaks in the spring and sampling was conducted in February. Similarly, Chinese privet may have contributed little to minimum forest floor mass, due to its rapid decomposition rate. Forest floor maximum mass was greater for sites with increased NPP (Table 1and Figure 5).

Forest floor turnover rates were estimated by percent change from maximum to minimum mass. The rough estimates of decomposition did not mimic trends documented in the decomposition study (Chapter 2), which had more rapid decomposition rates in sites with higher percent Chinese privet. However, turnover rates determined from forest floor samples are only crude estimates of decomposition. Turnover of forest floor litter was more rapid in the uninvaded sites compared to the moderately and severely invaded sites (Table 1). P content in the uninvaded sites were significantly higher than the maximum and minimum samples, indicating that forest floor may serve as an important nutrient pool on uninvaded sites (Table 1).

Litterfall

Estimates of litterfall in this study indicate that these systems are comparable to the more productive systems referenced in Clawson et al. (2001). The high productivity is similar to that of other floodplain forests in Georgia (Cuffney 1988, Clawson et al. 2001) and across the Southeast U.S. (Brinson et al. 1980, Conner and Day 1992). There was a trend of moderately invaded sites having higher productivity compared to the uninvaded and severely invaded sites (Figure 5) which were similar to the observations of

Brantley (2008). Moderately invaded sites have nutrient input from both the native overstory trees plus the dense midstory of Chinese privet, while the uninvaded sites have litter input from the native trees and the severely invaded sites have the majority of their input from Chinese privet with few overstory native trees (Chapter 2, Table 11).

Litterfall nutrient dynamics were explained largely by stand productivity. For example, nutrient content relationships for C and N were primarily determined by litterfall mass, and both had curvilinear regressions (Figures 3 and 7) peaking in moderately invaded sites similar to productivity in Brantley (2008). Therefore, lower litterfall mass in uninvaded and severely invaded sites contributed to the differences in C and N content for year 2 (Figures 4, 5, and 6). However, mass differences did not explain all the trends in nutrient content and there were increased N concentrations in the sites with moderately invaded sites (Figure 9). The combination of higher productivity and higher N concentration drove significantly greater N content in moderately invaded sites compared to uninvaded sites, (Figures 3, 5, 9).

In comparison to other studies, the N and P content in litterfall were greater than values noted on either the Altamaha or Satilla Rivers of Georgia (Shilling and Lockaby 2005). All sites also had a greater N concentration than those in the Georgian coastal plain (Jolley 2008). Findings here were similar to Jolley (2008) which both indicated there was increased N concentration in the year with greater rainfall. Furthermore, seasonal variation in N and P concentrations suggests that Chinese privet altered the timing and quantity of nutrient to forest floor as discussed by Ehrenfeld et al. (2001). Also, there was a greater concentration of N in the moderate and severely invaded sites in summer and spring in comparison to uninvaded sites for those seasons.

Seasonal differences in mean C:N and N:P ratios among classes suggest Chinese privet modifies litter quality (Figures 12, 13, respectively) by also narrowing ratios similar to Japanese barberry in Ehrenfeld et al. (2001). Seasonal variation in C:N ratios occurred among classes with moderately and severely invaded sites having narrower C:N ratios in comparison to the uninvaded sites (Figure 12). Furthermore, ratios of C:N (Figure 12) were lowest in the spring in each class due to increased N concentration (Figure 10) in the reproductive parts and new foliage as noted in Clawson et al. (2001). Wider N:P ratios (Figure 13) occurred in the moderate and severely invaded sites for all seasons possibly resulting from higher N concentrations (figure 10) and lower P concentrations (Figure 11) of Chinese privet that occurs in those sites.

The ranges of C:N ratios of litterfall (Figure 12) were similar to those in Baker et al. (2001), Shilling and Lockaby (2006), and other Southeastern U.S. floodplain forests. The narrower ratios of severely invaded sites likely result from the late winter-early spring abscission of high quality Chinese privet leaves, which have narrower C:N ratios, compared to the native species that abscise leaves with wider C:N.

N:P ratios (Figure 13) were similar to observed ratios in the Flint, Altamaha, and Satilla River floodplains by Clawson et al. (2001) and by Schilling and Lockaby (2006), respectively. The narrower N:P ratios which occurred consistently on uninvaded sites suggest more N limitations than on moderately and severely invaded sites. However, N:P ratios were less than 12 which is suggested by Lockaby and Conner (1999) to indicate a balanced system. Chinese privet is likely to influence this shift in N availability since their leaves have greater N concentration than native species.

Trends of N availably were influenced by both Chinese privet and land use; however, there were indications that all sites were N limited. Positive regressions for litterfall C content and litterfall with N-mineralization (Figures 26 and 27, respectively) supported that all sites were N limited to some extent. As a greater amount of N is available, productivity is boosted. Similar trends have been described for productivity in urban systems with high stream nutrient levels, especially N (Groffman et al. 2002). Brantley (2008) noted increased NPP at sites with increased stream nitrate in the same study area.

Nutrient Use Efficiency

Urbanization is frequently associated with altered nutrient availability (Pouyat and Carreiro 2003) and increased photoperiod may explain increased litter production that was observed in this study (Chaney 2002). It is possible that higher nitrate availability in urban streams may contribute to increased productivity (Figure 5) in urban sites and elevated N content (Figure 4) in leaves (Brantley 2008). These changes in N use and availability contribute to the observations in the urban sites that had a low N-NUE in comparison to developing, rural, and pasture sites (Figure 14). These sites cluster together in year 1 (Figure 14a), when streams which have high N loads regularly overtopped their banks (Chapter 2, Figure 33) in the three urban sites which produce litter with high N content while having a high ratio of N to litterfall mass (Brantley 2008). This suggests that urban sites were inefficient, and they have increased nutrient availability enabling them to have high productivity, reinforcing the idea that Vitousek (1982) presented stating that N-NUE is influenced by site nutrient availability. In year 2, when streams did not overtop their banks, urban sites had N-NUE along the curve of the other sites (Chapter 2, Figure 33). Therefore, in riparian systems, N-NUE may be greatly influenced by stream nutrient load and its contact with neighboring floodplains. However, N-NUE for these systems was comparable with those of the Southeastern U.S. in Brinson et al. (1980) and Burke et al. (1999).

There was no trend for P-NUE for either abundance of Chinese privet or land use in this study but was similar to findings of Burke et al. (1999) in the coastal plain of South Carolina. In these systems, P may not be the primary nutrient limiting productivity, since alterations in leaf P concentration did not coincide with increased litterfall (Figure 15) in a similar situation described in Lockaby and Conner (1999).

Major cations can also limit system productivity as in Shilling and Lockaby (2006) where Ca and K deficiencies were suggested to have limited productivity on the blackwater, Satilla River floodplain, while lack of Mg may have limited production on the redwater, Altamaha River floodplain. In west Georgia, it is possible that Mg and Ca are limiting productivity to some degree (Figure 16). Mg-NUE was lower in uninvaded sites than moderately and severely invaded sites, which may indicate that Chinese privet requires greater quantities of Mg compared to native species (Figure 16a). Inefficient use of Ca on severely invaded sites suggested that Chinese privet was not limited by Ca availability (Figure 16c).

Comparisons between cation NUE (Figure 16) and cations soil availability (Chapter 2) were conducted for west Georgia data. Uninvaded sites had inefficient use of Mg (Figure 16a) and a higher amount of Mg in soil (Chapter 2) than moderately invaded sites. However, severely invaded sites also had a high amount of Mg in soil but were less efficient than uninvaded sites in nutrient utilization. It is possible that Chinese privet is less efficient or has a greater Mg demand than native species.

Ca-NUE and soil availability of Ca also had interesting trends since severely invaded sites had high Ca availability in the soil and inefficient Ca circulation (Figure 16c and Chapter 2). Uninvaded sites clustered together and had a greater amount of Ca per gram of leaf tissue (Figure 16c) possibly due to an understory comprised of mostly dogwood. The leaves of dogwoods have a greater concentration of Ca than co-occurring species and decompose rapidly, thereby increasing the amount of plant available Ca in the forest floor (Thomas 1969, Holzmueller et al. 2007, Jenkins et al. 2007). Furthermore, uninvaded sites have high soil availability of Ca (Chapter 2) and are more efficient than invaded sites for circulating Ca (Figure 16c). In contrast, productivity on moderately invaded sites may be limited by Ca availability because Ca-NUE was lower and there is a lower availability of Ca in the soil compared to the uninvaded and severely invaded sites (Chapter 2). Although NUE can give indications of nutrient limitations it is not definitive proof of nutrient limitations in a stand.

Differences in NUE among sites were not as great as the differences observed between red- and blackwater systems observed by Schilling and Lockaby (2006). However, there were similar N, Ca, and Mg limitations on productivity in west Georgia and the redwater systems of the Altamaha River as suggested by high NUE (Schilling and Lockaby 2006). Furthermore, the differences among sites for cation NUE observed in this study reinforce the importance of cation cycling and limitations in riparian systems such as those in Schilling and Lockaby (2006).

Resorption Efficiency/Proficiency

Nutrient resorption can serve as a nutrient conservation strategy by plants to reduce the amount of nutrients required by plants to be taken up from soil pools. Killingbeck (1996) determined that resorption proficiency values can be used to compare nutrient limitations across systems and proposed minimum concentrations (*i.e.* maximum proficiency) in senesced leaves. Therefore, it is possible to compare resorption proficiency across sites and these may suggest relative differences in nutrient availability (Killingbeck 1996).

In this study, there were greater differences for resorption proficiency (Figure 17) and efficiency (Figure 18) among species rather than among sites. Sweetgum exhibited resportion efficiencies similar to those in Burke et al. (1999) for sweetgum in South Carolina. However, Chinese privet, as hypothesized, was not as efficient as sweetgum since it abscised leaves with higher concentration of N. This may have contributed to Chinese privet leaves having high litter quality and decomposing rapidly.

Killingbeck (1996) suggested that specific resorption values indicate the completeness of resorption, values less than 0.7% represent complete resorption for N and values greater than 1.0% indicate incomplete resorption for N (Figure 18). Using these values, both Chinese privet and sweetgum had complete resorption (Killingbeck 1996) but Chinese privet had significantly lower resorption efficiency than sweetgum. This different resulted from the higher N concentration in green and senesced leaves for Chinese privet compared to sweetgum (Figure 18). Chinese privet also had significantly higher N resorption proficiency (Figure 17) or N remaining in leaves after senescence which is credited by Ehrenfeld (2003) as a possible driver for changes in both N and C cycling.

Nitrogen Mineralization and Microbial Biomass

The presence of Chinese privet did not have a significant influence on microbial biomass and the soil process of N-mineralization (Figures 21-27). Microbial biomass was similar to that of the Altamaha River floodplain in Georgia of Schilling and Lockaby (2005). Some studies (Vitousek 1994, Ehrenfeld et al. 2001, Ehrenfeld 2003, Kourtev et al. 2003) have noted the capability of exotic species to alter soil conditions Chinese privet may have also altered the overall extent of microbial activity on these study sites. With time, the changes in altered timing and quality of Chinese privet foliage may influence a shift in species of soil microorganisms similar to those shifts in other studies (Kourtev et al. 2002, Hawkes et al. 2005, Carney and Matson 2006, Kao-Kniffin and Balser 2007).

This study investigated the related changes of Chinese privet on the soil process of N-mineralization. N-mineralization rates observed in this study were similar to those described by Idol et al. (2003) in upland hardwood forests but greater than those of Jolley (2008) in ephemeral floodplains in the coastal plain of Georgia. N-mineralization had a positive regression with system productivity in west Georgia similar to the positive relationship reported by Newman et al. (2006). Both this study and Newman et al. (2006) observed that when rates of N-mineralization increased there was a greater amount of available N for plant uptake which then helped drive productivity. In summer months, N-mineralization rates were higher in severely invaded sites, possibly because of the higher N composition of litterfall on those sites in the spring and summer.

CONCLUSIONS

The influence of Chinese privet on nutrient cycling in riparian forests was observed in several variables. There was a noticeable influence of Chinese privet leaf litter on nutrient cycling in riparian forests, but there was also a land use influence observed in this study. Differences in annual N and C content were related to dominant land use classifications and associated dynamics of site productivity. Although, urban sites did not appear to be as limited by N availability as the other sites, they still were N limited in drought periods. This was evidenced by their reduced productivity and N concentration, and altered N-NUE during year 2 which had drought conditions. It is possible that greater stream N availability or prolonged photoperiod enables urban stands to be more productive and have lower N efficiency. However, Chinese privet may be similar to other exotic species by being able to boost available N due to altered timing of senescence and high N concentration in litterfall compared to native species.

Among the Chinese privet classes there were observable modifications in leaf chemistry, such as increased N concentration in the moderately and severely invaded sites. Cation differences in litterfall may be influenced by increasing abundance of Chinese privet, since moderately and severely invaded sites have different Mg- and Ca-NUE in comparison to uninvaded sites. Mean N-mineralization was significantly greater for severely invaded sites in comparison to uninvaded sites for summer samples. Severely invaded sites had a trend of increased N-mineralization in other seasons compared to the other Chinese privet classes. Also, there was increased productivity on sites with greater N-mineralization where with excess N may be contributed by Chinese privet.

Nutrient composition of Chinese privet leaves was compared to native leaves. Chinese privet exhibited higher resorption proficiency for N compared to native sweetgum, indicating greater potential for internal nutrient circulation in the latter species. There were distinct seasonal patterns of nutrients in litterfall, microbial biomass, and N-mineralization associated with the sites that had Chinese privet contributing to litterfall. Therefore, Chinese privet does alter timing and quality of leaf litter as it invades a site. Not only did Chinese privet alter species composition and regeneration in forests (Burton et al. 2005, Burton and Samuelson 2007, Brantley 2008), it has further capability to alter sites by changing biogeochemical dynamics as observed in this study. More in-depth investigation on nutrient requirements of Chinese privet would improve the knowledge base of possible biogeochemical changes that may result from Chinese privet in a forest.

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Table 1. Forest floor biomass and nutrient content among classes of Chinese privet in understory in west Georgia. One-way ANOVA results presented with standard error in parentheses. Percent change was calculated by the following equation [(maximum-minimum)/maximum]*100.

forest floor	Class of Chinese privet in understory			$F_{df\ 2,61}$	p-value
	uninvaded	moderately invaded	severely invaded		
dry weight g/m^2					
maximum	780.0 (79.1)	687.6 (66.9)	860.1 (112.3)	1.23	0.32
minimum	355.8 (89.9)	450.2 (83.4)	526.5 (89.3)	1.21	0.33
% change	54.9 (6.2)	34.8 (11.4)	37.5 (5.2)	1.26	0.32
C content g/m^2					
maximum	350.5 (38.9)	308.4 (33.8)	378.8 (52.1)	1.06	0.37
minimum	146.3 (45.9)	183.5 (31.6)	224.6 (37.4)	1.49	0.26
% change	59.1 (6.9)	41.5 (8.8)	39.9 (4.5)	1.83	0.20
N content g/m^2					
maximum	5.4 (0.5)	5.9 (0.6)	7.1 (1.0)	1.41	0.28
minimum	3.3(0.9)	4.9 (0.7)	5.6 (1.1)	1.81	0.20
% change	37.3 (10.5)	18.1 (12.7)	20.2 (6.1)	0.86	0.50
P content g/m^2					
maximum	1.2 (0.1)	0.9 (0.1)	1.1 (0.1)	2.86	0.09
minimum	0.5 (0.1)	0.6 (0.1)	0.7 (0.1)	0.55	0.59
% change	55.8 (5.0)	31.4 (10.2)	37.9 (4.4)	2.26	0.14

Table 2. Forest floor biomass and nutrient content comparisons among dominant land-use classification in watershed in west Georgia. One-way ANOVA results presented with standard errors are in parentheses. Percent change was calculated by the following equation [(maximum-minimum)/maximum]*100.

forest floor g/m^2	dominant land-use in watershed				$F_{df\ 2,\ 61}$	p-value
	urban	developing	rural	pasture		
dry weight						
maximum	1090 (124)^{A}	713.0 (58.0)^{B}	723.1 (44.1)^{B}	734 (83.9)^{B}	5.56	0.01
minimum	606 (60.7)	439 (44.4)	442 (68.7)	435(183)	0.76	0.50
% change	42.5 (0.1)	38.3 (3.7)	37.3 (11.4)	44.4 (16.8)	0.10	0.96
C content						
maximum	479 (49.0)^{A}	318 (29.5)^{B}	330 (20.6)^{B}	316 (36.0)^{B}	5.04	0.02
minimum	261 (29.2)	189 (22.0)	179 (29.2)	178 (72.5)	0.97	0.40
% change	44.2 (8.4)	40.1 (3.1)	45.2 (9.4)	47.2 (15.3)	0.10	0.96
N content						
maximum	6.3 (1.0)	7.13 (1.1)	6.1 (0.6)	6.0 (0.8)	0.34	0.80
minimum	5.9 (0.6)	4.9 (0.6)	4.8 (1.0)	4.4 (1.7)	0.34	0.80
% change	3.3 (7.3)	29.0 (6.6)	24.2 (0.1)	29.3 (19.1)	1.10	0.40
P content						
maximum	1.1 (0.2)	1.0 (0.08)	1.1 (0.1)	1.0 (0.2)	0.38	0.77
minimum	0.7 (0.1)	0.6 (0.07)	0.7 (0.1)	0.6 (0.2)	0.18	0.91
% change	38.3 (5.1)	40.0 (5.3)	37.3 (11.7)	42.0 (12.4)	0.04	0.99

Different letters represent significant differences in means by Tukey's HSD (p=0.05).

Table 3. Mean concentrations of nutrients in litterfall in west Georgia riparian forests divided by year and classes of Chinese privet in the understory. One-way ANOVA results for comparisons among classes for each year, p, F, and degrees of freedom (df) are presented.

		class					
year	nutrient concentration (mg/kg)	uninvaded	moderately invaded	severely invaded	p	F	df
1	N	12,300 (300)^{ab}	13,400 (300)^{a}	12,000 (200)^{b}	0.001	6.7	2,698
	P	2,000 (50)^{a}	1,800 (40)^{b}	1,600 (20)^{c}	<0.0001	31.8	2,685
	C	474,000 (1,000)^{a}	472,500 (1,000)^{a}	467,300 (900)^{b}	<0.0001	12.6	2,698
2	N	10,600 (400)^{b}	12,100 (300)^{a}	11,600 (200)^{ab}	0.007	5.0	2,689
	P	1,900 (70)^{a}	1,700 (50)^{b}	1,700 (40)^{b}	0.005	5.4	2,683
	C	468,300 (1,300)^{ab}	472,000 (900)^{a}	465,400 (1,400)^{b}	0.004	5.5	2,698
1&2	N	11,500 (300)^{b}	12,700 (200)^{a}	11,800 (1,400)^{a}	0.0001	8.9	2,1399
	P	2,000 (40)^{a}	1,700 (30)^{b}	1,600 (20)^{c}	<0.0001	24.8	2,1371
	C	471,200 (900)^{a}	472,000 (700)^{a}	466,300 (800)^{b}	<0.0001	14.5	2,1399

Different letters represent significant differences in means by Tukey's HSD (p=0.05).

Table 4. Mean litterfall mass, N, C, and P content in west Georgia riparian forests divided by year and classes of Chinese privet in the understory. One-way ANOVA results for comparisons among classes for each year, p, F, and degrees of freedom (df) are presented.

		class				
year	mass and nutrient content (g/m^2)	uninvaded	moderately invaded	severely invaded	p	$F_{2,13}$
1	mass	675.8(4.3) ^{a}	850.2(47.4) ^{a}	817.8(55.3) ^{a}	0.2	1.9
	N	7.4(0.3) ^{b}	10.3(0.5) ^{a}	9.2(0.4) ^{ab}	0.01	6.2
	P	1.20(0.04) ^{a}	1.35(0.06) ^{a}	1.17(0.07) ^{a}	0.2	2.1
	C	338.1(1.7) ^{a}	426.1(23.9) ^{a}	410.3(28.5) ^{a}	0.2	1.8
2	mass	564.4(5.5) ^{a}	697.5(33.0) ^{a}	669.0(26.3) ^{a}	0.05	3.8
	N	5.1(0.1) ^{b}	7.6(0.4) ^{a}	6.9(0.2) ^{ab}	0.002	11.2
	P	0.94(0.04) ^{a}	1.08(0.05) ^{a}	0.98(005) ^{a}	0.3	1.5
	C	278.2(3.6) ^{b}	346.0(16.2) ^{a}	743.5(39.7) ^{a}	0.049	3.8
1&2	mass	620.1(3.7) ^{a}	773.8(39.3) ^{a}	743.5(39.7) ^{a}	0.1	2.6
	N	5.9(0.1) ^{b}	8.5(0.4) ^{a}	7.5(0.3) ^{a}	0.002	10.1
	P	1.07(0.05) ^{a}	1.22(0.05) ^{a}	1.07(0.06) ^{a}	0.2	2.1
	C	290.4(2.8) ^{a}	365.2(17.5) ^{a}	347.3(18.9) ^{a}	0.1	2.7

Different letters represent significant differences in means by Tukey's HSD (p=0.05).

Table 5. One-way ANOVA comparisons for nutrients in seasonal litterfall among classes, F, p, and degrees of freedom (df) are presented.

nutrient	season	year 1			year 2			year 1 and 2		
		p	F	df	p	F	df	p	F	df
N (mg/kg)	fall	0.03	3.7	2,186	0.2	1.6	2,139	0.01	4.7	2,328
	winter	0.003	6.0	2,235	0.6	0.5	2,184	0.3	1.2	2,422
	spring	0.02	4.0	2,131	0.0006	7.6	2,228	<0.0001	10.5	2,402
	summer	0.003	6.1	2,137	0.0005	8.0	2,138	<0.0001	11.2	2,278
C:N	fall	0.1	2.0	2,186	0.4	0.8	2,139	0.14	2.0	2,328
	winter	0.2	1.9	2,235	0.04	3.5	2,184	0.29	1.23	2,422
	spring	0.04	3.2	2,131	0.0009	7.3	2,228	0.0002	8.7	2,362
	summer	0.0008	7.6	2,137	<0.0001	11.7	2,138	<0.0001	19.8	2,278
P (mg/kg)	fall	<0.0001	24.1	2,186	<0.0001	11.0	2,138	<0.0001	33.2	2,328
	winter	<0.0001	18.1	2,222	0.13	2.1	2,175	<0.0001	11.8	2,402
	spring	<0.0001	10.1	2,129	0.03	3.6	2,223	0.0001	9.2	2,355
	summer	0.002	6.7	2,136	0.8	0.3	2,138	0.15	1.9	2,277
N:P	fall	<0.0001	27.4	2,186	<0.0001	17.1	2,138	<0.0001	43.9	2,327
	winter	<0.0001	14.7	2,224	0.002	6.5	1,175	<0.0001	19.8	2,402
	spring	0.0003	8.6	2,129	<0.0001	13.7	2,223	<0.0001	20.2	2,355
	summer	<0.0001	10.8	2,136	<0.0001	11.7	2,138	<0.0001	21.5	2,277
C:P	fall	<0.0001	18.1	2,186	<0.0001	10.7	2,138	<0.0001	26.5	2,327
	winter	<0.0001	18.1	2,224	0.2	1.8	2,175	0.0009	7.2	2,402
	spring	<0.0001	10.2	2,129	0.08	2.6	2,223	0.0005	7.7	2,355
	summer	0.002	6.7	2,137	0.5	07	2,138	0.06	2.8	2,277

Different letters represent significant differences in means by Tukey’s HSD (p=0.05).

Table 6. One-way ANOVA results for comparisons between all species for N and P (mg/kg) concentrations in green and abscised foliage, p, F, and degrees of freedom (df) are presented..

	p	F	df
abscised N concentration	<0.0001	9.9	6,35
green N concentration	<0.0001	10.1	8,33
abscised P concentration	<0.0001	8.6	6,35
green P concentration	<0.0001	7.4	8,33

Table 7. One-way ANOVA results for comparisons of N-mineralization, microbial C and microbial N, p, F, and degrees of freedom are presented.

	nitrogen mineralization g ha^{-1} d^{-1}			microbial C µg g^{-1}			microbial N µg g^{-1}		
season	p	F	df	p	F	df	p	F	df
fall	0.2	1.8	2,46	0.2	1.8	2,23	0.1	2.6	2,23
winter	0.7	0.4	2,111	0.0006	8.0	2,93	0.0004	8.6	2,93
spring	0.1	2.2	2,41	0.008	5.2	2,93	0.008	5.1	2,93
summer	0.046	4.2	2,10	0.07	2.7	2,61	0.009	5.1	2,61

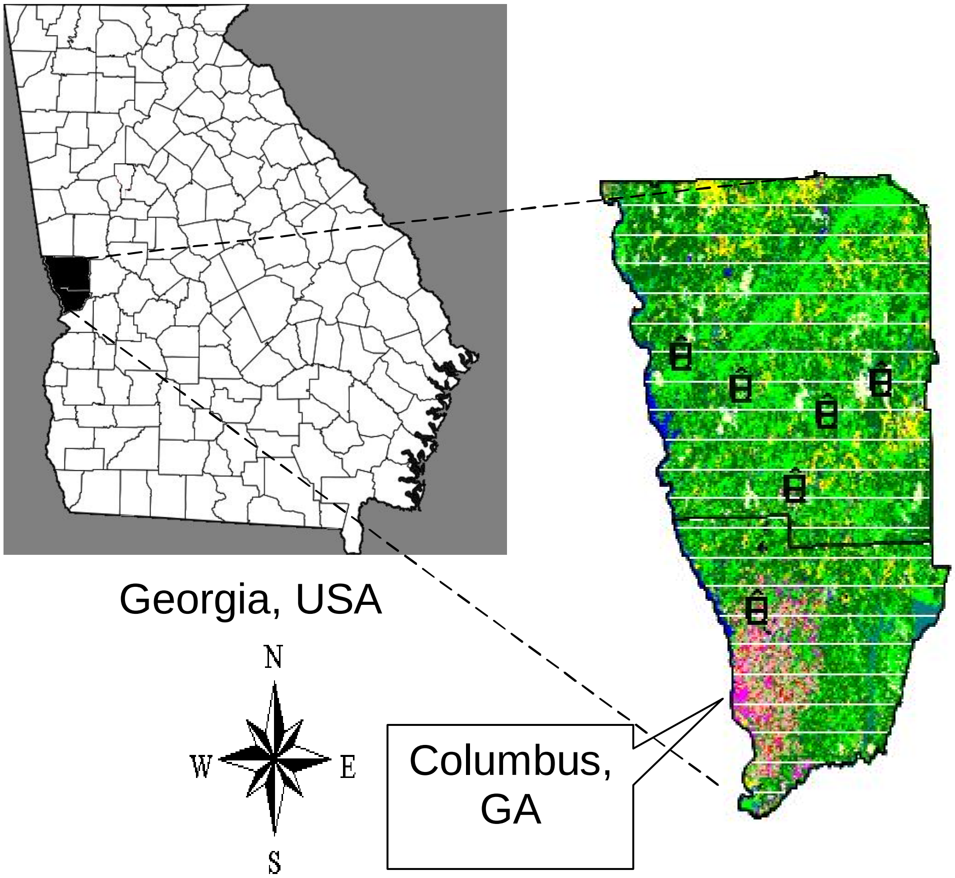


Figure 1. Map showing the location of the six study site watersheds in Muscogee and Harris counties, west Georgia. Chinese privet in understory ranged from 0 for uninvaded sites to 100% for severely invaded sites.

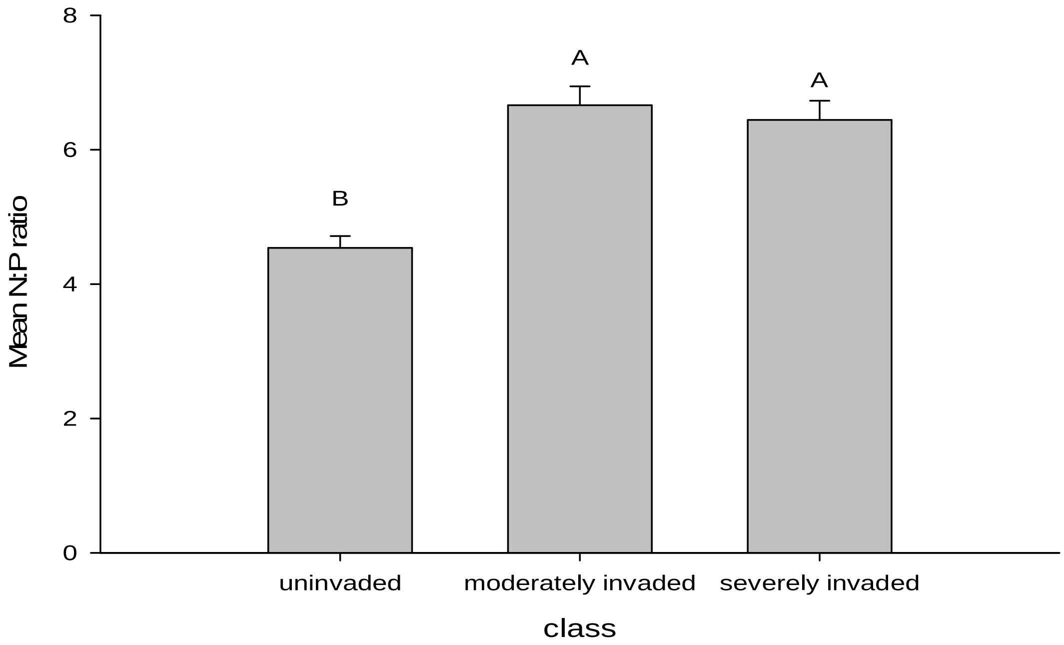


Figure 2. Comparison of N:P ratios for forest floor annual maximum mass among classes of Chinese privet in understory in west Georgia riparian forests. Letters represent significant differences at $p<0.05$ by Tukey's post hoc test. Error bars represent standard error.

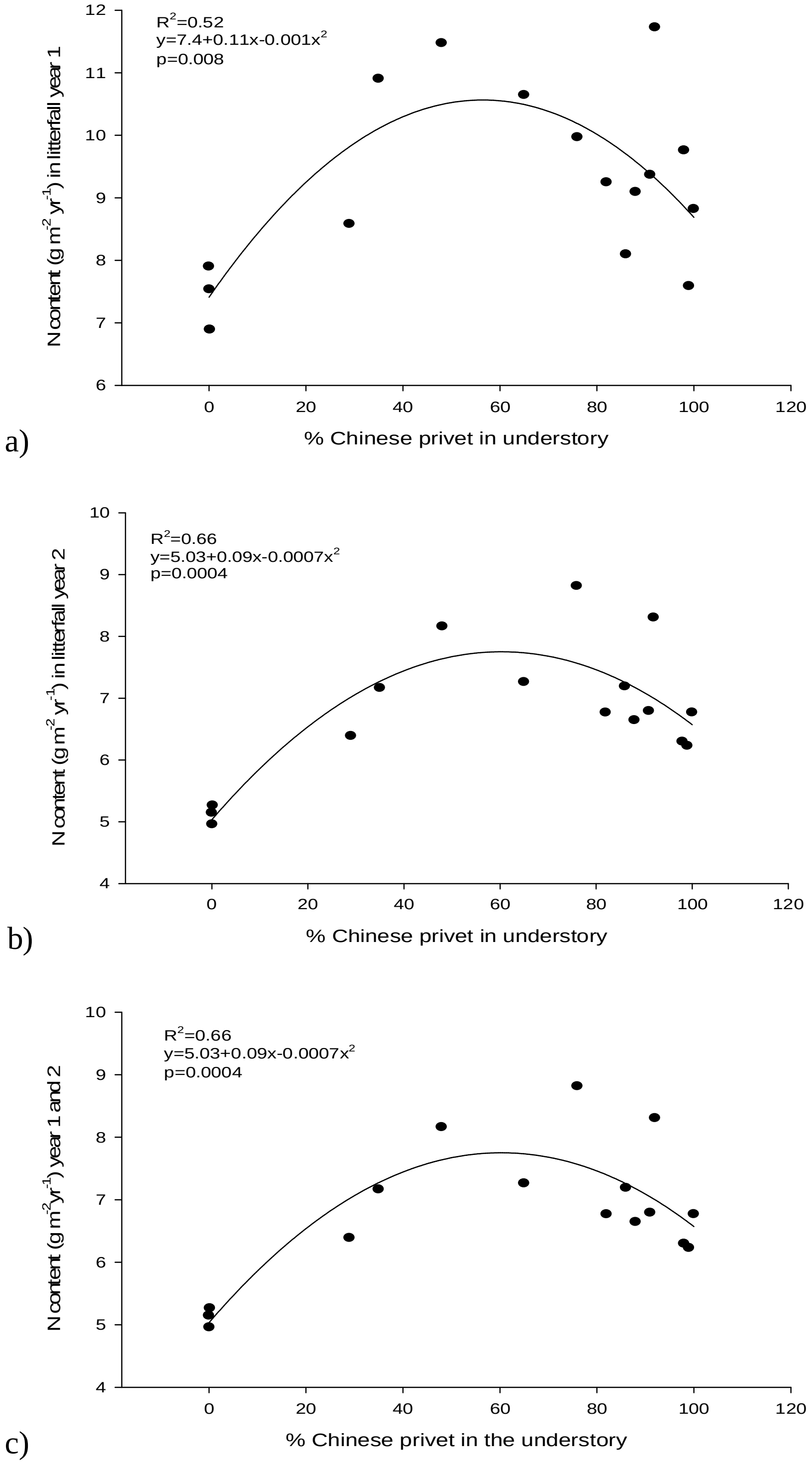


Figure 3. Curvilinear regression relationships between N content in litterfall (including twigs) and percent Chinese privet in understory of riparian forests in west Georgia by a) year 1, b) year 2 and c) year 1 and 2 combined.

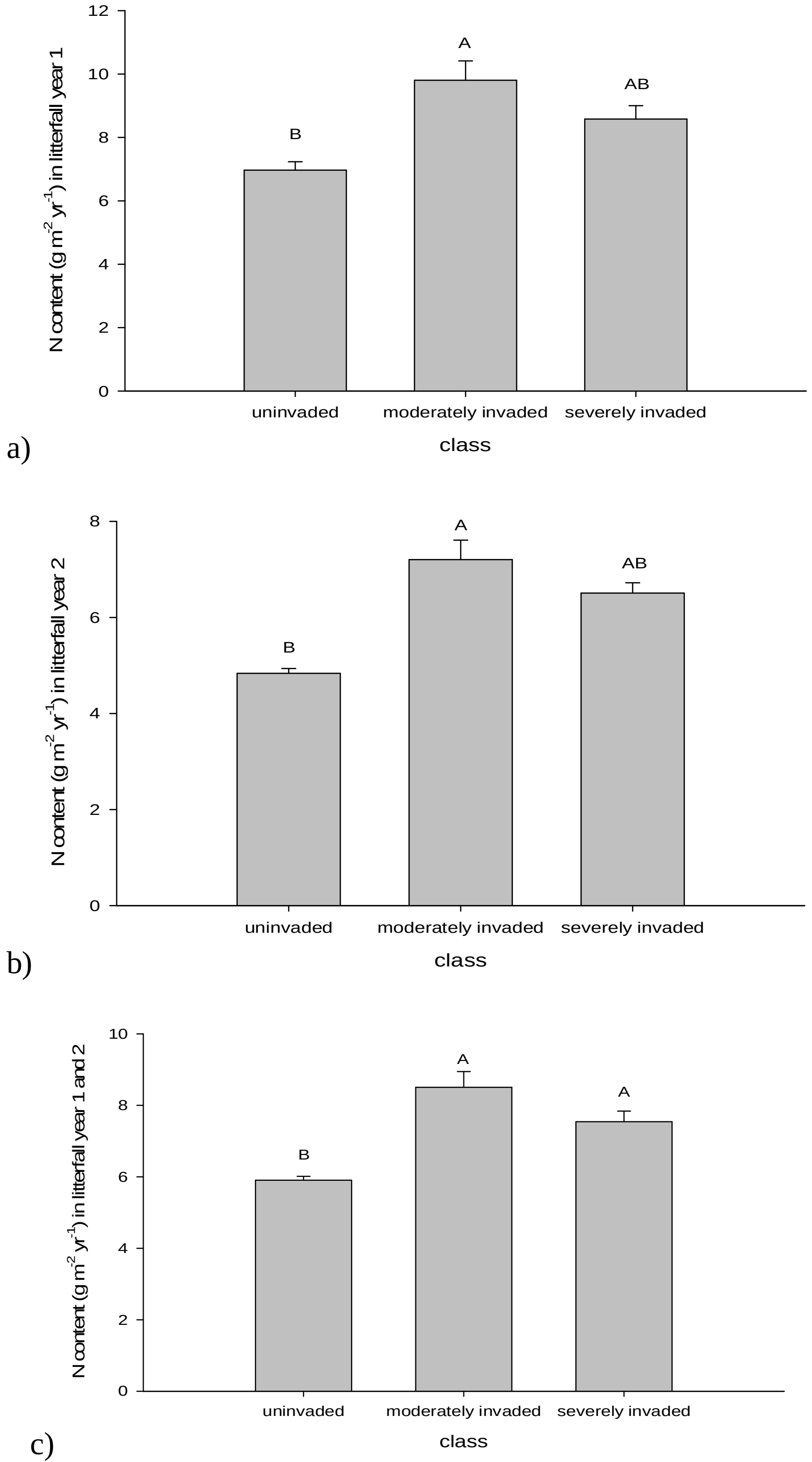


Figure 4. Comparisons of litterfall N content (g m^{-2} yr^{-1}) among classes of Chinese privet in west Georgia for a) year 1, b) year 2, and c) year 1 and 2 combined. Letters represent significant differences at $p<0.05$ by Tukey's post hoc test. Error bars represent standard error.

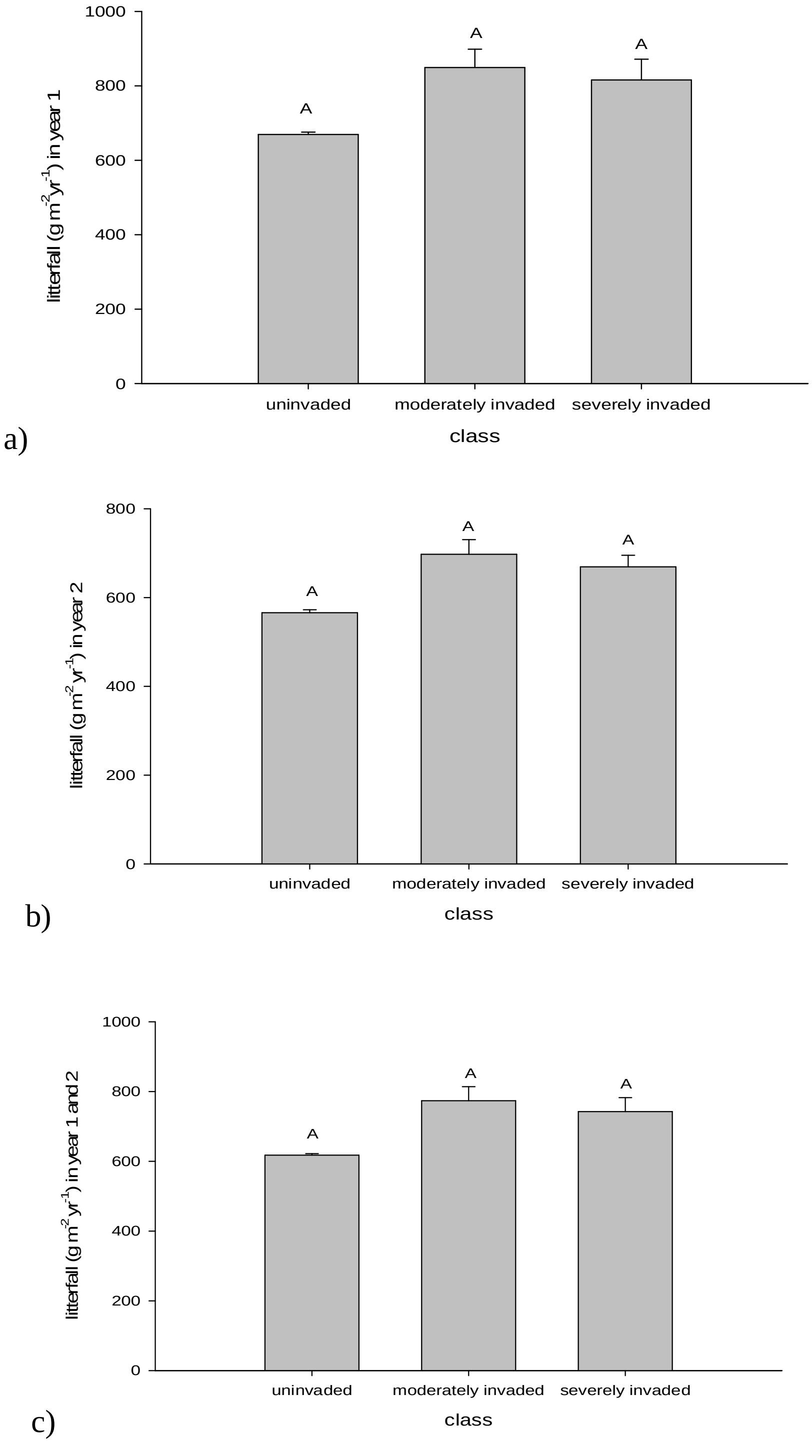


Figure 5. Comparisons of litterfall mass in a) year 1, b) year 2, and c) year 1 and 2 combined among classes of understory Chinese privet in riparian forests in west Georgia (Brantley 2008). Letters represent significant differences at $p<0.05$ by Tukey's post hoc test. Error bars represent standard error.

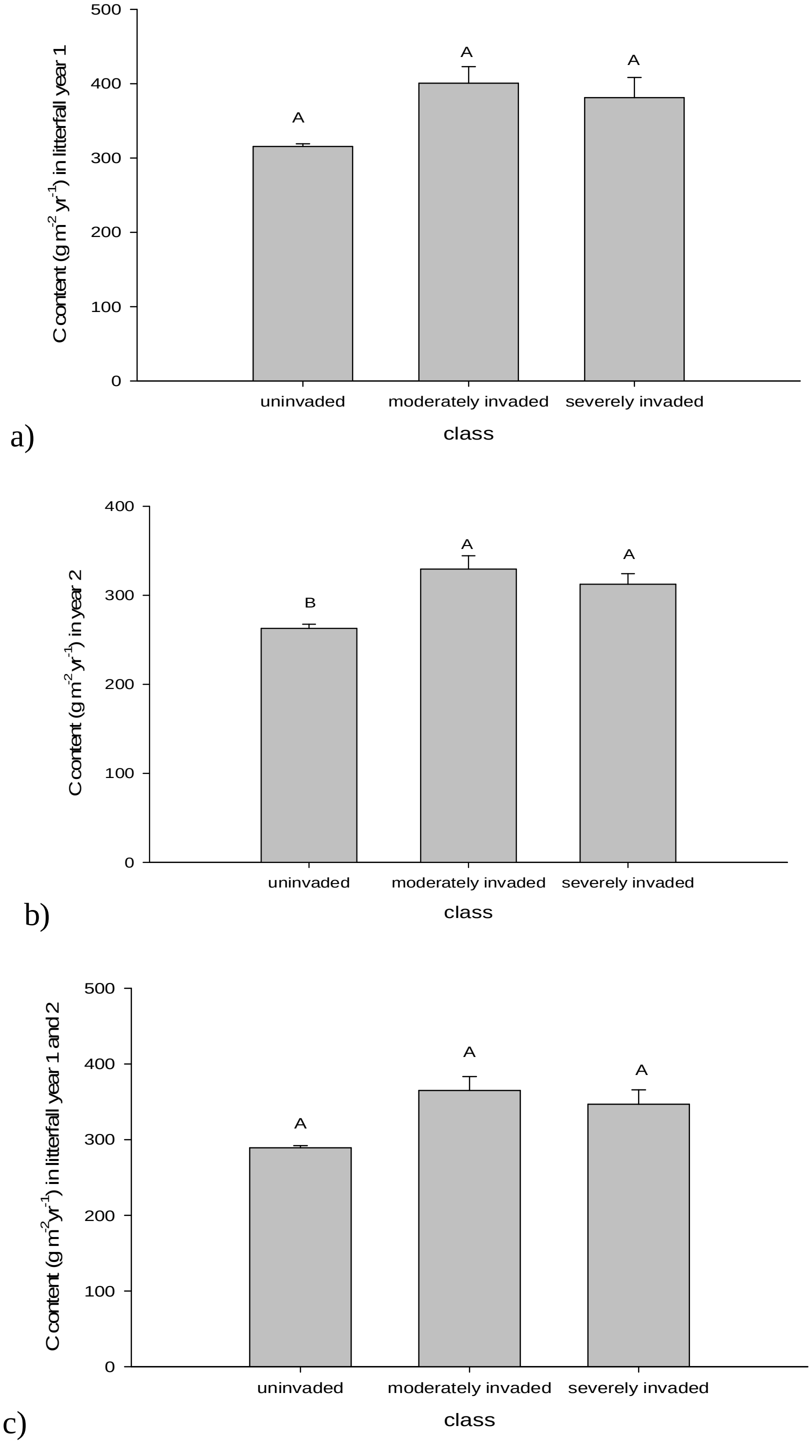


Figure 6. Comparisons of carbon content in a) year 1, b) year 2, and c) year 1 and 2 litterfall combined among classes of understory Chinese privet in riparian forests in west Georgia. Letters represent significant differences at $p<0.05$ by Tukey's post hoc test. Error bars represent standard error.

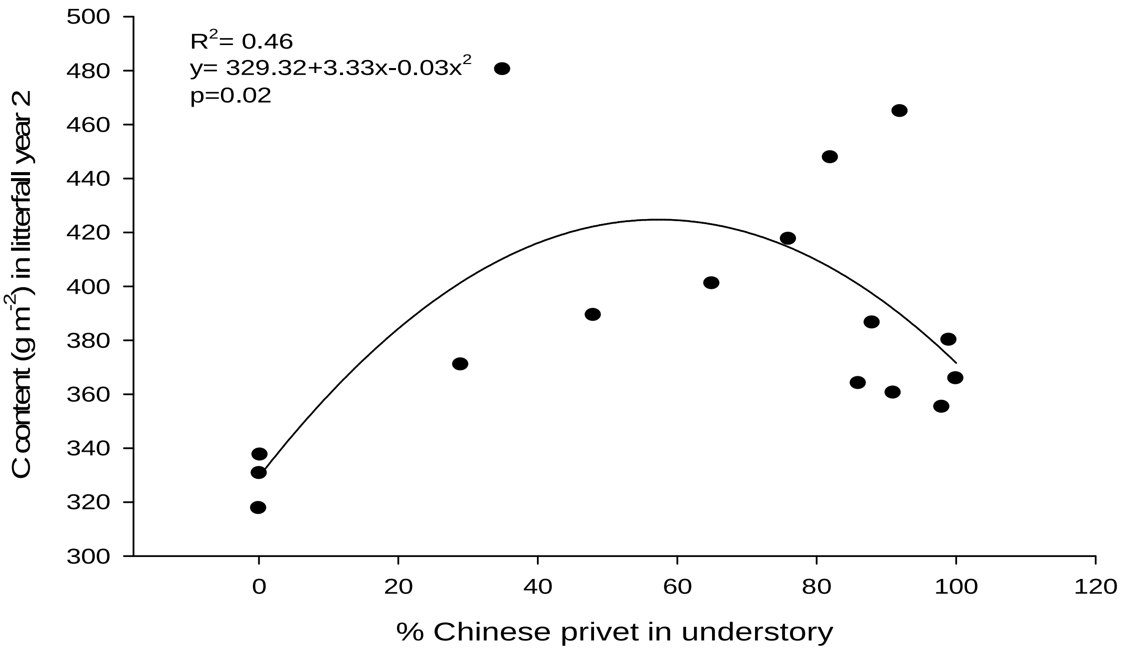


Figure 7. Curvilinear regression relationship between C content in litterfall including twigs and percent Chinese privet in understory of riparian forests in west Georgia for year 2.

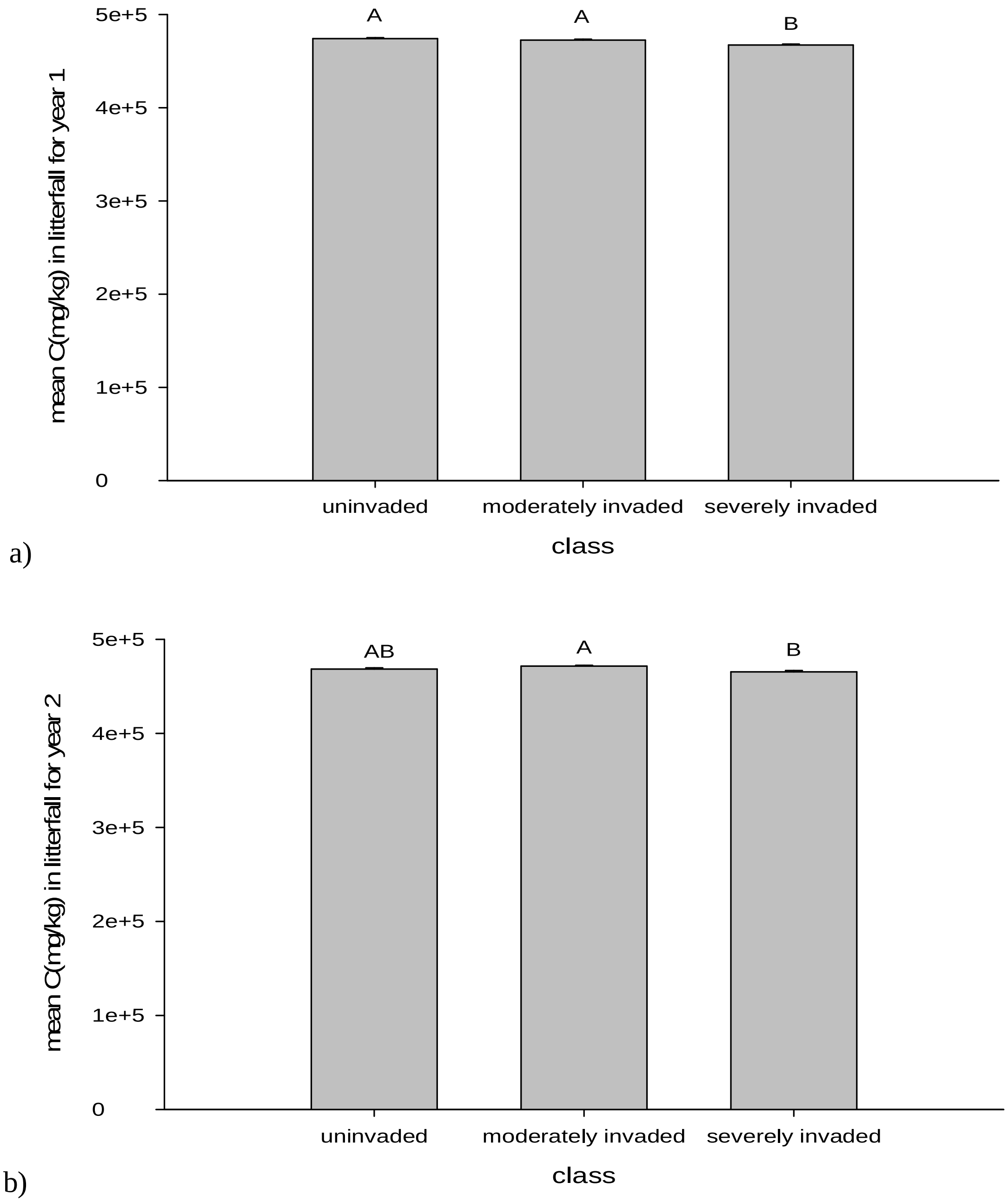


Figure 8. Comparisons of C concentration in a) year 1 and b) year 2 litterfall among classes of understory Chinese privet in riparian forests in west Georgia. Letters represent significant differences at $p<0.05$ by Tukey's post hoc test. Error bars represent standard error.

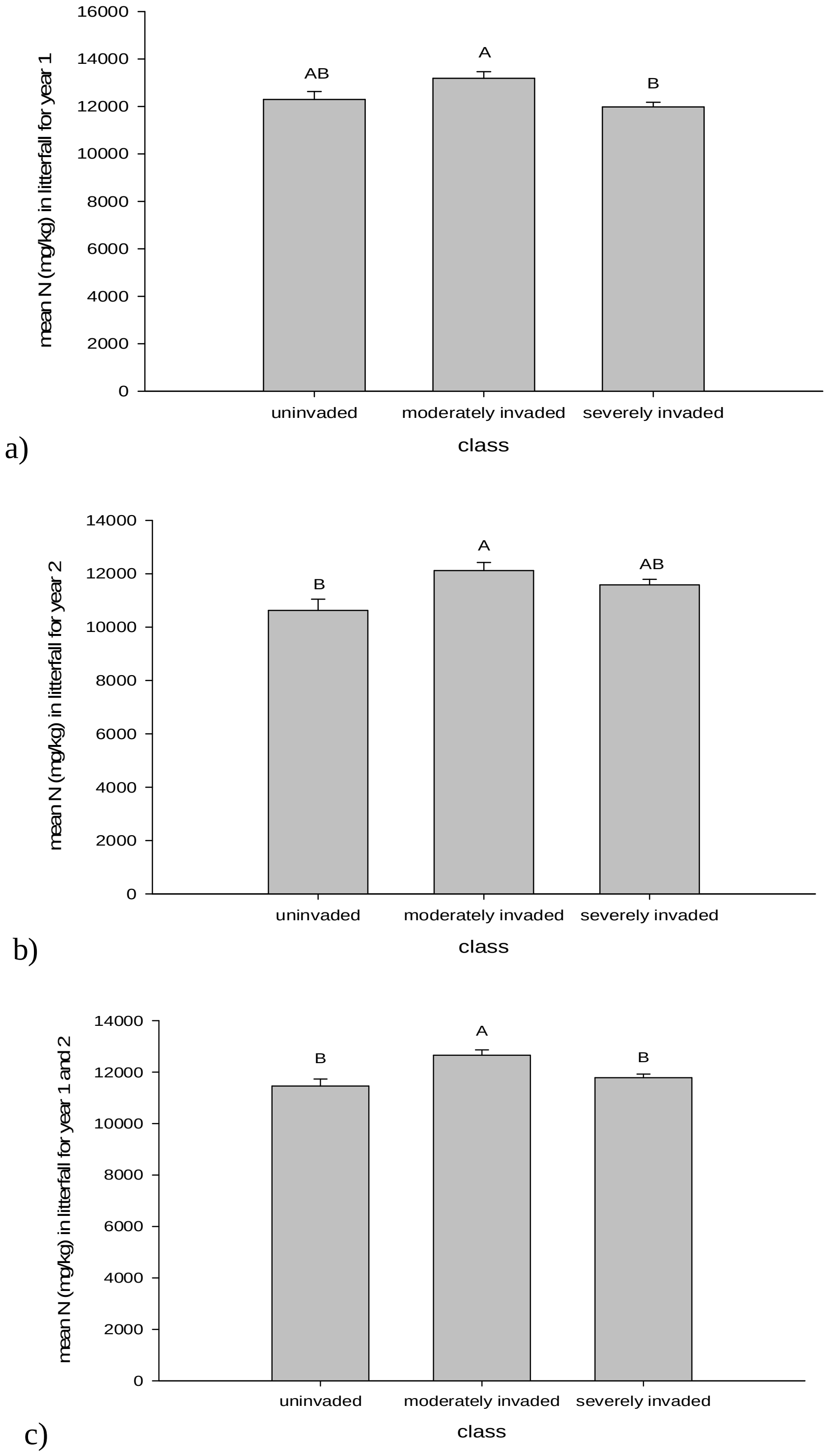
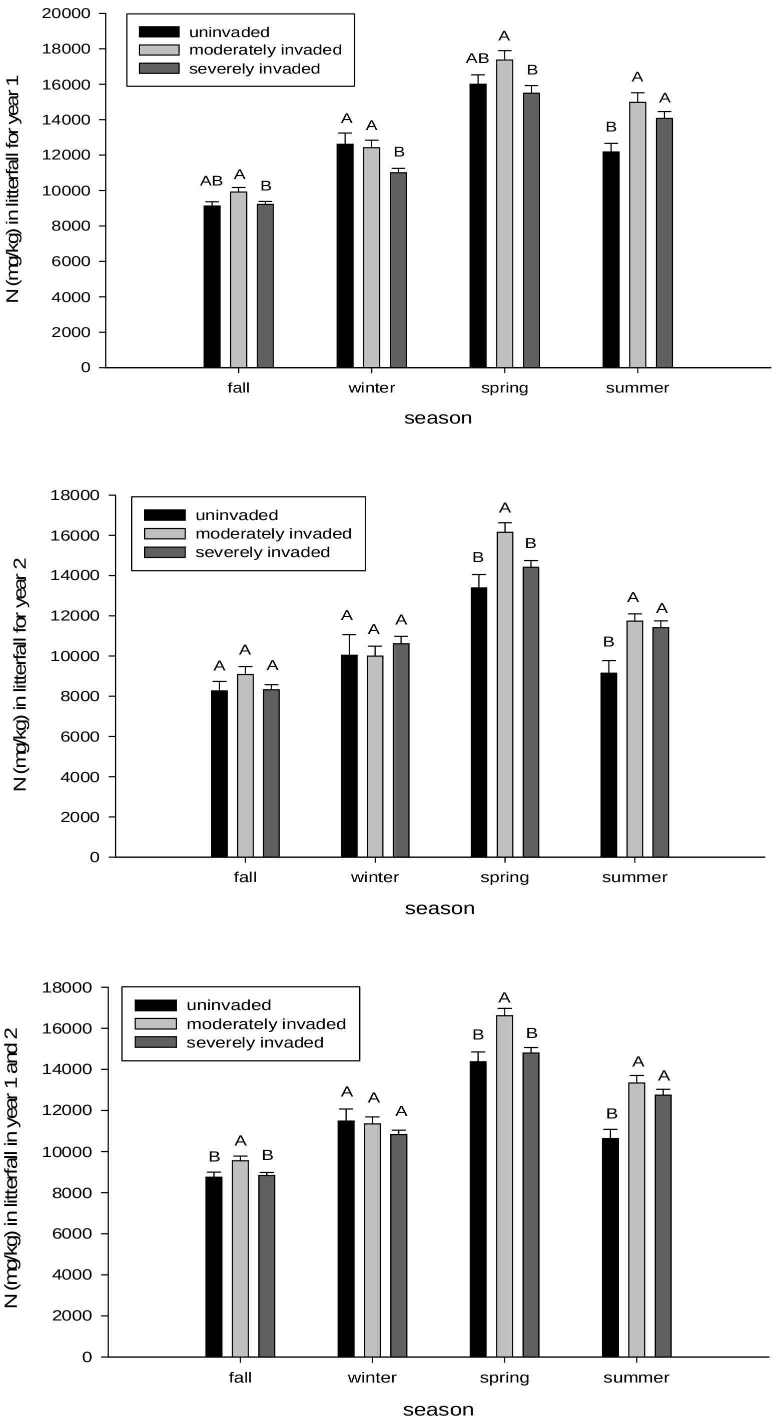


Figure 9. Comparisons of litterfall N concentration among classes of Chinese privet in west Georgia for a) year 1, b) year 2, and c) year 1 and 2 combined. Letters represent significant differences at $p<0.05$ by Tukey's post hoc test. Error bars represent standard error.



a)

b)

c)

Figure 10. Comparisons of mean N concentration in litterfall including twigs among classes of understory Chinese privet in riparian forests in west Georgia by season for a) year 1, b) year 2, and c) years 1 and 2 combined. Comparisons were conducted among classes by seasons. Letters represent significant differences at $p<0.05$ by Tukey's post hoc test. Error bars represent standard error.

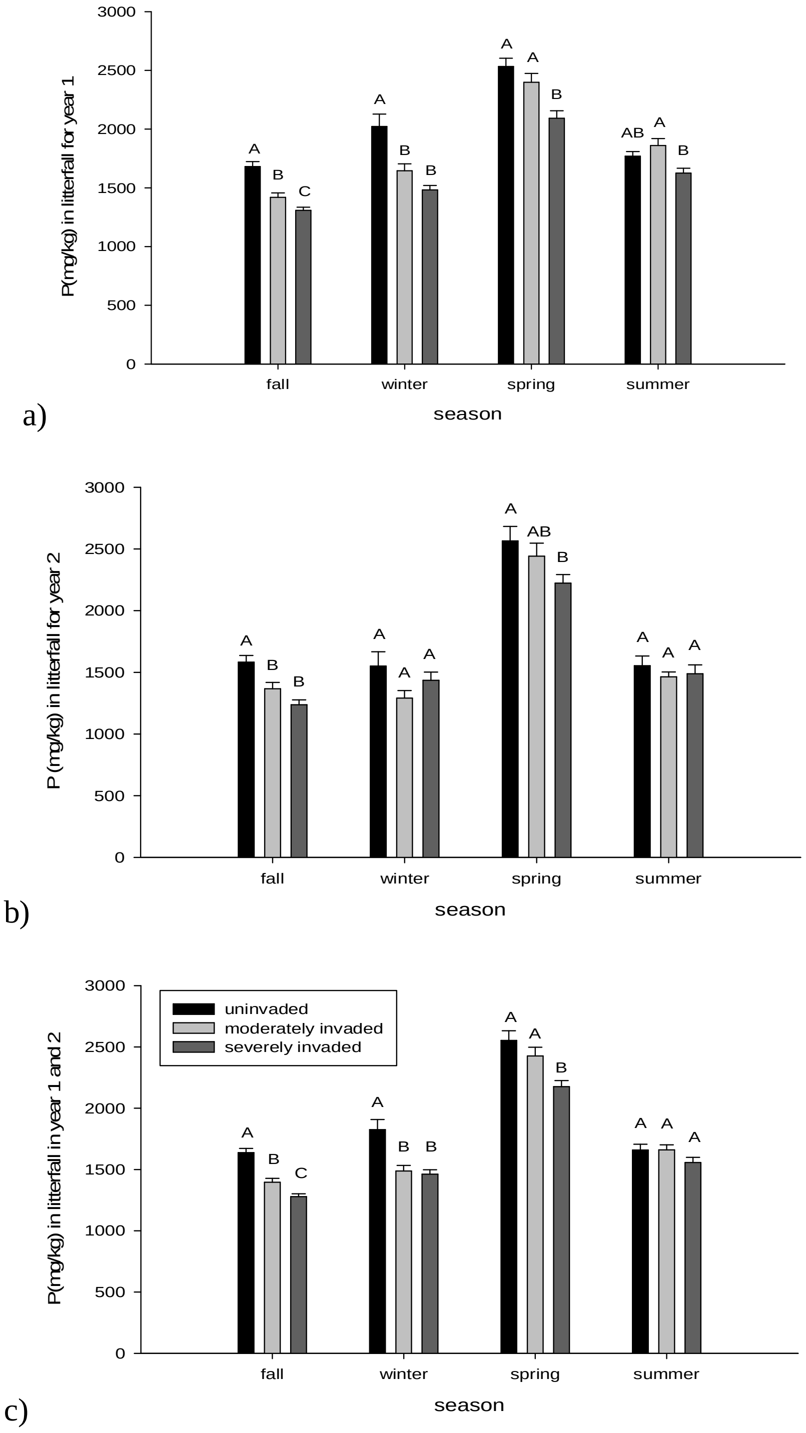


Figure 11. Comparisons of mean P concentration for litterfall among classes of understory Chinese privet in riparian forests in west Georgia for a) year1, b) year 2, and c) years 1 and 2 combined. Comparisons were conducted among classes by season. Letters represent significant differences at p<0.05 by Tukey’s post hoc test. Error bars represent standard error.

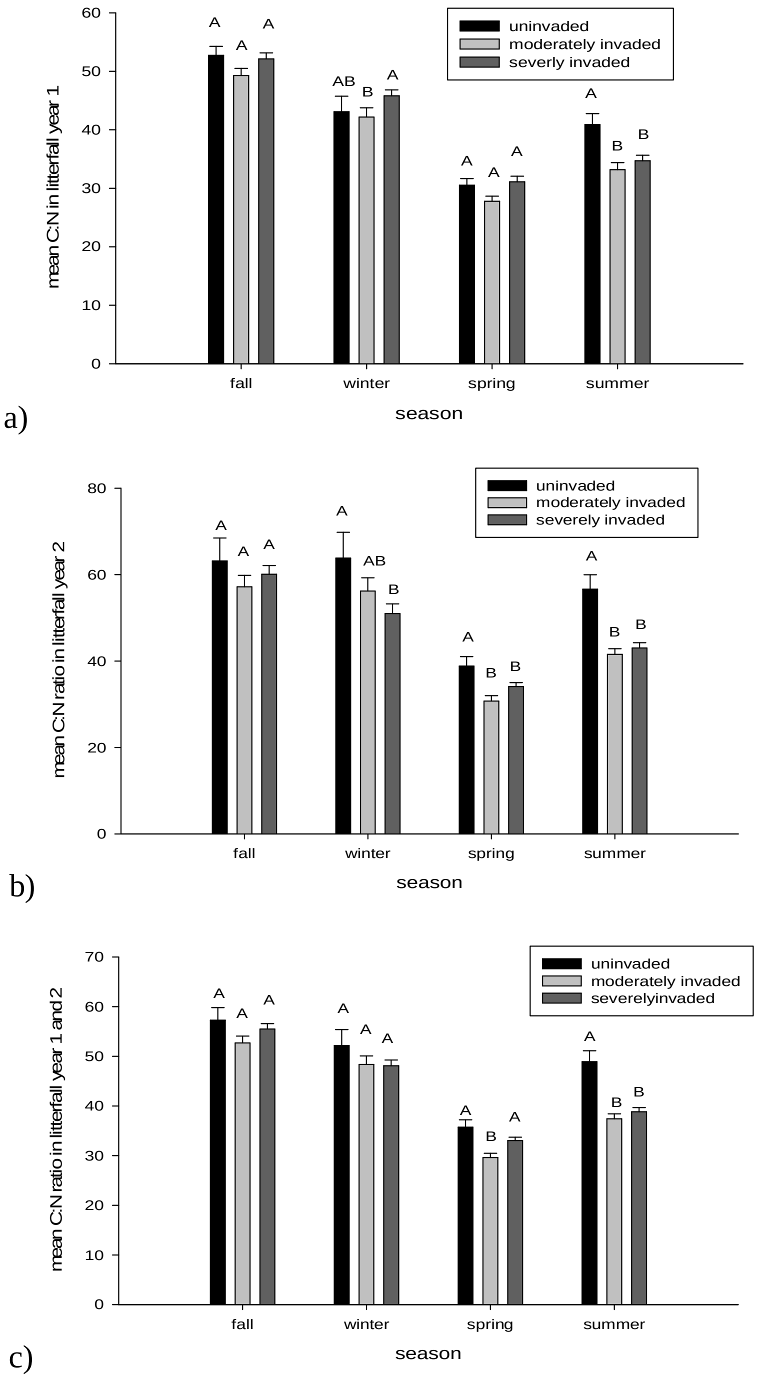


Figure 12. Comparisons of mean C:N ratios in litterfall including twigs among classes of understory Chinese privet in riparian forests in west Georgia by season for a) year 1, b) year 2, and c) year 1 and 2 combined. Comparisons were conducted among classes by season. Letters represent significant differences at $p<0.05$ by Tukey's post hoc test. Error bars represent standard error.

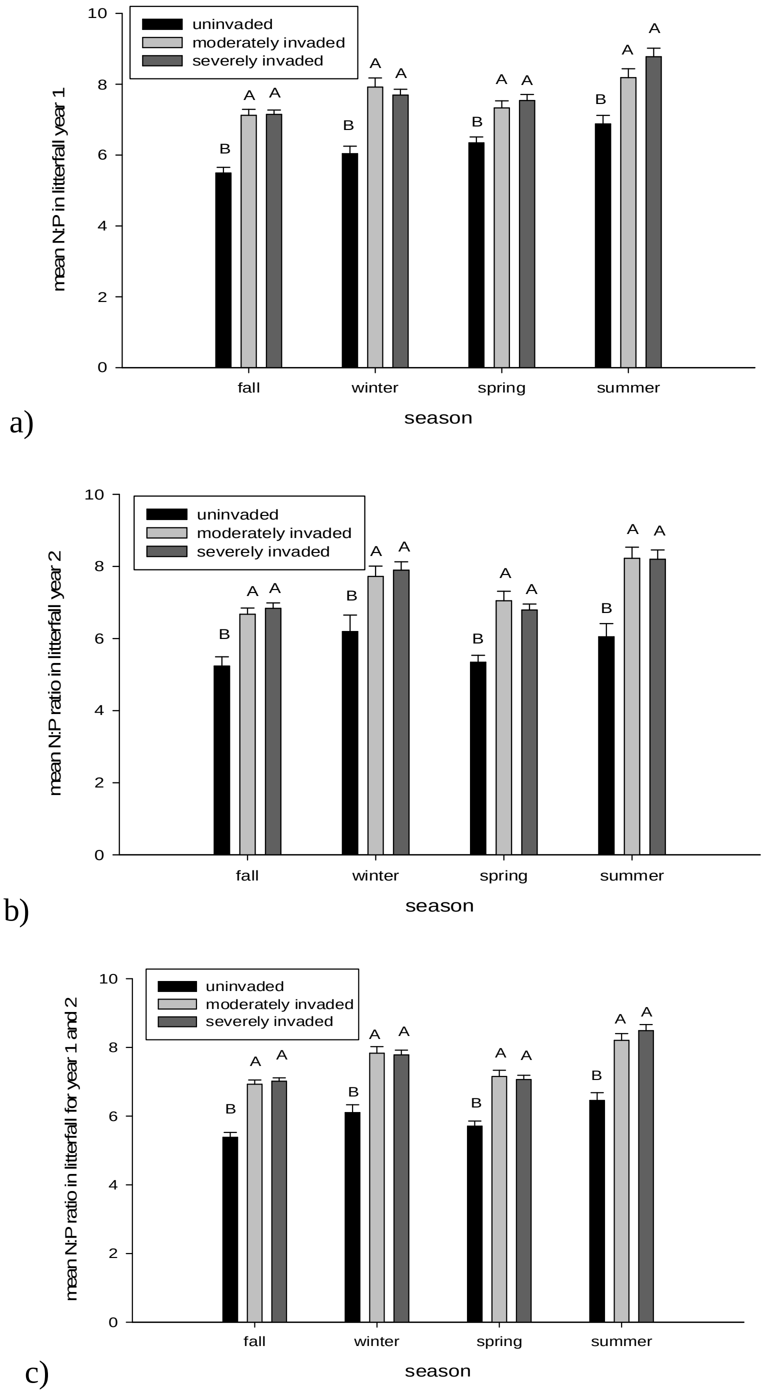


Figure 13. Comparisons of mean N:P ratios for litterfall among classes of understory Chinese privet in riparian forests in west Georgia for a) year 1, b) year 2, and c) years 1 and 2 combined. Comparisons were conducted among classes by season. Letters represent significant at $p<0.05$ by Tukey's post hoc test. Error bars represent standard error.

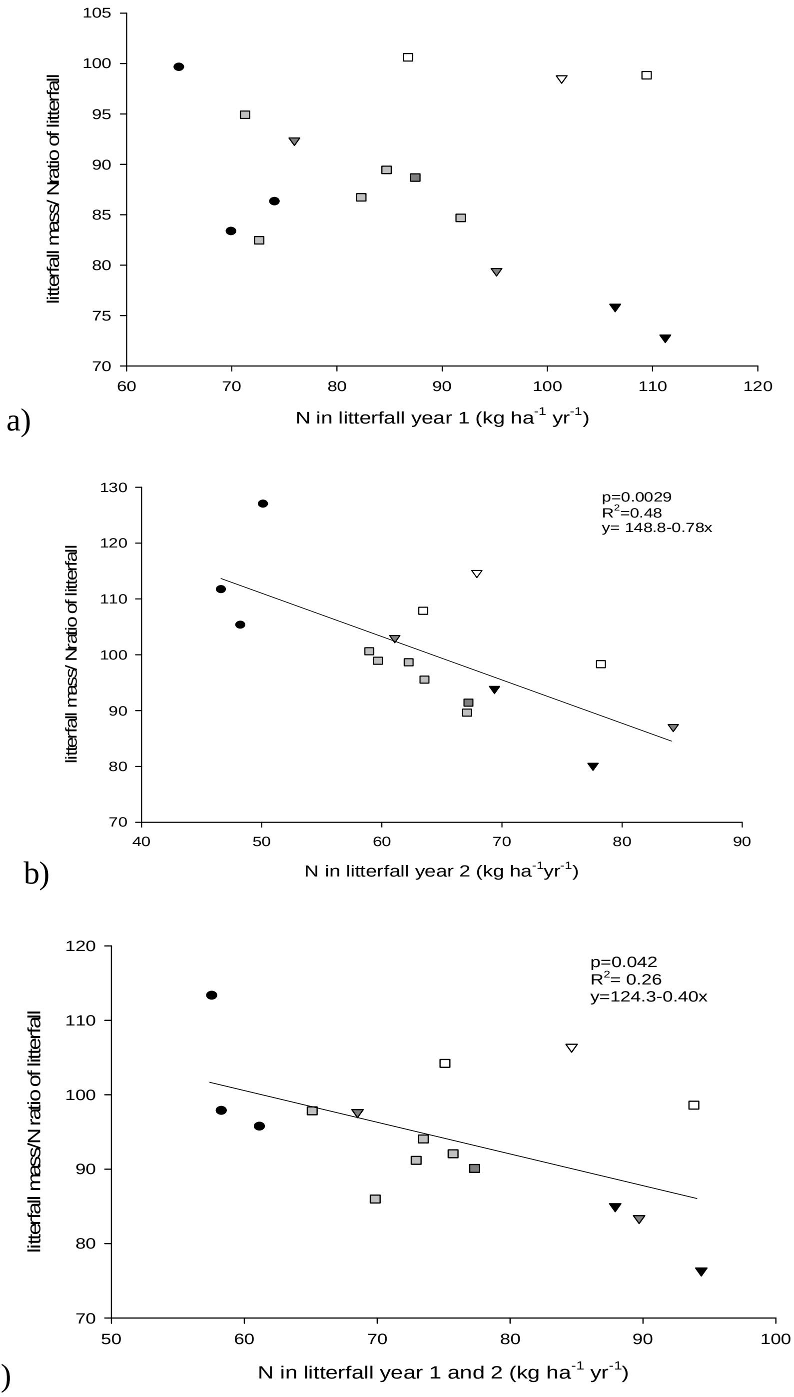


Figure 14. Annual nitrogen content graphed against the litterfall mass/N ratio of litterfall for riparian forests in west Georgia a) year 1, b) year 2, and c) year 1 and 2 combined for sites in riparian forests in west Georgia from May 2005 to April 2007 for different classes of Chinese privet (circle =uninvaded sites, triangle = moderately invaded sites, and squares = severely invaded sites). Land use categories are indicated by shading (black= rural, dark gray=pasture, light gray= developing, white=urban).

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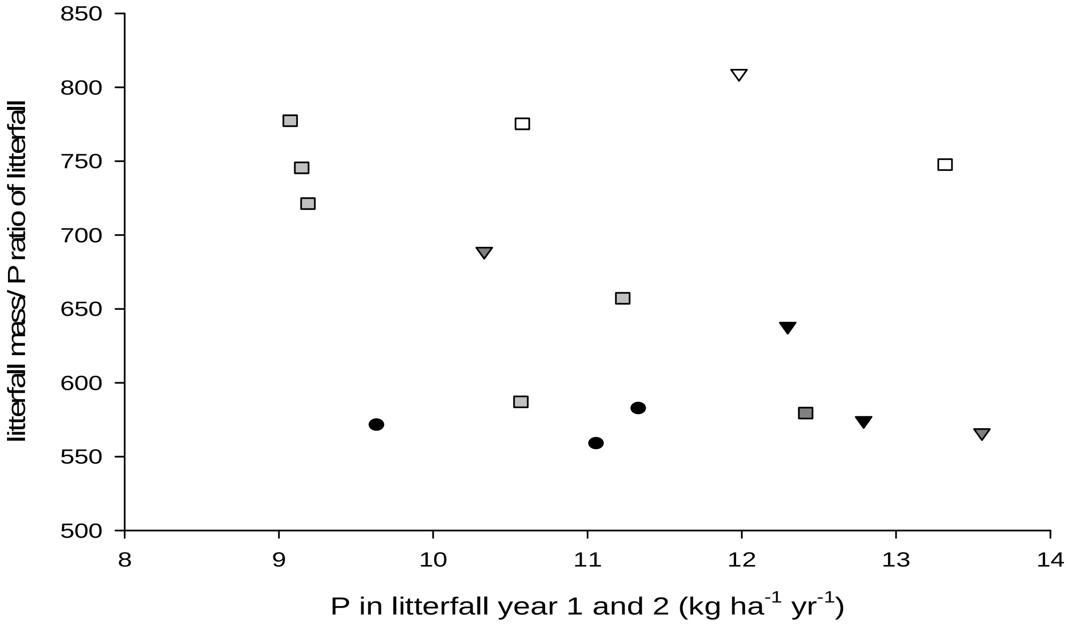

Figure 15 Annual phosphorus content graphed against the litterfall mass/P ratio of litterfall for classes of Chinese privet (circle=uninvaded sites, triangle=moderately invaded sites, and squares=severely invaded sites). Land use categories are indicated by shading (black=rural, dark gray=pasture, light gray=developing, white=urban).

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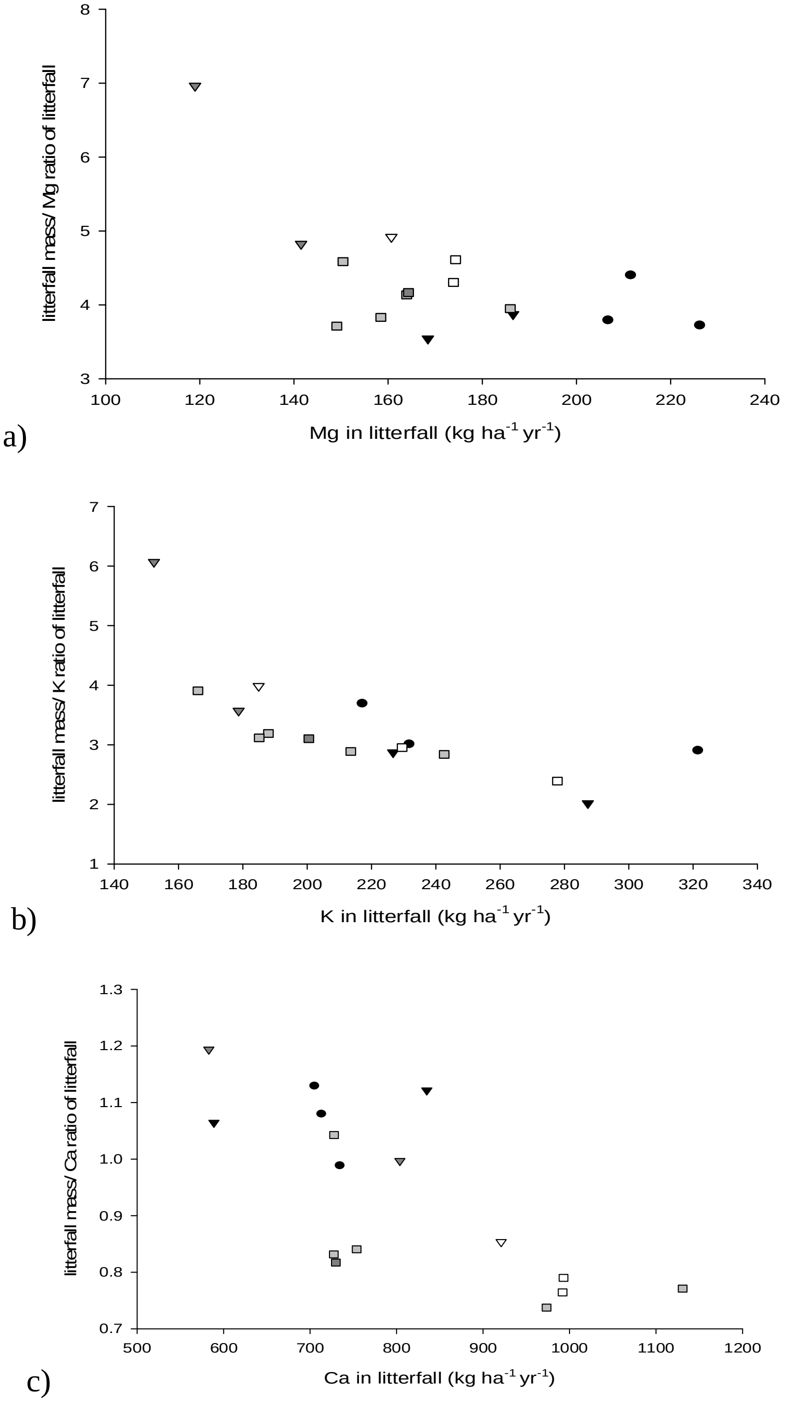


Figure 16. Annual nutrient content graphed against litterfall mass/ nutrient ratio of litterfall a) magnesium, b) potassium, and c) calcium for sites in riparian forests in west Georgia, USA from May 2006 to April 2007 for classes of Chinese privet (circle=uninvaded sites, triangle=moderately invaded sites, and squares=severely invaded sites). Land use categories are indicated by shading (black=rural, dark gray=pasture, light gray= developing, white=urban).

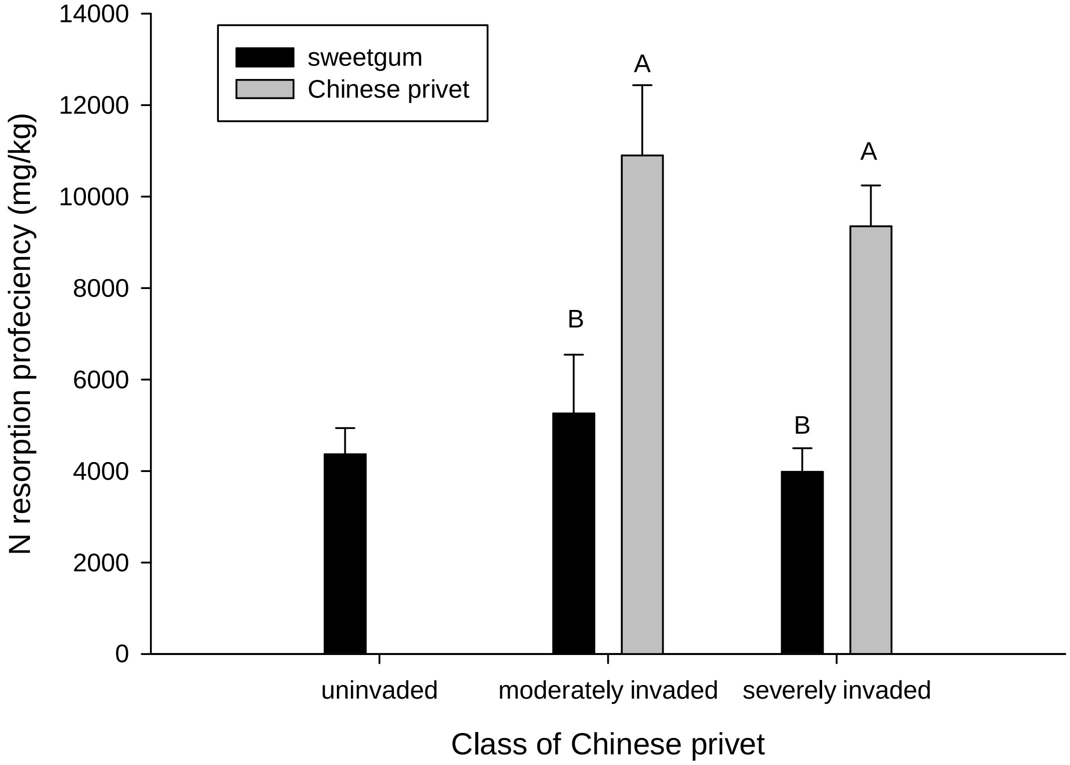


Figure 17. N resorption proficiency by class of Chinese privet in the understory for the two most common species; Sweetgum found on 14 sites and Chinese privet on 13 sites. Letters represent significant differences at p<0.05 by Tukey's post hoc test within Chinese privet classes. Error bars represent standard error.

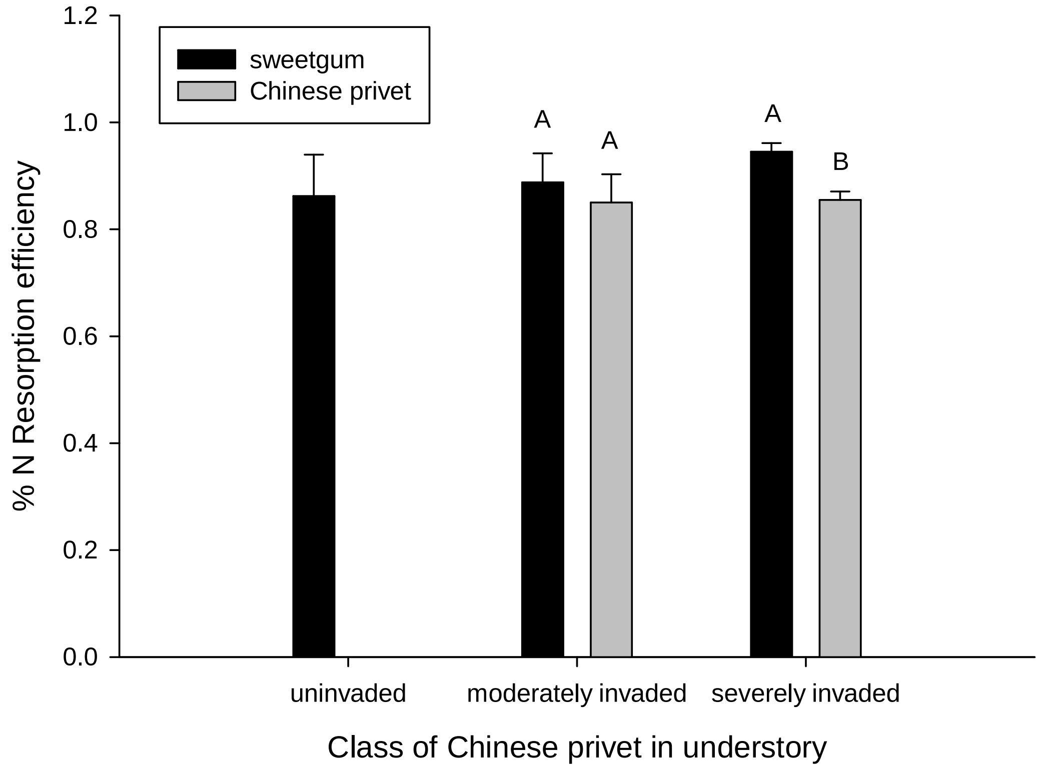


Figure 18. N resorption efficiency by class of Chinese privet in the understory for the two most common species; Sweetgum found on 14 sites and Chinese privet on 13 sites. Letters represent significant differences at $p<0.05$ by Tukey's post hoc test within Chinese privet classes. Error bars represent standard error.

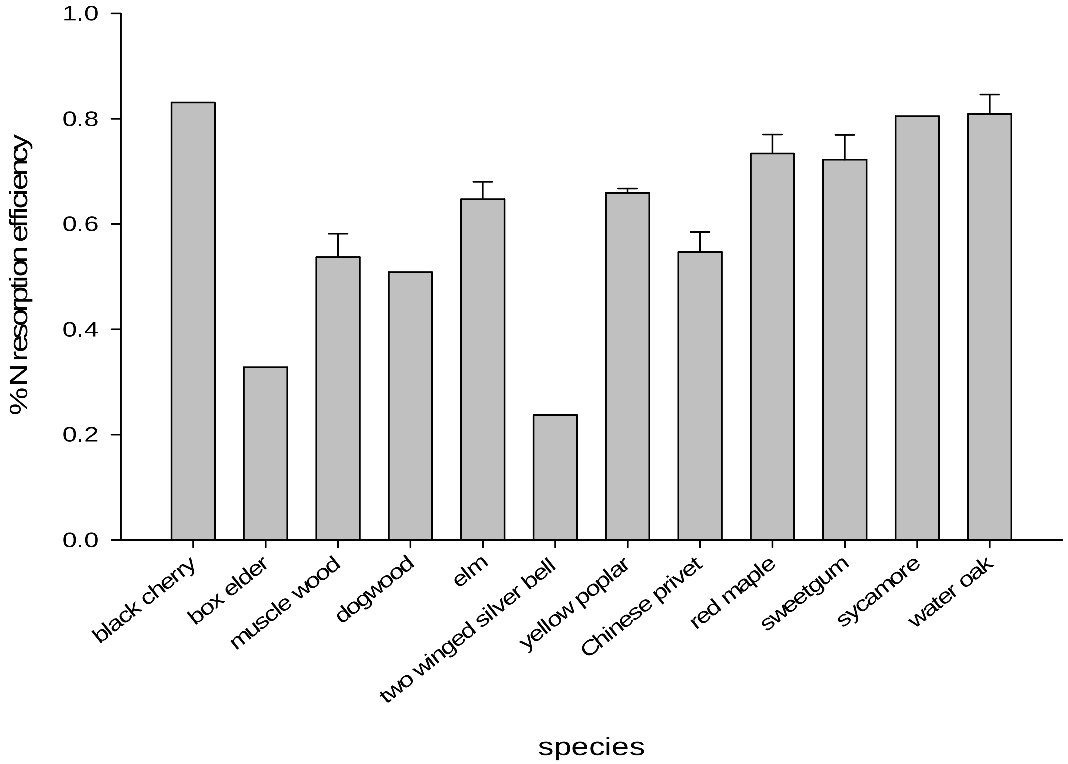


Figure 19. Nitrogen resorption efficiencies are presented for species occurring on sites with 0-100% Chinese privet in their understory in riparian forests in west Georgia. There was only one sample for those species with no error bars. Error bars represent standard error.

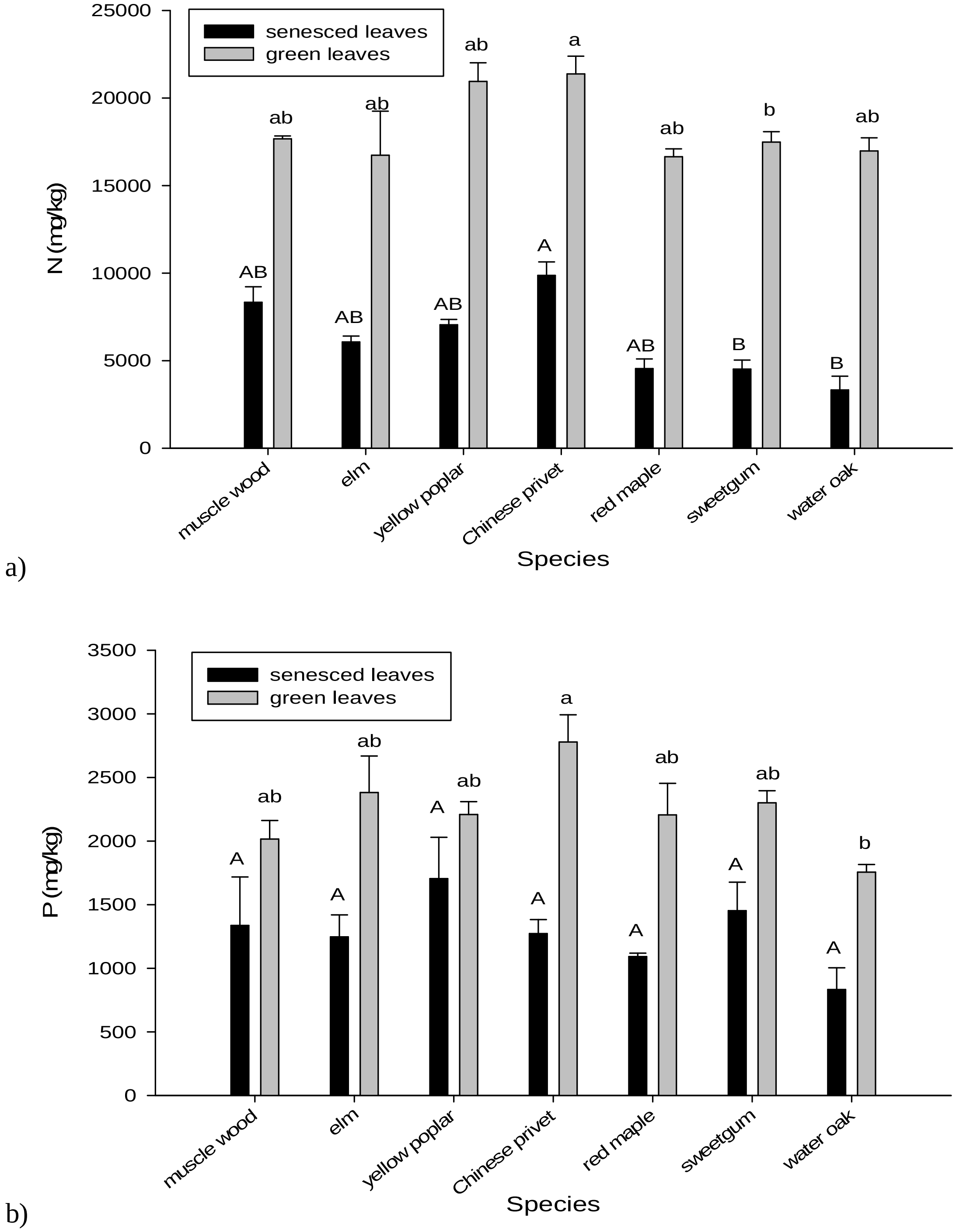


Figure 20. Concentration of a) nitrogen and b) phosphorus for green and senesced leaves in west Georgia. Letters represent significant differences at $p<0.05$ by Tukey's post hoc test, capital letters are for comparisons across senesced leaves and lower case letters are for comparisons across green leaves. Error bars represent standard error.

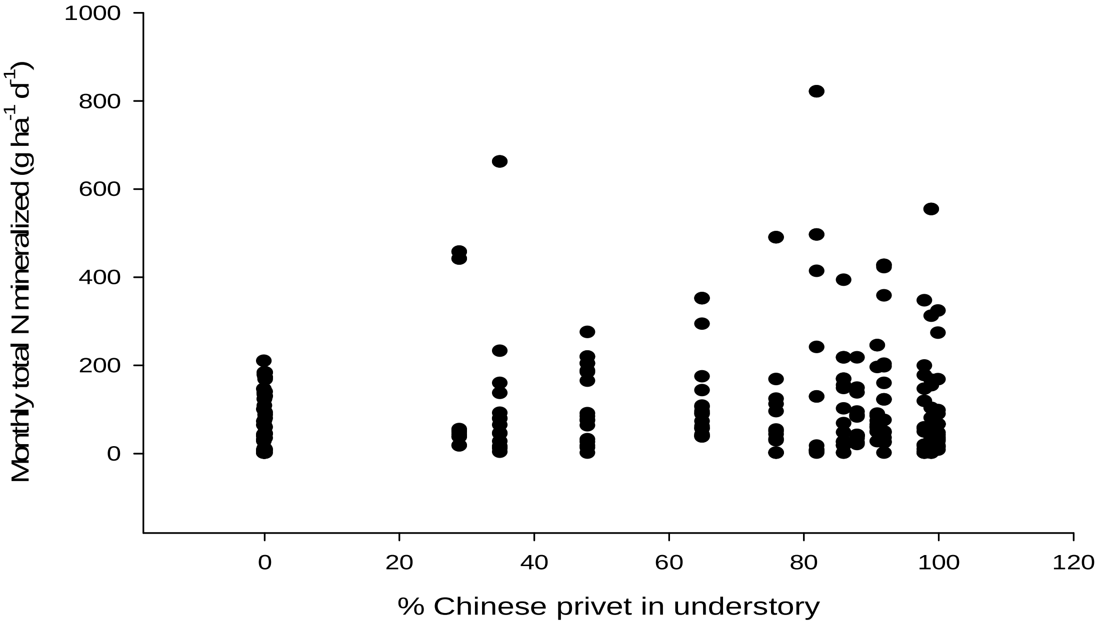
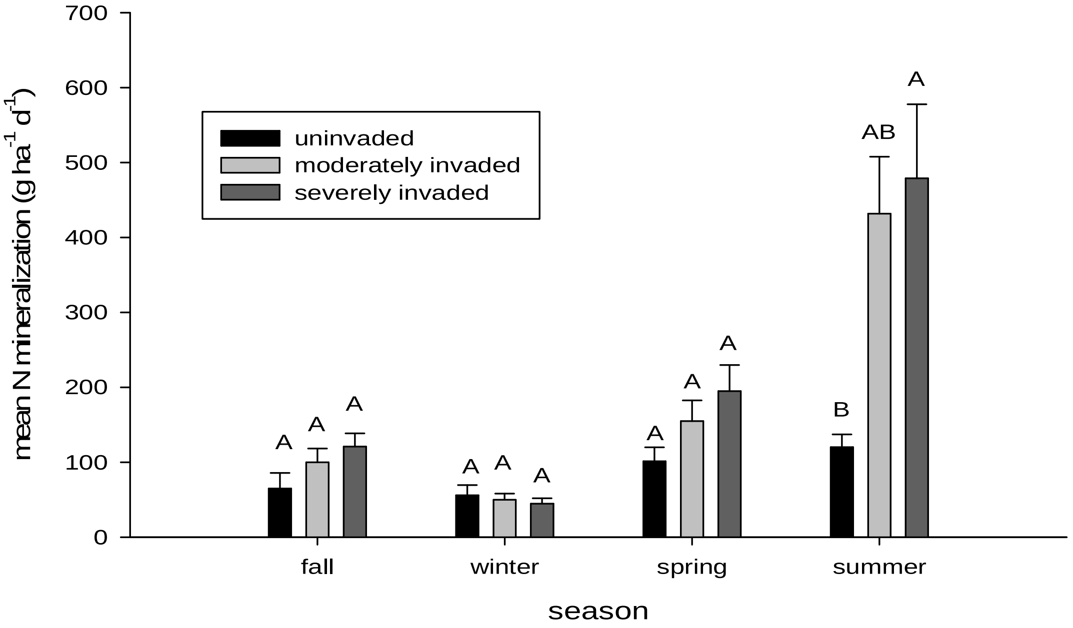


Figure 21. Graph of monthly total nitrogen mineralized and percent of understory composed of Chinese privet in west Georgia.



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igure 22. Seasonal comparisons among understory Chinese privet classes for mean nitrogen mineralization rates in riparian forests in west Georgia. Letters represent significant differences at $p<0.05$ by Tukey's post hoc test. Error bars represent standard error.

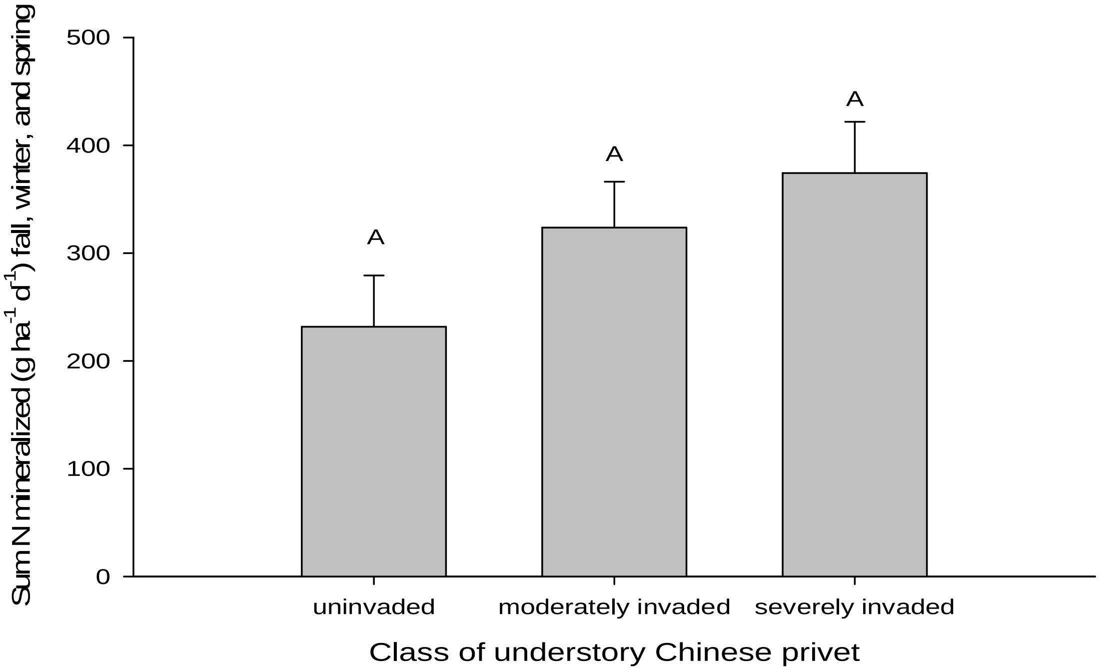

Figure 23. Comparison of total nitrogen mineralized in fall, winter, and spring among classes of Chinese privet for west Georgia riparian forests. Letters represent significant differences at $p<0.05$ by Tukey's post hoc test.   Error bars represent standard error.

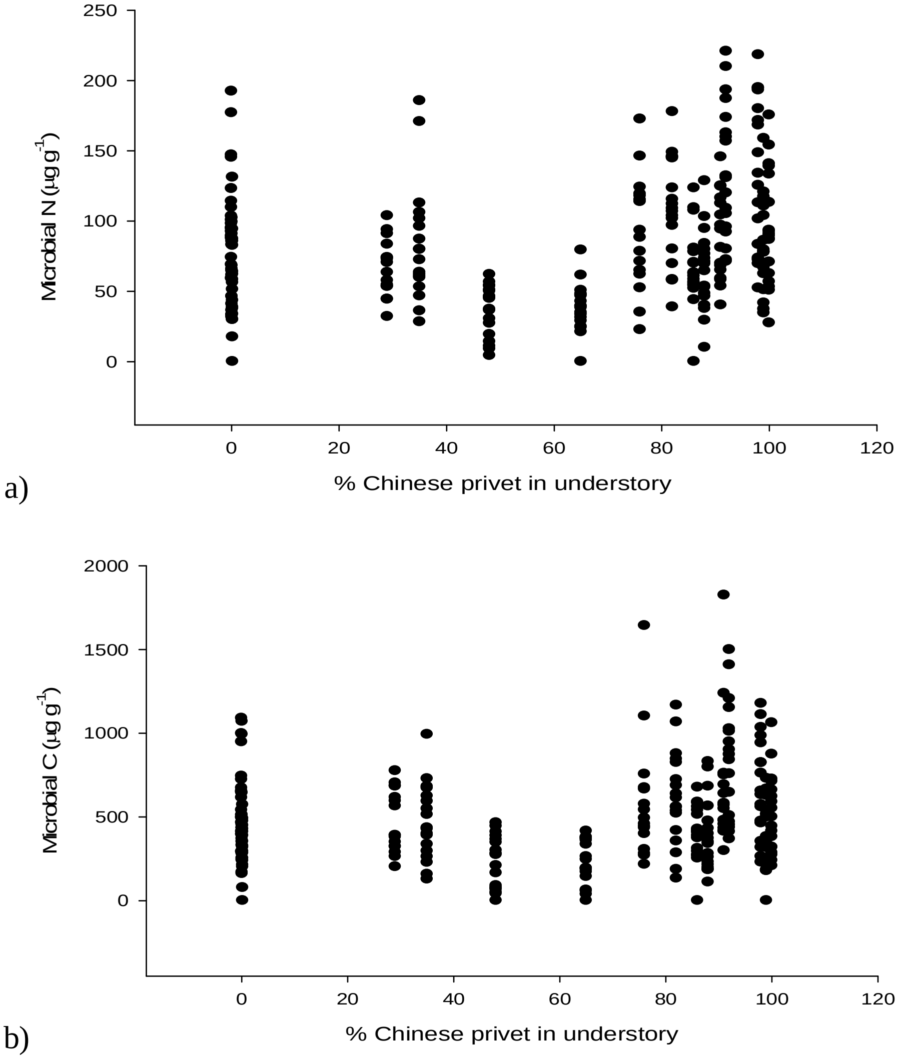

Figure 24. Graph of microbial N (a) and C (b) biomass by percent Chinese privet in the understory for riparian forests in west Georgia.

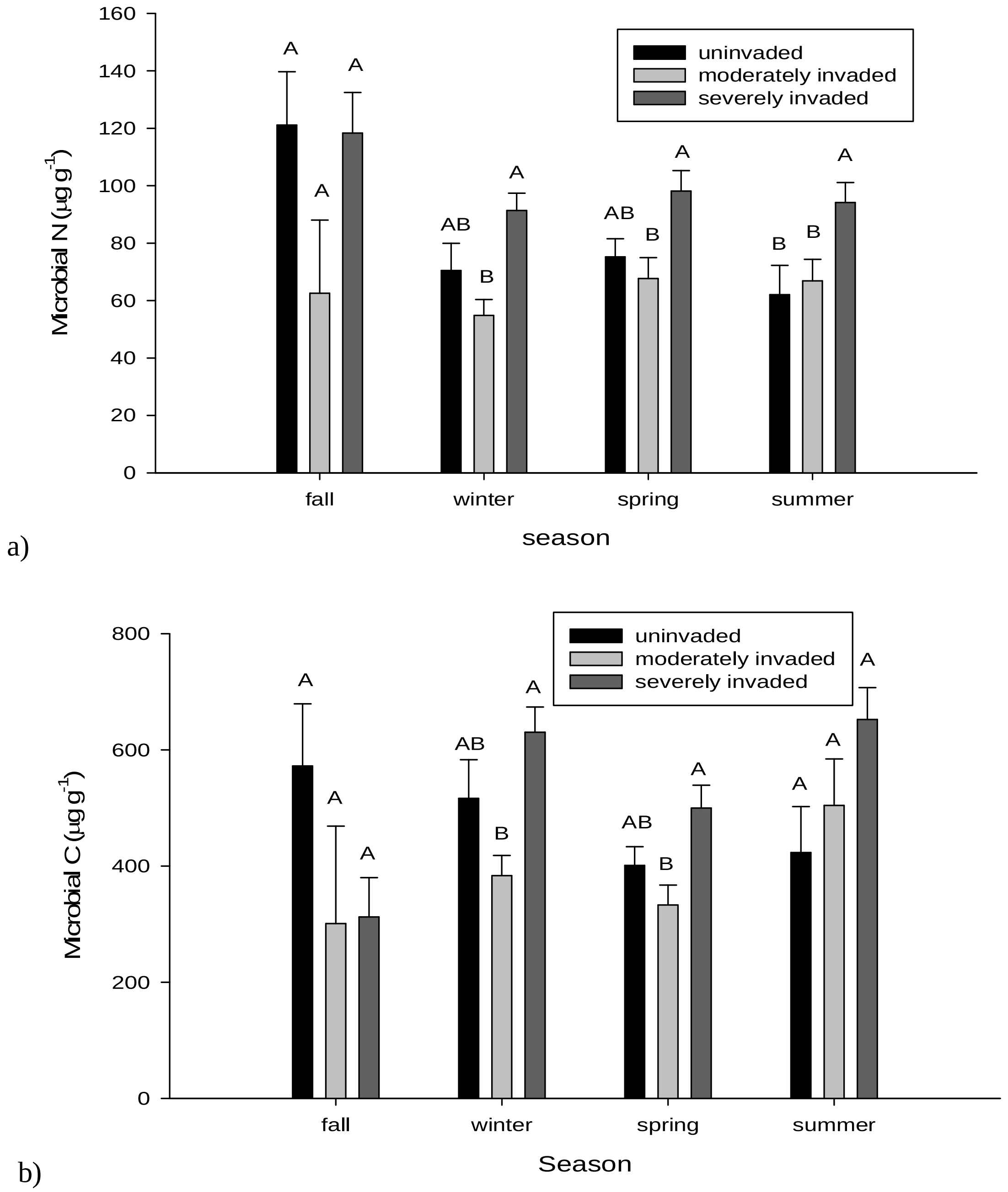

Figure 25. Comparisons of mean microbial biomass among classes of Chinese privet in understory for riparian forests by season in west Georgia a) microbial N and b) microbial C. Letters represent significant differences at $p<0.05$ by Tukey's post hoc test. Error bars represent standard error.

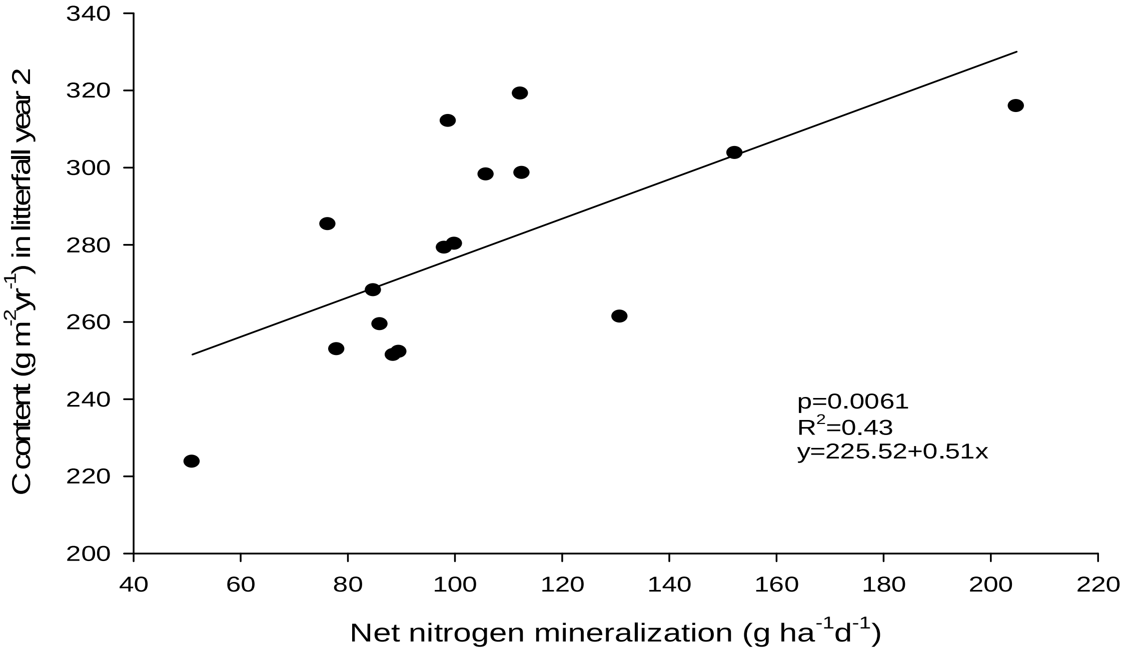

Figure 26. Linear regression for carbon content in litterfall versus mean nitrogen mineralization by site in riparian forests in west Georgia for year 2.

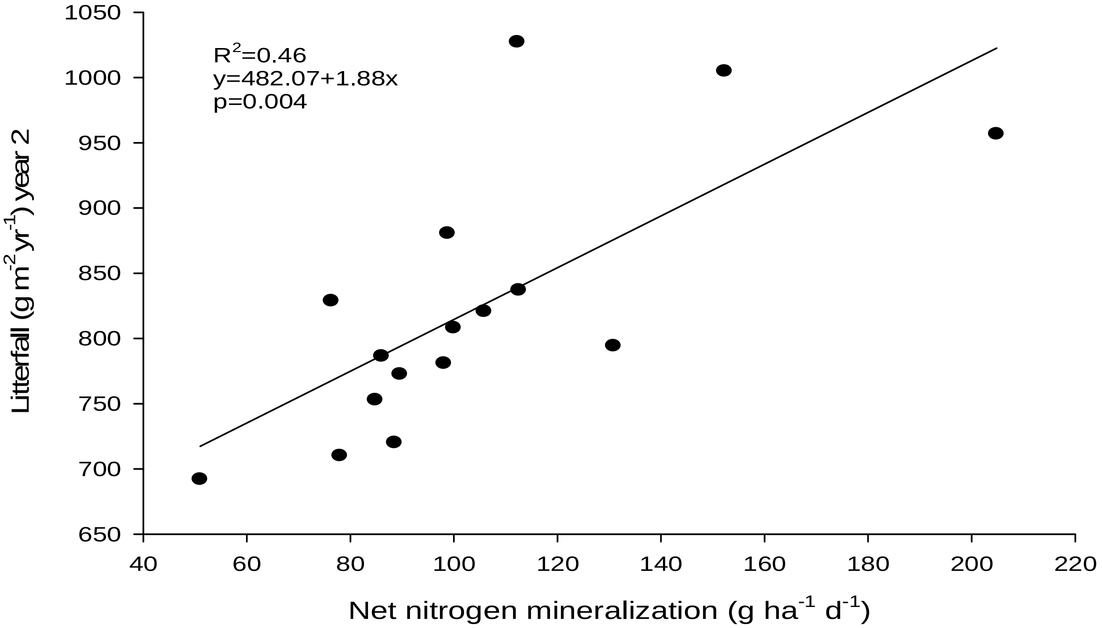

Figure 27. Linear regression for litterfall mass including twigs versus mean nitrogen mineralization by site in riparian forests in west Georgia for year 2.

CHAPTER IV

OYSTER HARVEST IN APALACHICOLA BAY AND THE INFLUENCE OF CHANGES IN WATER QUALITY AND QUANTITY ON THE OYSTER ECONOMY

ABSTRACT

Apalachicola oysters are widely known for their size and flavor, but the oyster industry is currently threatened by many factors. These factors include land use conversion, rising fuel cost, and altered water quality and quantity. This research examined changes in oyster harvests from 1994 to 2006 and the economic repercussions from altered land use and fresh water quality. Data utilized were collected and provided by the Florida Department of Agriculture and Consumer Services. Data were available for weight and value of harvests and for closures of harvesting areas. Water quality and quantity were examined using fecal coliform abundance, salinity, and discharge from the USGS gauging station near Blountstown, FL. Land use data were analyzed for 1995, 2000, and 2005 to quantify the amount of change occurring between those years. From 1994-2006, Apalachicola oysters contributed 3.6-7% to U.S. oyster harvest and 95.3-98.7% to the Florida oyster harvest. The average unrealized value of oyster harvest when >0-25% of the Bay was closed was $43,375 per month. The unrealized value increased as a greater proportion of the Bay was closed. As closures increased in frequency, there

was a negative relationship with both the weight and the value of oysters harvested. Furthermore, there was a significant negative relationship between freshwater discharge at the Blountstown gauge and the amount of oysters harvested. Although decreased freshwater flow was associated with elevated oyster harvests, there are temporal limitations for high productivity. Land use conversion had little influence on changes in fecal coliform (FC) abundance and closures in the Bay; therefore, greater land use conversion near the Bay may need to occur before changes in water quality are observed. Oyster harvests still maintain their importance to the economy of Apalachicola, providing $1.5 to 4.8 million annually, and they should be considered when making decisions that will influence runoff into the Bay and discharge levels of the Apalachicola River.

INTRODUCTION

Apalachicola Bay is located at the mouth of the Apalachicola River, which begins at the confluence of the Chattahoochee and Flint Rivers. The entire drainage basin spans parts of western Georgia, eastern Alabama, and the Florida Panhandle with an area of approximately 48,500 km^2 (Livingston 1991). Recently, increased water demand in Atlanta from the Chattahoochee River has decreased flow reaching the Bay. In the Bay, salinity is controlled by freshwater from the Apalachicola River, rainwater, drainage from Tate’s Hell Swamp, and salt water input at three narrow openings to the Gulf of Mexico. Tides slightly influence both the Bay and River and are classified as “unsymmetrical and semidiurnal except during periods of strong wind effect” (Gorsline 1963). Salinity of the Bay ranges from 0 near the mouth to 19 g/kg in East Bay (Livingston et al. 1997). In this shallow system, with a mean depth of 2.6 m and an approximate area of 62,879 ha, eastern oysters (*Crassostrea virginica* [Gmelin]) flourish (Livingston 1991). Oyster reefs are estimated to cover 7% of the bottom of the Bay (4,359 ha); water conditions are suitable for oysters in 40% of the Bay but solid substrate is lacking in the remaining 33% of suitable water areas (Livingston 1984, Whitfield and Beaumarriage 1977).

Throughout history, oysters have been important to the inhabitants of Apalachicola. In the past, Apalachicola oysters have represented approximately 90% of those sold from Florida and 10% in the U.S. (Whitfield and Beaumarriage 1977). Recent changes in water quantity and quality threaten the profitability of oyster harvest and productivity of oysters in the Bay (Kirkland 2006, Parker 2006).

Conditions in the Bay are ideal for oyster growth because of optimal salinities and temperatures. In high salinity, oyster predators proliferate and in low salinity water there is an increased incidence of disease in mature oysters, so optimal salinity is required for maximum oyster production. Water temperatures appropriate for spawning range between 26.5^{o}C and 28^{o}C and typically occur from late March to October (Ingle 1951). Oysters have rapid growth rates in the Bay and can reach harvestable size in 18 months, a situation associated with elevated mean water temperatures (Ingle and Dawson 1952, 1953). Furthermore, oysters in Apalachicola Bay have been described as having prolonged growing periods, rapid growth rates, and early sexual development (Hayes and Menzel 1981).

Regulation of quantity and method of oyster harvest in Apalachicola have been designed to reduce the possibility of overharvesting. Harvesters in Apalachicola Bay utilize hand-held tongs instead of dredging which reduces the damage to oyster beds during harvesting (Parker 2006). In a single day, oystermen are allowed to harvest up to 20 bags which weigh approximately 27.2 kg each (City of Apalachicola 2008).

The purpose of this study was to examine the economic significance of closing harvesting areas because of degraded water quality. There are several factors that interweave to influence oyster productivity which can be taken into account, including alterations in water quantity and quality from the Apalachicola River such as hurricane occurrence, salinity, disease, predation, and harvest intensity. This study focused on the influence of water quality and quantity on oyster harvesting. Water quality and quantity were measured using freshwater discharge, fecal coliform (FC) abundance, and salinity as variables. The influence of percent area closed on harvesting was an indicator of FC contamination in the Bay. Lastly, the influence of changes in land use patterns on water quality was assessed.

Water Quantity and Productivity

Apalachicola River water quality and quantity has changed in the past few decades. Atlanta is removing increasing quantities of water from the Chattahoochee River for industry and to meet the needs of its expanding population (Marchman 1997). As a result of decreased flow from the Chattahoochee River into the Apalachicola River and more frequent drought conditions, bay-wide salinity has been increasing since the mid-1970s (ANERR 2000). Furthermore, increased nutrients from agriculture in the Flint River, which also feeds the Apalachicola River, drainage basin are added to the Bay (Marchman 1997). Freshwater volume and nutrient inputs to the Bay have highly complex interactions that influence bay-wide productivity. When nutrients are in excess, algal blooms may occur causing the system to become anoxic. However, secondary productivity in the Bay is controlled by photosynthetic organisms occurring in the Bay rather than from food webs connected to the Apalachicola River (Chanton and Lewis 2002). Along with alterations to the nutrient dynamics of the Bay, more frequent incidence of nearshore harmful algal blooms (HAB) have been noted to decrease Bay productivity (Livingston et al. 2000, Flewelling et al. 2001). Other factors, such as the construction of dams, dredging for barge traffic, and irregular weather patterns of hurricanes and droughts, that obscure efforts to relate changes in Bay productivity to a single controlling factor (Marchman 1997, Livingston et al. 2000, Marchman 2000).

Oyster productivity is linked to the trophic structure and nutrient inputs to the Bay. Livingston et al. (1997) attributed the altered trophic structure and decreased productivity to clearer water in the Bay. They also noted changes in herbivore and omnivore dynamics resulting from altered river physiochemical factors (Livingston et al. 1997). A hypothetical explanation for the complex interaction between low flow and oyster productivity is that primary production increases due to greater water clarity allowing increased secondary production (Livingston et al. 1997). However, if nutrients are not replenished, primary productivity will decrease, and in turn, oyster productivity will also decline (Livingston et al. 1997). Therefore, there is a limit to the duration of low flow conditions and high productivity in the Bay. Furthermore, Livingston et al. (2000) noted that, as salinity increased, there was increased disease and predation by crabs and birds, which contributed significantly to oyster mortality.

There is a delicate balance between salinity and oyster productivity (Livingston et al. 2000, Turner 2006). Relationships between productivity, kilograms of oysters harvested, and salinity were observed during 1959-1977, which indicated oyster harvests were inversely correlated with river flow (Meeter et al. 1979). Similarly, Wilber (1992) observed an inverse relationship between oyster catch per unit effort and flow conditions between 1960 and 1984. Turner (2006) observed an inverse relationship between river flow and harvest in several bays across the Gulf of Mexico. There was a corresponding exceptionally large catch during the 1980-1981 drought (Wilber 1992). Since flow of the Apalachicola River controls the salinity of the Bay, it is possible to examine the impact of salinity on harvested oysters.

Oyster reefs provide several ecological services including filtering pollutants, providing vital nursery habitat for fishes, and stabilizing the bottoms and shores (Henderson and O'Neil 2003). Permanent reduction in flow into the Apalachicola Bay could result in the reduction of oyster reefs. Loss of oysters in the Bay would have detrimental repercussions on both the economy of the area and long-term water quality in the Bay. Reduced river flow into the Bay would cause salinity to increase, possibly allowing predators such as the oyster drill (*Thais haemastoma*) and the stone crab (*Menippe mercenaria*) to flourish (Menzel et al. 1958). Another common parasite which causes mortality in mature oysters under high salinity conditions is Dermo (*Perkinsus marinus*) (Mackin 1959). Optimal salinity zones for oyster productivity vary across bays and oyster populations (Turner 2006, Wang et al. 2008).

The impacts of urbanization and increased water demand have influenced oyster productivity in other systems. Bergquist et al. (2006) found a negative relationship between oyster density, percent reef cover, and salinity in the Suwannee River where flow is being reduced by anthropogenic demands as population and development in that basin increases. This is similar to the changes occurring in the area surrounding the Apalachicola Bay (Bergquist et al. 2006). Unfortunately, the study design was not adequate to determine causal factors (Bergquist et al. 2006).

If flow reductions due to anthropogenic demands continue in Apalachicola's Chattahoochee and Flint River basins, low flow conditions during droughts may be intensified and/or extended, thereby reducing oyster productivity (Livingston et al. 2000). This outcome is supported by population models created by Wang et al. (2008) which projected that productivity would be negatively impacted due to low flow conditions during summer months, which typically reflect an important period of growth and reproduction for oysters. High oyster production occurred in areas that had highly variable salinity, but there was high mortality in areas with consistently high salinity (Livingston et al. 2000).

Ecosystem Services

Oysters improve bottom stability and water quality which are important ecosystem services often overlooked in evaluating the importance of oyster reefs in Apalachicola Bay. It is crucial to consider these services in making decisions that will influence the Bay and the oyster industry. As an example of the economic benefit, the fish and other marine life that utilize oyster reefs in North Carolina have greater economic importance than the oysters themselves (Henderson and O'Neil 2003). Many game fish use oyster beds to spawn and forage in their juvenile stages (Henderson and O'Neil 2003). Another example of a recognizable function of oyster beds was observed in the Chesapeake Bay, where the value of improved water quality due to oysters was estimated at $8 million per year (Henderson and O'Neil 2003). Also, oysters removed phytoplankton and sediment which improved water clarity for swimmers, boaters, and beach goers and, consequently, helped maintain tourism income as part of the $8 million (Henderson and O'Neil 2003).

An individual oyster is capable of filtering 5 L of water h^{-1} g^{-1} dry mass and removes the majority of pollutants, particulate organic carbon, microorganisms, sediments, and phytoplankton from the water (Newell 1988). Organic material that is not assimilated into the oyster biomass is excreted and provides food for benthic organisms (Tolley et al. 2005). Therefore, major reductions in oyster populations have caused a negative feedback loop regarding water quality in the Chesapeake Bay. Poor water quality and overharvesting have been attributed to the oyster population decline and reduced filtering capacity in the Chesapeake Bay, and as a result, water quality has further deteriorated without oyster filtering (Mackenzie 2007). Loss of oyster populations may have caused severe oxygen depletion and increased frequency of anoxia in summer months in the Chesapeake Bay (Baker 1992).

Water Quality and Oyster Health

Increases in human pathogens do not directly harm oysters; however, the toxins in harmful algal blooms (HAB) can kill oysters. Oyster fecundity can be impacted by HAB and oysters experience increased susceptibility to disease in response to deteriorated water quality (Chu and Hale 1994, Anderson et al. 1996, Anderson et al. 1998, Kim et al. 2001, Fleming et al. 2006). Oyster mortality has occurred when toxins produced by HAB are present in water bodies, and their more frequent occurrence may be responsible for decreasing oyster populations in general (Fleming et al. 2006).

Human Health, Water Quality, and Oysters

Although bacterial contamination associated with FC bacteria does not directly influence oyster survival, it does raise concern for human health. Recently there has been a decline in oyster consumption (Dedah et al. 2007, Mackenzie 2007). The main reason for this decline is public awareness of health risks from consuming contaminated oysters. Since oysters are filter feeders, they are capable of concentrating pollutants in their tissues (Burkhardt and Calci 2000). Several human pathogens can be consumed with raw or under cooked oysters, such as typhoid, hepatitis A virus, norovirus, human enteric viruses, and vibrio virus (Burkhardt and Calci 2000). Gastrointestinal problems can result from ingesting oysters contaminated with FC bacteria. Bacterial contamination by FC results from direct sewage dumping or non-point source runoff in areas that oysters are harvested (Marchman 2000). More than 30% of closings of shellfish harvesting areas in the U.S. are directly related to wastewater treatment plant discharges (Alexander 1998, Calci et al. 1998, Shieh et al. 2003). Careful monitoring of FC in harvest areas and stringent harvesting regulations are intended to decrease the incidence of harvesting contaminated oysters.

Further concern for increased FC in the water of Apalachicola Bay is reinforced by a study that showed in late November through January oysters selectively took up bacteria which caused gastrointestinal illness (Burkhardt and Calci 2000). Increased viability and abundance of human pathogenic bacteria during winter relates to increased rates of illness. Reduced solar radiation in the winter has been shown to increase residence time of bacteria in comparison to other season for coastal waters and contributes to higher concentrations of FC and other disease causing micro-organisms (Solic and Krstulovic 1992). November to January also coincides with higher reports of human illness from Norwalk-like viruses due to oyster consumption (Glatzer 1998).

As areas become more developed, there is a trend of increased FC abundance in water bodies, especially in coastal areas (Mallin et al. 2000). A study in Portugal found significantly greater accumulation of FC in clams (which are also filter feeders) in more urbanized study areas compared to undeveloped areas (Campos and Cachola 2007). FC abundance can require area closures for both shellfish harvesting and recreational activities, such as swimming or boating. This study will focus on the impacts of FC, the resulting changes in oyster harvests, and the economic impact for Apalachicola Bay.

Study Objectives

Apalachicola Bay's coastal zone is currently experiencing conversion from timberland to development for tourism. As private land is developed along the waterfront, there is increased risk of FC contamination in the Bay. This study investigated the economic impact of changes in oyster harvests as water quality and land use has changed since 1994. Although many factors influence the productivity of oyster beds in Apalachicola Bay, this work examined FC contamination, resulting closure of harvest areas, and economic ramifications. There are several possible scenarios for the oyster industry as the percent of the Bay that is open for harvesting fluctuates. Oystermen will work longer hours in order to maintain their harvest despite increased areas of the Bay being closed, decreasing their catch per unit effort. Decline in harvest quantities may cause a significant negative impact on the economy of Apalachicola Bay.

METHODS

Oyster Harvest Data

Commercial landing data were provided by the Florida Department of Agriculture and Consumer Services (FDACS) available online at http://www.floridamarine.org/features/view_article.asp?id=19224. Data on harvest weight (kilograms), value (in U.S. dollars), and number of licenses for Franklin and Gulf counties were available on a yearly basis from 1994 to 2006. Monthly data on oyster harvest weight, value, and number of trips taken by oystermen were also available by contacting the FDACS directly. Dollar value was converted to 2006 dollars to compensate for inflation and to allow direct comparisons by using the consumer price index for 1994-2006 from yearly values taken from the following website: ftp://ftp.bls.gov/pub/special.requests/cpi/cpiai.txt. All dollar values presented here are in 2006 U.S. dollars, unless otherwise indicated.

Harvest areas are clearly defined and regulated by the FDACS in the Shellfish Environmental Assessment Section (SEAS). Areas are closed when either discharge of the Apalachicola River in Blountstown, Florida exceeds a predetermined flow or when the 3-day rainfall total at the airport in Apalachicola, Florida exceeds a predetermined quantity. FDACS uses an equation to relate discharge or rainfall in order to predict FC levels in the Bay and then based closure decisions on these predictions. Minimum discharge and rainfall quantities in each management area vary depending on proximity to the mouth of the Apalachicola River. However, the equation for this relationship was unavailable for examination. SEAS has chosen these discharge and precipitation values because they reflect FC levels that are considered too high for harvested oysters to be safe for human consumption. Data on closures for each harvesting area were available for the years 1984 to 2006 by contacting SEAS.

Data for national oyster harvest price and quantity were found on the NOAA Fisheries website at http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html. Harvest information on kilograms harvested and price adjusted to 2006 U.S. dollars was available for all states that harvest oysters.

Water Quality and Quantity Data

SEAS monitored FC, salinity, and temperature at multiple sampling stations across the Bay. Water quality data were available from 1984 to 2007, but only 1994-2006 were used in this study because of changes in boundaries of harvest areas in previous years. Harvest areas are declared open or closed daily, and decisions are based on measured FC levels, rainfall, and river discharge thresholds. Once an area is closed, it is not reopened until the sampled geometric mean of FC abundance in all sampling stations in that area are 14 mpn (most probable number)/100ml or less and the percentage of stations with FC counts greater than 43mpn/100ml is less than 10%. Some sampling stations are included in multiple harvest areas. Areas can be closed based on high FC concentrations which are either predicted or directly measured, but areas are only reopened when samples of Bay water indicate acceptable FC concentrations.

Water quantity data reflect discharge of the Apalachicola River at the USGS gauge near Blountstown. These data were accessed online at http://ida.water.usgs.gov/ida/available_records.cfm?sn=02358700 for 1994 to 2006.

Fecal coliform. All FC laboratory analyses were conducted by SEAS. All of the numbers for FC abundance presented were directly measured. The method for quantifying FC in seawater was the modified A-1 M mpn method described in the Recommended Procedures and Association of Official Agricultural Chemists Methods (Horwitz 1980). In this method, the presence of FC growth is indicated by gas production after 24 hours. Fifteen tubes with three dilution series were used to determine the MPN of FC bacteria with calculations based on the number of tubes with positive growth. A-1 media was used to grow FC. Samples were collected, kept at or below 10^{o}C but not frozen, and analyzed within 30 hours. Homogenized samples were inoculated into media with the following dilutions: 5 test tubes with 10ml of sample into A-1 double strength media, 5 tubes 1ml sample into single strength A-1 media, and 5 tubes 0.1ml sample into single strength A-1 media.

Tubes were incubated at 35+/- 0.5 ^{o}C for 3 +/- 0.5 hours with an inverted vial in them. Tubes were then transferred to a water bath which was maintained at 44.5 +/-0.2 ^{o}C for 21 +/- 2 hours. Tubes were examined for the presence of gas bubbles and other indications of growth after incubation. Positive results for the presence of FC were indicated by a bubble of gas in the inverted vial or by active effervescence in the tube when gently shaken. To determine MPN, positive tubes were counted and results were compared to published tables (Recommended procedures and AOAC Methods 4th edition) to find the MPN/100ml of sample.

Statistical Analysis

For mean comparisons using one-way analysis of variance (ANOVA), 5 classes (0%, >0-25%, >25-50%, >50-75%, and >75% closed to oyster harvest) were created based on average percent closure in a month for oyster harvest in the Apalachicola Bay (PROC GLM, SAS Institute 2002-2003). If significant at $\alpha=0.05$, a Tukey's post hoc mean separation test was performed. Linear regressions were also utilized to determine relationships between variables in this study (PROC REG, SAS Institute 2002-2003). Data analysis used SAS version 9.1 (SAS Institute 2002-2003).

RESULTS

Bay Closures and Harvest

The percent of the Bay closed each month ranged from 0 to 100% with an average of 16% closure. Yearly average of the percent Bay closed was highest in 2005 at 32% (Figure 1, $p=0.0005$ $F_{12, 143}=3.2$). There were significant differences among classes of Bay closure for both harvest quantity and value (Figure 2, $p< 0.0001$, $F_{4,151}= 12.3$, and $p< 0.0001$, $F_{4,151}= 13.3$, respectively). Water quality measured by mean FC had a significant positive regression relationship with the percent of the Bay closed (Figure 3, $p=0.006$, $F=9.51$). There were significant negative regressions for percent of the Bay closed and the number of trips oystermen took (Figure 4, $p<0.0001$, $F=56.1$) and between the amount of oysters harvested (Figure 5a, $p<0.0001$, $F=63.2$). Similarly, there was a negative regression for the value of harvests and the percent of the Bay closed (Figure 5b, $p<0.0001$, $F=58.9$).

Changes in Harvest Over Time

Since 1994, both the kilograms of oysters harvested (Figure 6a, $p=0.006$, $F=7.8$) and the value of the harvests have increased (Figure 6b, $p<0.0001$, $F=17.7$). However, when data were examined from 1980 to 2006, there were considerably fewer kilograms harvested in recent years (Figure 7). The proportion of the total harvest from Apalachicola oysters has decreased from the commonly cited values of 10% to U.S. sales and 90% of Florida sales (Table 1). In the past decade, Apalachicola Bay accounted for 95% of the oysters from Florida and 5% of the U.S. oysters (Table 1). There were differences among years for average kilograms of oysters harvested on a monthly basis (Figure 8a, $p<0.0001$, $F_{12,143}=5.7$), with 2001 having the greatest average monthly harvest of 88,714±10,445 kilograms and the lowest being 0 kilogram when the entire Bay was closed for September and October 2005 due to Red Tide. The average monthly value of oysters was greatest in 2006 at \$400,191 ± 31,994 and lowest in 1995 at \$136,080 ± 19,277 (Figure 8b, $p<0.001$, $F_{12,143}=6.8$). Price per kilogram had a positive linear slope and significant linear regression indicating that price per kilogram has increased since 1994 (Figure 9, $p<0.0001$, $F=31.8$). The unadjusted price per kilogram of Apalachicola Bay oysters fluctuated based on the average price per kilogram of oyster across the entire U.S. (Figure 10, $p=0.0008$, $F=20.8$).

Water Quantity Influence on Harvest

Discharge of the Apalachicola River into the Bay was examined at the gauging station near Blountstown, FL, which is used to determine harvesting area closures. Since 1994, there has been a slow decrease in discharge at the Blountstown gauge (Figure 11, p=0.02, F=6.0). As expected, discharge at Blountstown station had a significant negative relationship with surface and bottom salinity in the Bay (Figure 12a, p<0.0001 F=57.0) and (Figure 12b, p<0.0001, F=47.9), respectively. Discharge at the Blountstown gauge was positively related to mean FC in the Bay (Figure 13, p<0.0001, F=21.8). Furthermore, discharge at the Blountstown gauge had a significant negative relationship with kilograms of oysters harvested (Figure 14, p=0.007, F=7.5). Despite the relationship of discharge with salinity and with quantity of oysters harvested, there was not a significant relationship between salinity and quantity of oysters harvested (Figure 15a, p=0.011, F=3.1, surface and Figure 15b, p=0.4, F=0.7, bottom).

Fecal Coliform

During 1994 to 2006, the mean monthly measured FC concentration in the Bay has decreased (Figure 16, p<0.0001, F=19.0). Despite the positive linear relationships between discharge and mean FC MPN/100ml and the negative linear relationship between discharge and quantity of oysters harvested, there was no significant relationship between mean FC MPN/100ml and the quantity of oysters harvested (Figure 17a, p=0.92, F=0.01). Nor was there a significant relationship between FC MPN/100ml and value of the harvest (Figure 17b, p=0.9, F=0.03) or the price per kilogram (Figure 17c, p=0.48, F=0.5).

Oystermen and Harvest

When more oystermen were licensed to harvest, kilograms of oysters harvested increased linearly (Figure 18a, p=0.006, F=11.4). A similar positive relationship existed between the number of oystermen and the value of the harvest (Figure 18b, p=0.008, F=10.1). However, there was no relationship between the number of oystermen and the price per kilogram (Figure 18c, p=0.84, F=0.04). Similarly, there was no observable trend between year and the number of licensed harvesters from 1994 to 2006 (Figure 19). Rather, fluctuations in the number of licenses followed trends in quantity of oysters harvested. However, there are fewer oystermen in the early 2000's compared to the late 1980's and there was a similar decline in harvested kilograms (Figure 20).

Land Use Change

In the three years examined in this study, the forest and wetland forests declined by more than 25,000 hectares in Franklin and Gulf counties between 1995-2005 (Table 2, Figure 21). 2,000 hectares have been converted to urban and residential land uses (Table 2, Figure 21). The effect of land use change on oyster harvest over time and fecal coliform abundance were analyzed using regressions. First, land use data for 1995, 2000, and 2005 data were fit in against oyster harvest over time, then the same land use change data were fit against fecal coliform abundance. There was not a significant effect of land use change on these two parameters. Also, no significant relationships were found between land use data and annual average percent Bay closures.

DISCUSSION

Bay Closures and Harvest

There is a complex interaction between the factors that control water quality, water quantity, and the population of harvestable oysters. In months when >0-25% of the Bay was closed, an average of 8,700 kilograms of oysters was harvested and the value of the harvest had an unrealized value of $45,375 (Figure 2). Therefore, even small closures in the Bay result in the loss of major economic potential. In the months when > 75% of the Bay was closed, the unrealized value was $275,000 (Figure 2).

Closures may also occur due to hurricanes or red tide. These factors may obscure the relationship between Bay closures and land use patterns near the Bay. It should be noted that closures due to hurricanes occurred in the summer harvesting season but were infrequent. Harvesting areas were closed during and after hurricanes because of extreme precipitation events that caused sedimentation. Several oyster processing facilities were destroyed by storm surges, during summer closures in 2004 and 2005, which limited quantities that could be processed later. Also, closures due to red tide occurred throughout the sampling period but were not as frequent as closings due to management for precipitation or discharge of the Apalachicola River.

New regulations anticipated to be adopted in 2010 will likely increase the frequency of Bay closures to oyster harvesting because of the presence of the human pathogen *Vibrio vulnificus* (personal communication, Christopher Brooks, SEAS, 2008). In order to reduce the incidence of vibrio illness, boats will be required to install cooling systems or quickly return harvested oysters to shore. Maintaining low temperatures will prevent oysters from increasing the pathogenicty of *V. vulnificus*. Other methods for controlling vibrio illness have a range of costs and include irradiation, heat shock, special freezing, hydrostatic pressure, and several other treatments (personal communication, Christopher Brooks, SEAS, 2008). However, these changes may result in further decline of the oyster industry, which is challenged by development pressures, rising fuel cost, and decreasing demand for oysters (Kirkland 2006, Parker 2006). The unrealized value of oyster harvest will increase as there are more frequent closures in the Bay, and harvesting efforts may increase in other areas of the Gulf to compensate.

Changes in Harvest Over Time

Oyster harvests increased in the 12 year period from 1994-2006 (Figure 7a). However, harvests are considerably lower from 1990-2005, than they were in the early 1980's, although harvests had begun to increase (Figure 6). Changes in harvest regulation, labeling requirements, and hurricane frequency are often described as the leading cause of declining harvests in the early 1990's (Dedah et al. 2007), and the industry has not yet fully recovered (Figure 6). Apalachicola Bay has typically been described as contributing 10% of the entire U.S. harvest; however, from 1994-2006 it provided only about 5% (Table 1**)**. Other oyster producing areas in Florida have greatly reduced their production, so in recent years Apalachicola accounts for nearly 97% of Florida oysters harvested. These contribution values suggest that Apalachicola oysters are not as important to the national oyster industry as they once were, but that they dominate the Florida oyster industry.

Water Quantity Influence on Harvest

The relationship between discharge of the Apalachicola River and oyster harvest in the Bay was confounded since discharge influences both salinity and FC abundance in the Bay. Nevertheless, there was a significant inverse relationship between the discharge of the Apalachicola River at the Blountstown gauge and oyster harvests (Figure 13), which is similar to the findings of by Turner (2005) and Wilber (1992). Although Berquist et al. (2006) observed relationships between surface salinity and oyster harvest, similar trends in the study were not significant (Figure 15). The high variation of salinity in the Bay and irregular sampling regime may have reduced detectability of the relationship between oyster harvest and salinity (Figure 15).

Fecal Coliforms

Linking changes in land use with alterations in FC can be difficult to discern. Concentrations of FC in Bay waters decreased over the period of study, regardless of land use conversion (Figure 17). As land use change occurred, it is important that the equation used by SEAS to determine closures is updated consistently. Since the equation has not been published, the variability associated with FC predictions cannot be determined. It is especially difficult to conclusively make predictions in this setting where the old pipes that handle stormwater runoff are considered out of date and failing (Marchman 2000). In neighboring areas, there are old septic systems as well as new construction both which are responsible for FC input into the Bay and both are classified as impervious surface in Land use classification schemes (Marchman 2000). FC sources that most limit oyster harvesting in the Gulf of Mexico result from upstream contamination from human communities, wildlife, and individual wastewater treatment systems (NOAA 2005).

Contrary to most studies that investigate the relationship between water quality and urbanization (in this study time was used as a proxy for conversions of land cover), there was no increase in measured Bay FC associated with increased impervious surface cover (Figure 16). Irregular sampling periods and high variability associated with monitoring in the Bay could be factors which obscure land use and FC relationships. Periods of high discharge were associated with greater levels of FC being transported directly to the Bay in comparison to low discharge. Although discharge was inversely related to harvest (Figure 12), there was no detectable relationship between FC and harvest (Figure 16). Since discharge of the Apalachicola River controls the amount of fresh water going into the Bay there was a significant negative relationship for discharge and salinity (Figure 12). The interaction of discharge, FC, and salinity influences the success of oyster productivity and the frequency of Bay closures. Low discharge and increased harvest, in comparison to mean harvest, had the duration of two to three years in this study. Wilber (1992) noted that there was a two to three year lag time of decreased harvest after low salinities which resulted from the lag time associated with disease and predation in Apalachicola Bay. No such lag effect was observed in this study. However, longer periods of drought and lower flow than are currently experienced in the Apalachicola River would greatly increase salinity, possibly to a level where oyster predators and disease would be capable of reducing oyster populations (Livingston et al. 2000). A similar situation occurred in the Chesapeake Bay where contamination and disease decimated oyster populations causing the demise of Chesapeake oyster industry (Baker 1992).

Oystermen and Harvest

The seafood industry in Apalachicola Bay is dependent on the high diversity of economically important seafood, such as shrimp, game fish, oysters, and clams. In times of low oyster harvest, fishermen can switch between catches. It is common for commercial fishermen in Apalachicola to alternate between harvesting oysters and shrimp, depending on which are more abundant and economically valuable at the time (Kirkland 2006). However, increasing frequency of Bay closures has forced oystermen to seek jobs with more consistent paychecks instead of relying on the unpredictable income of the seafood industry (Kirkland 2006). Although the number of licensed commercial oystermen fluctuated from 371 to 580 in a pattern similar to harvest (Figure 17), there are dramatically fewer oystermen during the period of study compared to previous decades (Figure 20). If the frequency of Bay closures increases, more oystermen will be forced to find a more reliable source of income and the oyster industry of Apalachicola could be lost (Kirkland 2006). The loss of the industry would cause major economic repercussions in the area since the oyster industry accounts for a two to four million dollar annual economy.

Land Use Conversion

Changes in land cover in Franklin and Gulf counties are in early stages. Since most of the land in these two counties is forested, there could be major impacts from cutting and developing this forested land in the future. The potential for development is very high in this area (particularly along coastlines, Figure 21), and those changes have the potential to cause changes in water quality. Furthermore, pressures for development in the coastal area are reducing public access to waterfront property for launching and landing oyster boats. Several of the oyster houses in Apalachicola were damaged during the hurricane seasons of 2004 and 2005, and instead of being rebuilt as oyster houses, the land was sold to developers who will convert those areas into condominiums and dense residential development (Parker 2006). However, this study's findings suggests that rainfall patterns and discharge had a greater influence on water quality in the Apalachicola Bay than did changes in land cover from 1995-2005. Despite the steady conversion of forested land to urban, the changes were not extreme enough to be related to changes in water quality in the Bay. A possible explanation of these observations is that fecal contaminants only enter the water column at times of peak flow; therefore, FC enters the Bay only following significant rains at which is the signal for Bay closures for harvesting. However, if development continues and FC contamination becomes more abundant, small rain events will create FC levels requiring closures in the Bay and alterations in the SEAS equation.

CONCLUSIONS

Harvesting oysters is influenced by many factors such as harvest closures, demand for oysters, cost effectiveness of harvest, and others. All of these factors interact in a particular fashion to enable oystering to be a profitable industry in Apalachicola Bay, FL. Many of these factors, however, are changing in ways that may decrease future profitability of the industry. Although changes in water quality have not occurred during 1994-2006, there were changes in water quantity because of weather events such as drought and increased human consumption upstream. Decreased flow of the Apalachicola River had a two fold influence in increasing oyster harvest. Lower discharge was related to increased salinity which is known to increase oyster productivity. Also, decreased flows corresponded to smaller areas of the Bay being closed due to FC contamination. If harvest areas are closed more frequently (as may occur with new regulations in 2010), hundreds of thousands of dollars monthly may be unrealized. The predicted increase in closures is a response to increased water temperature in the Bay and because of increased understanding of vibrio illness in human consumers. Of all the factors influencing oyster harvest quantities studied here, water quantity had the greatest influence. Although decreased discharge resulted in increased production, extended duration of low flow conditions may cause a decline in harvests due to predation and disease that occur in extended high salinity conditions.

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Table 1. Harvests of oysters for entire U.S., Florida, and Apalachicola Bay. Percent contributed by oysters harvested from Apalachicola Bay was calculated for the U.S. harvest and the Florida harvest.

year	U.S. kg	Florida kg	Apalachicola kg	% of US harvest	% of Florida harvest
1994	16,606,755	958,602	913,081	5.5	95.3
1995	17,052,424	691,286	662,110	3.9	95.8
1996	17,525,879	657,580	640,444	3.6	97.4
1997	16,466,703	856,051	847,999	5.1	98.0
1998	15,288,208	716,513	697,978	4.6	97.4
1999	17,211,169	1,065,660	1,047,371	6.1	98.3
2000	18,339,177	1,167,686	1,144,134	6.2	98.0
2001	17,708,268	1,178,770	1,161,896	6.6	98.7
2002	17,136,683	899,300	882,398	5.1	98.1
2003	18,598,705	813,902	795,793	4.3	97.7
2004	17,704,288	764,813	746,173	4.2	97.6
2005	16,198,273	660,810	643,101	4.0	97.3
2006	15,462,225	1,111,961	1,086,951	7.0	97.8

Table 2. Land use cover data for Gulf and Franklin counties in Florida.

year	1995		2001		2005	
classification	hectares	% of total	hectares	% of total	hectares	% of total
water	7574	2.6	6343	2.2	8400	2.9
woody wetland	89986	30.6	110551	37.6	101895	34.6
emergent wetland	12951	4.4	15834	5.4	14049	4.8
forest	136334	46.31	114808	39	97945	33.3
shrub	23873	8.1	25336	8.6	47251	16.1
impervious surface	3737	1.3	3770	1.3	4130	1.4
barren	3371	1.2	3967	1.4	2219	0.8
grass	470	0.2	20	0	330	0.1
agriculture	3254	1.1	923	0.3	1275	0.4
unconsolidated	3354	1.1	3460	1.2	401	0.1
clearcut	4594	1.6	4023	1.4	5196	1.8
high residential	1427	0.5	1579	0.5	1607	0.6
medium residential	3104	1.1	3355	1.1	4215	1.4
low residential	1825	0.6	1949	0.7	2487	0.8

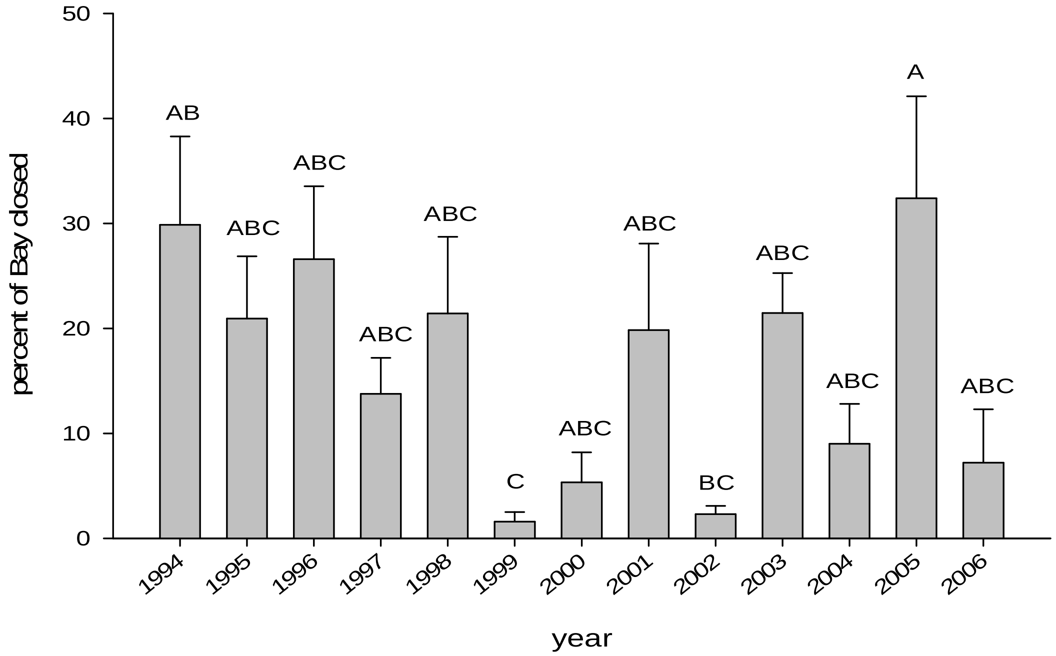


Figure 1. Monthly mean percent of the Bay closed on an annual basis in the Apalachicola Bay. Letters represent significant differences at p<0.05 by Tukey's post hoc test. Error bars represent standard error.

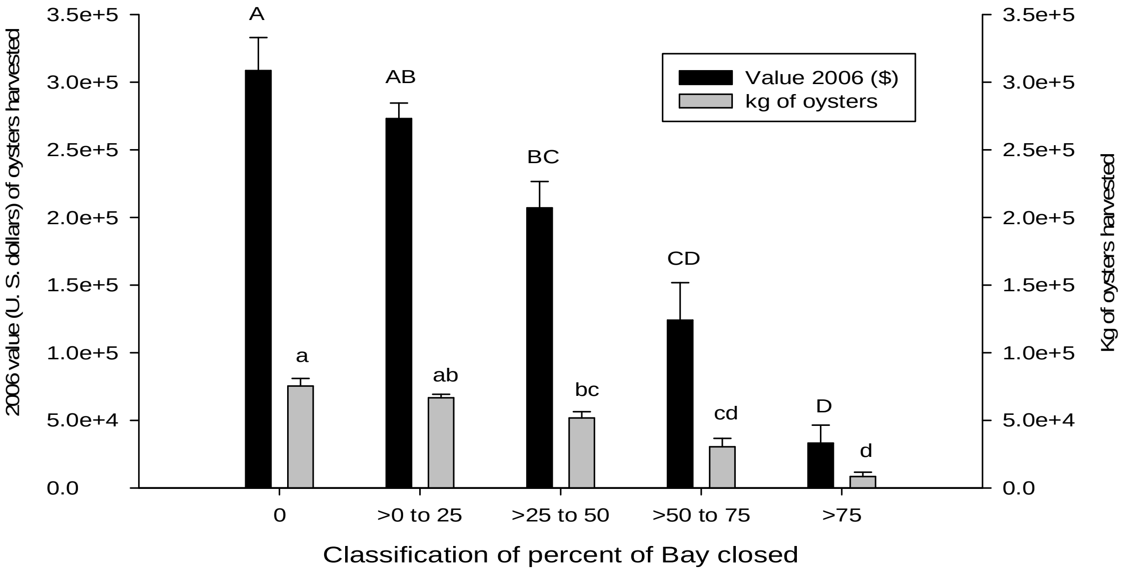


Figure 2. Average value of harvest in 2006 dollars and kilograms (kg) of oysters harvested for percent categories of closures in the Apalachicola Bay. Letters represent significant differences at p<0.05 by Tukey's post hoc test. Error bars represent standard error.

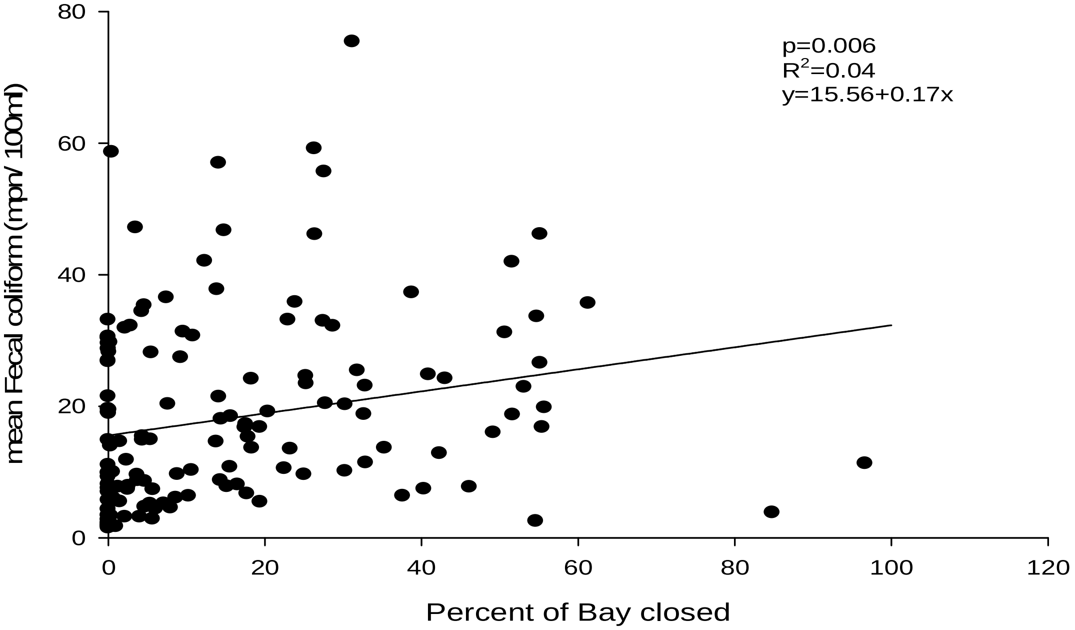


Figure 3. Percent of the Apalachicola Bay closed to oyster harvesting graphed against mean Fecal coliform concentration (mpn/ 100ml) in the Bay.

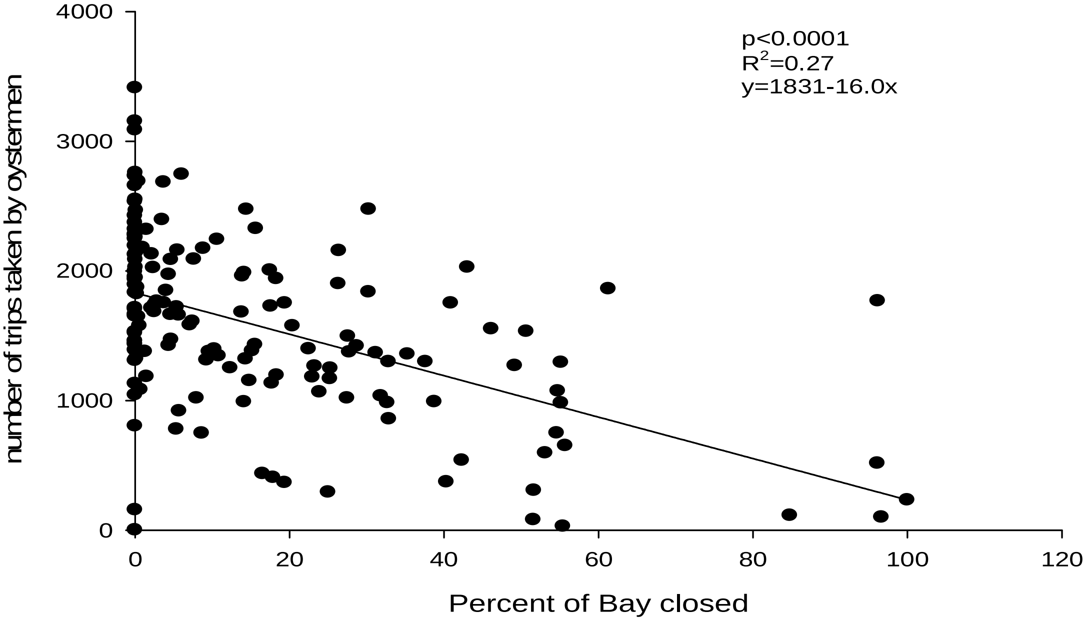
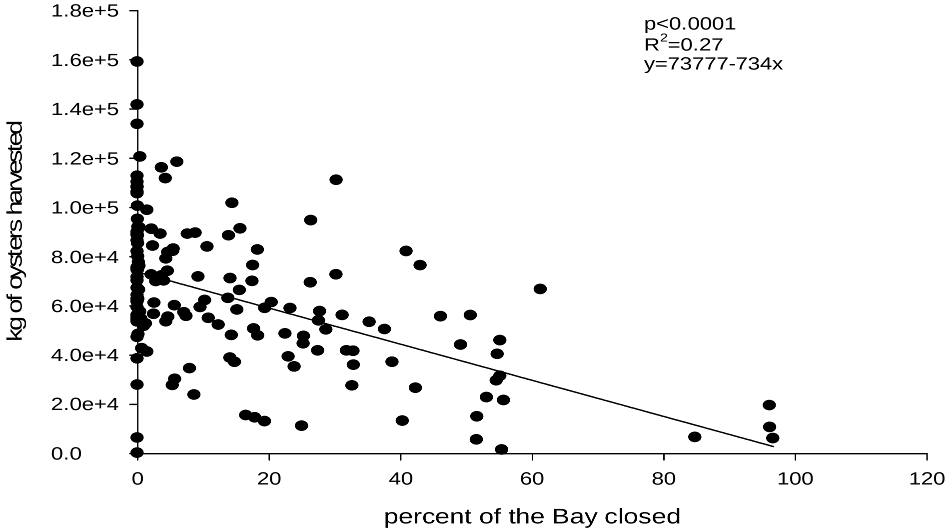
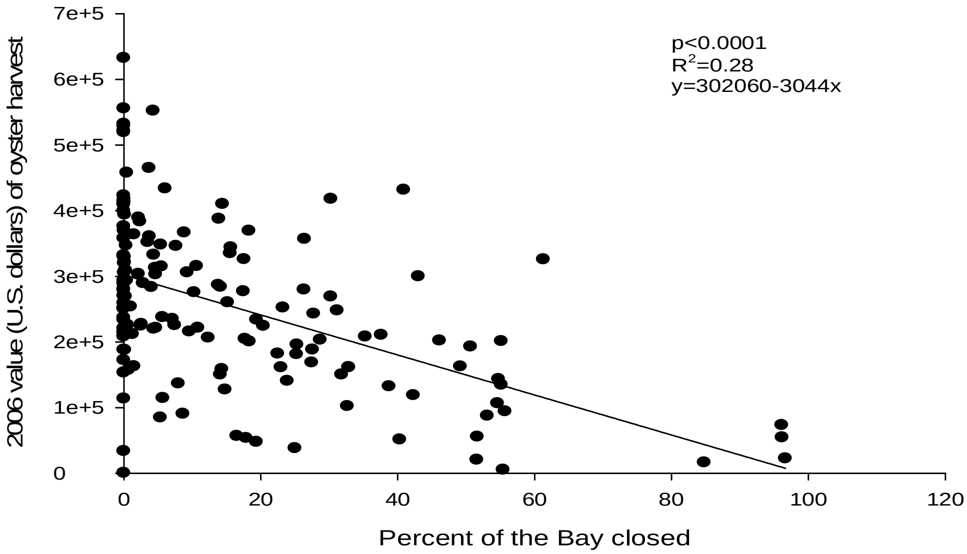


Figure 4. Percent of the Apalachicola Bay closed to oyster harvesting in relation to the number of trips taken by oystermen.

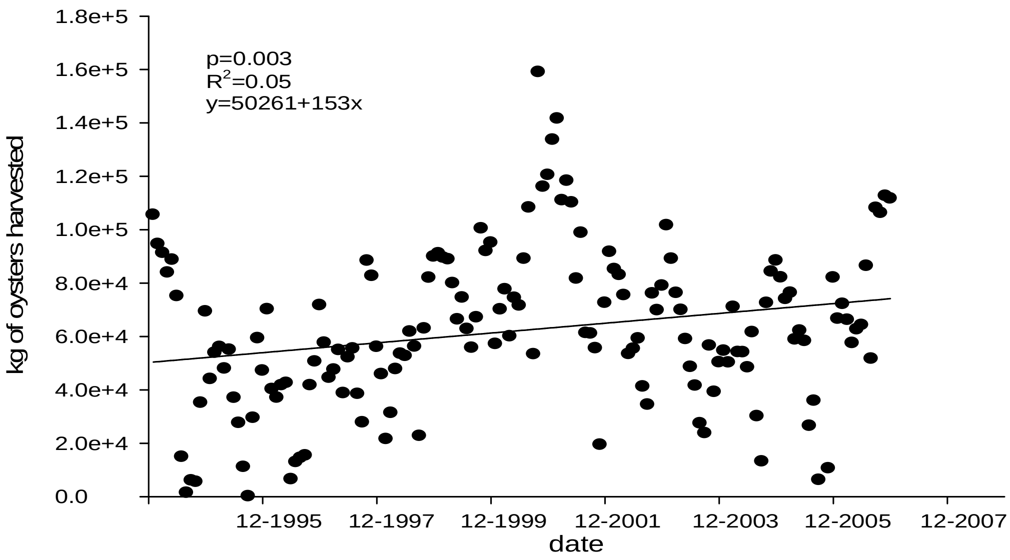


a)

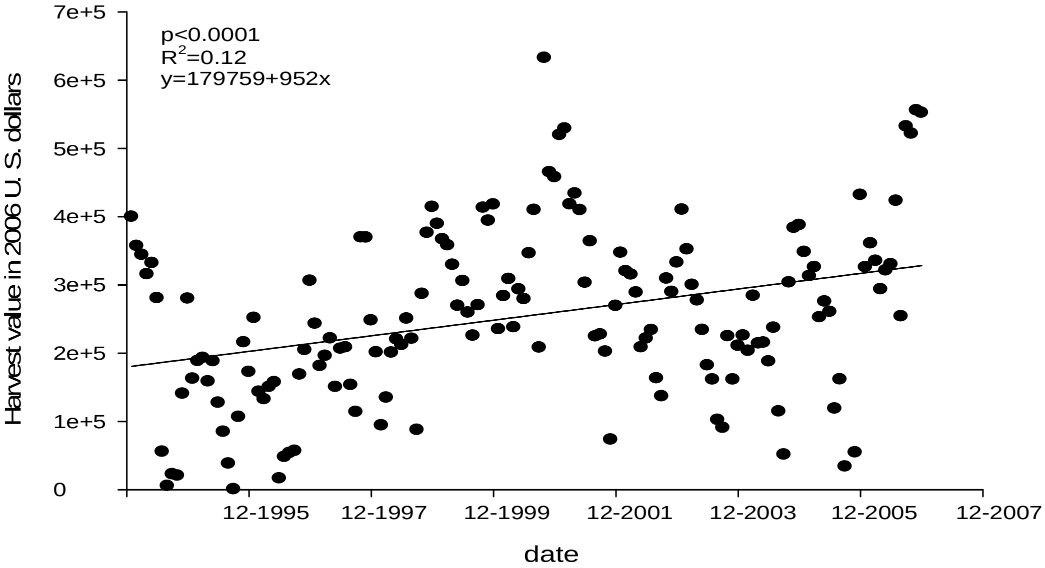


b)

Figure 5. Percent of the Apalachicola Bay closed to oyster harvesting in relation to a) kilograms (kg) of oysters harvested and b) value adjusted to represent the 2006 dollar value.



a)



b)

Figure 6. a) Kilograms (kg) of oysters harvested and b) value adjusted to the 2006 values based on monthly data for the Apalachicola Bay from 1994-2006.

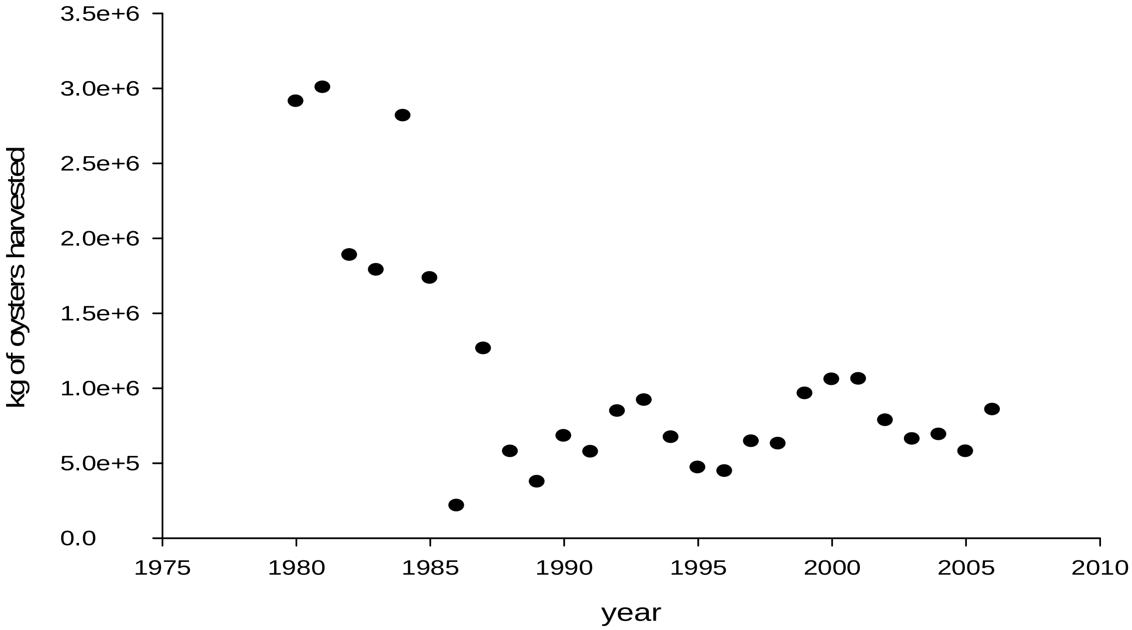


Figure 7. Kilograms (kg) of oysters harvested in Apalachicola Bay from 1980 to 2006.

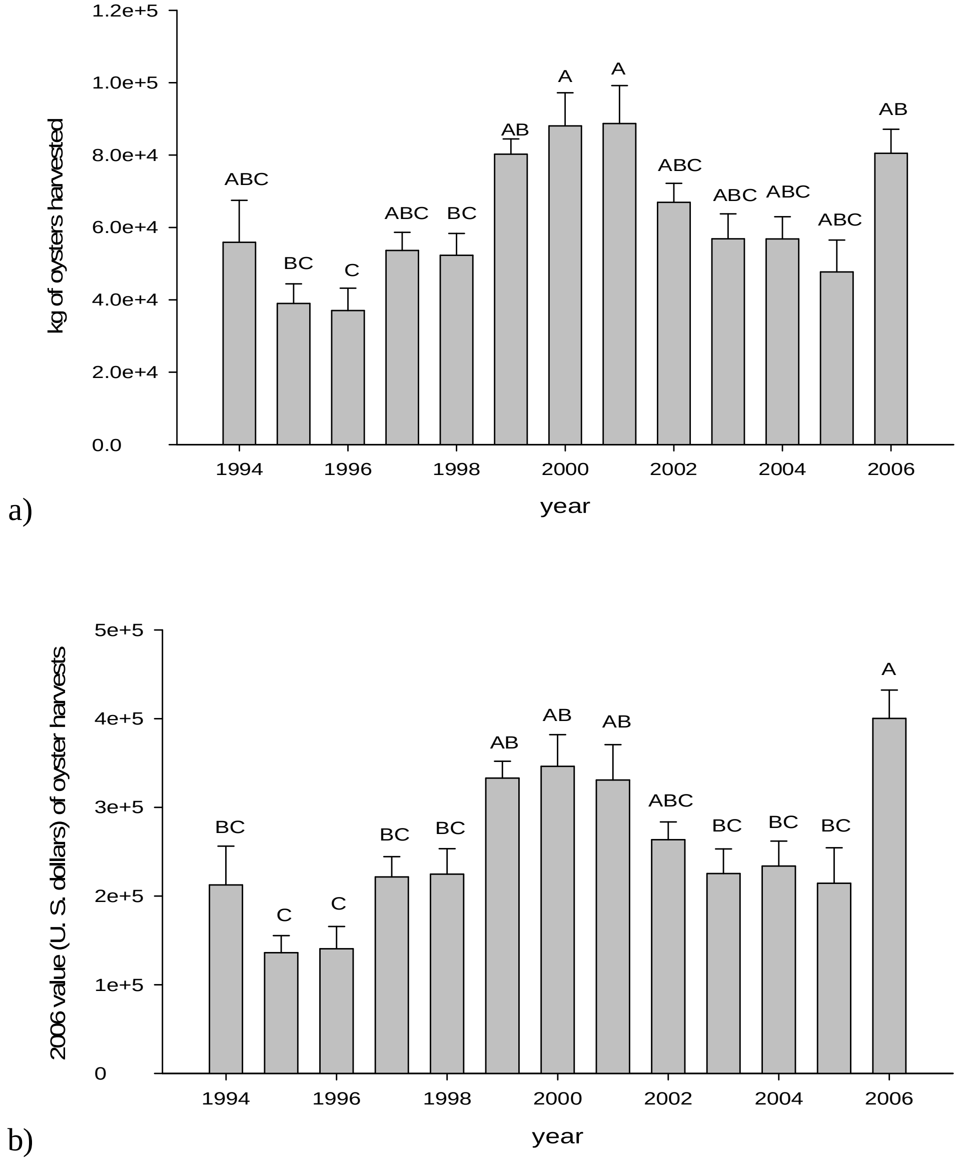


Figure 8. Monthly average of oysters harvested in Apalachicola Bay from 1994-2006 a) kilograms (kg) and b) 2006 value. Letters represent significant differences at $p<0.05$ by Tukey’s post hoc test. Error bars represent standard error.

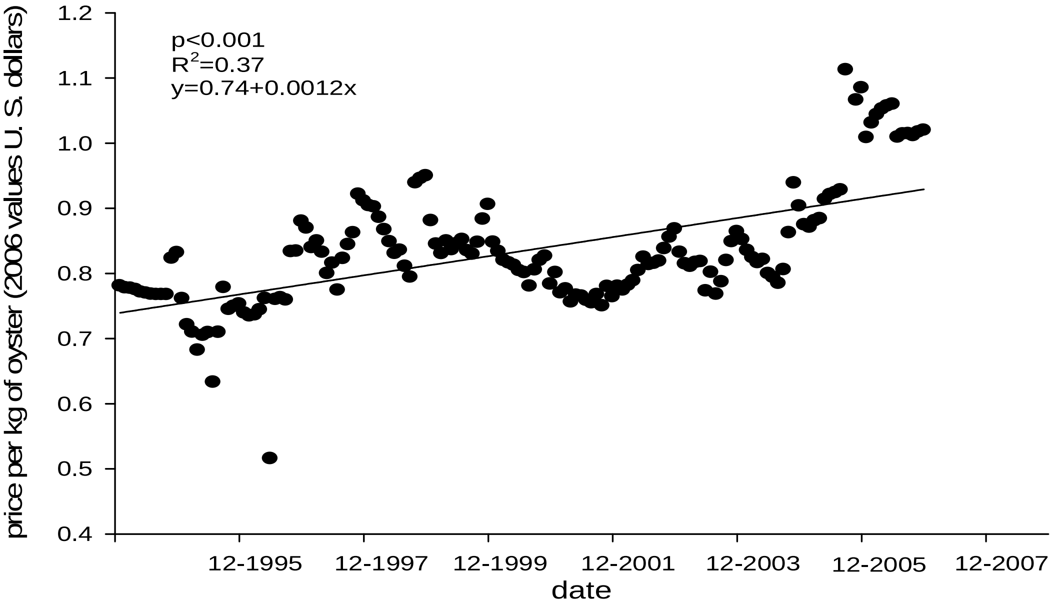


Figure 9. Monthly price (2006 value) per kilogram (kg) of oysters harvested in Apalachicola Bay from 1994-2006.

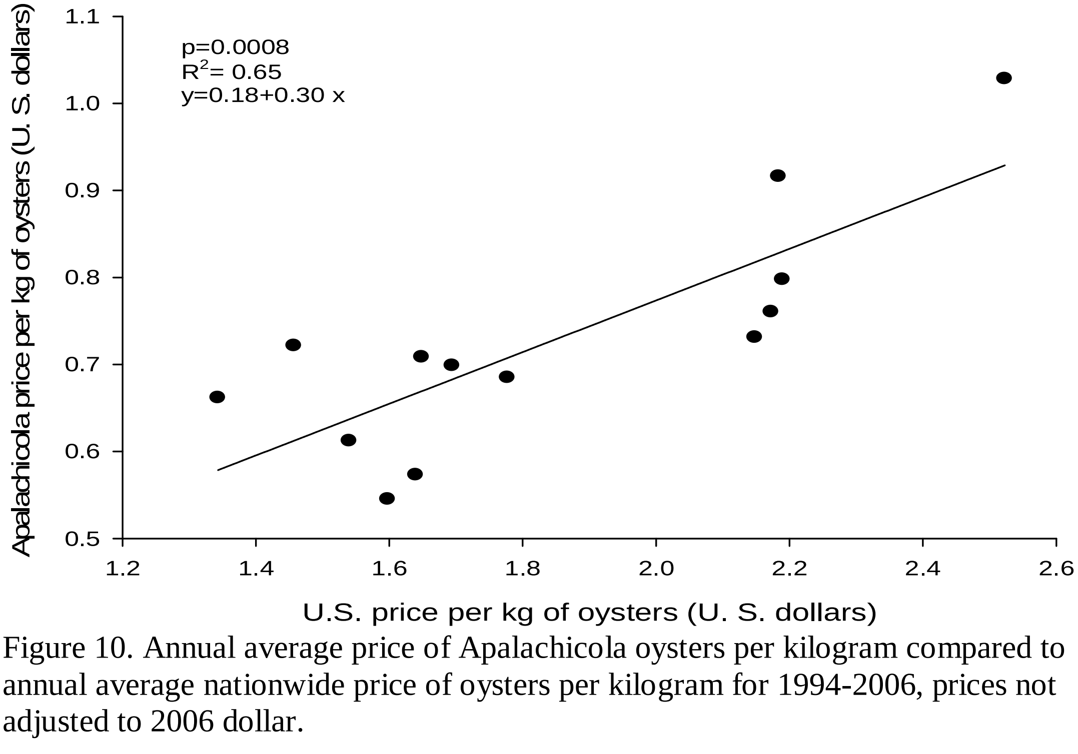


Figure 10. Annual average price of Apalachicola oysters per kilogram compared to annual average nationwide price of oysters per kilogram for 1994-2006, prices not adjusted to 2006 dollar.

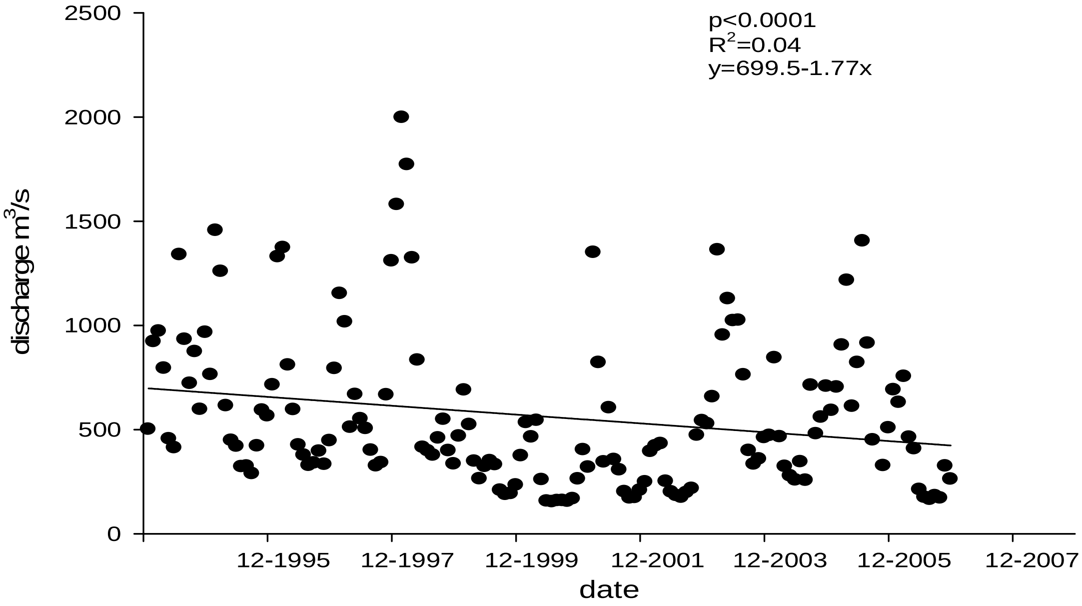


Figure 11. Mean monthly discharge (m^3/sec) from 1994-2006 at the gauge near Blountstown.

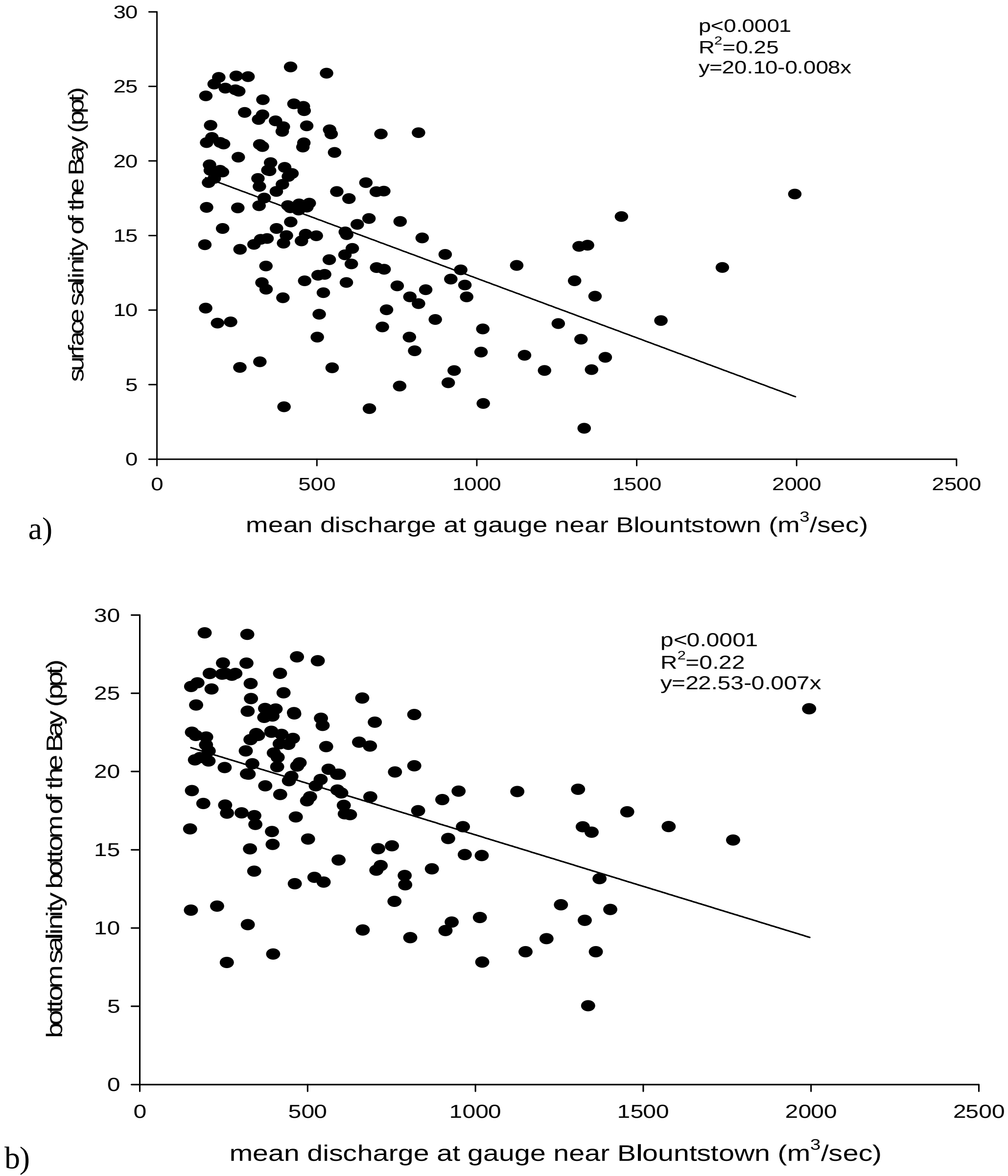


Figure 12. Relationship between mean monthly discharge (m^3/sec) recorded at the Blountstown gauge a) surface and b) bottom salinity.

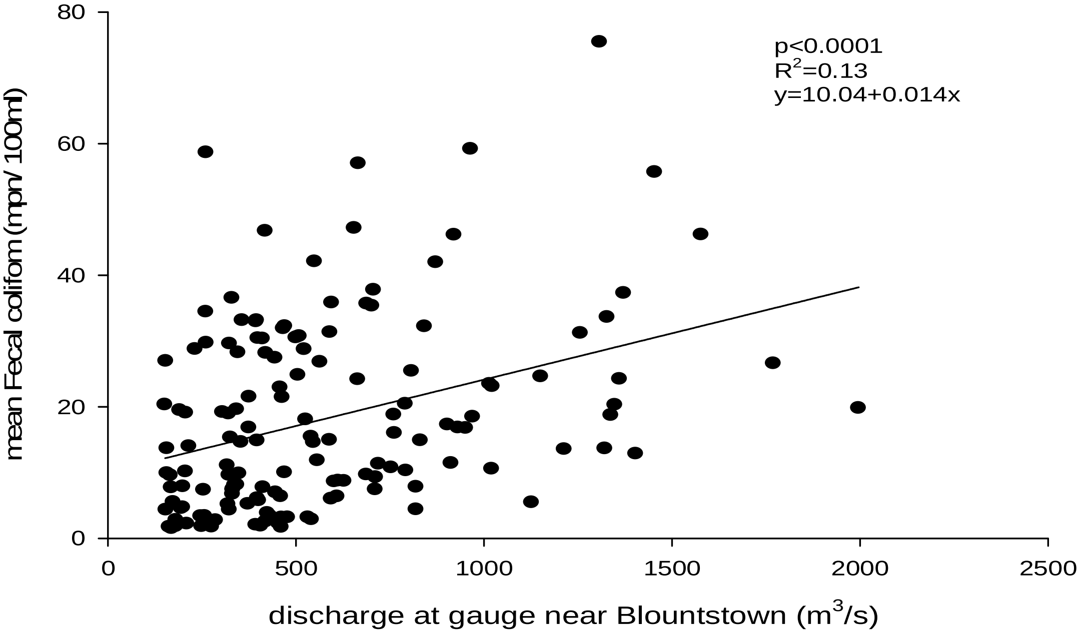


Figure 13. Relationship between mean monthly discharge (m^3/sec) at the Blountstown gauge and mean fecal coliform concentration (mpn/ 100ml) in Apalachicola Bay.

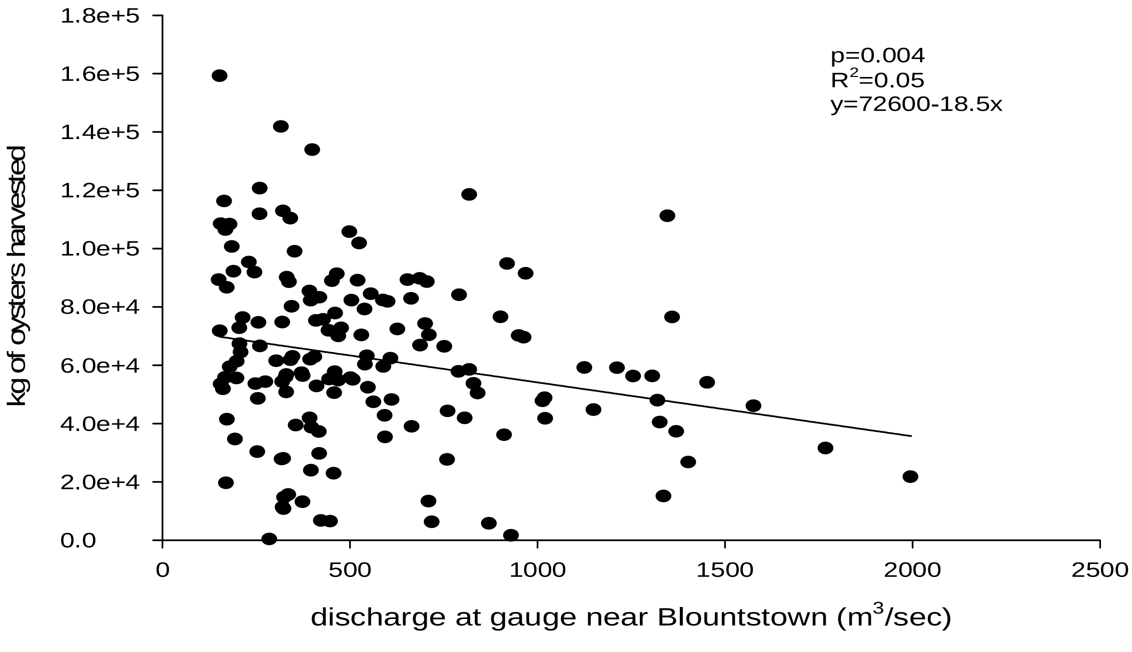


Figure 14. Relationship between mean monthly discharge (m^3/sec) at the Blountstown gauge and monthly kilograms (kg) of oysters harvested in Apalachicola Bay.

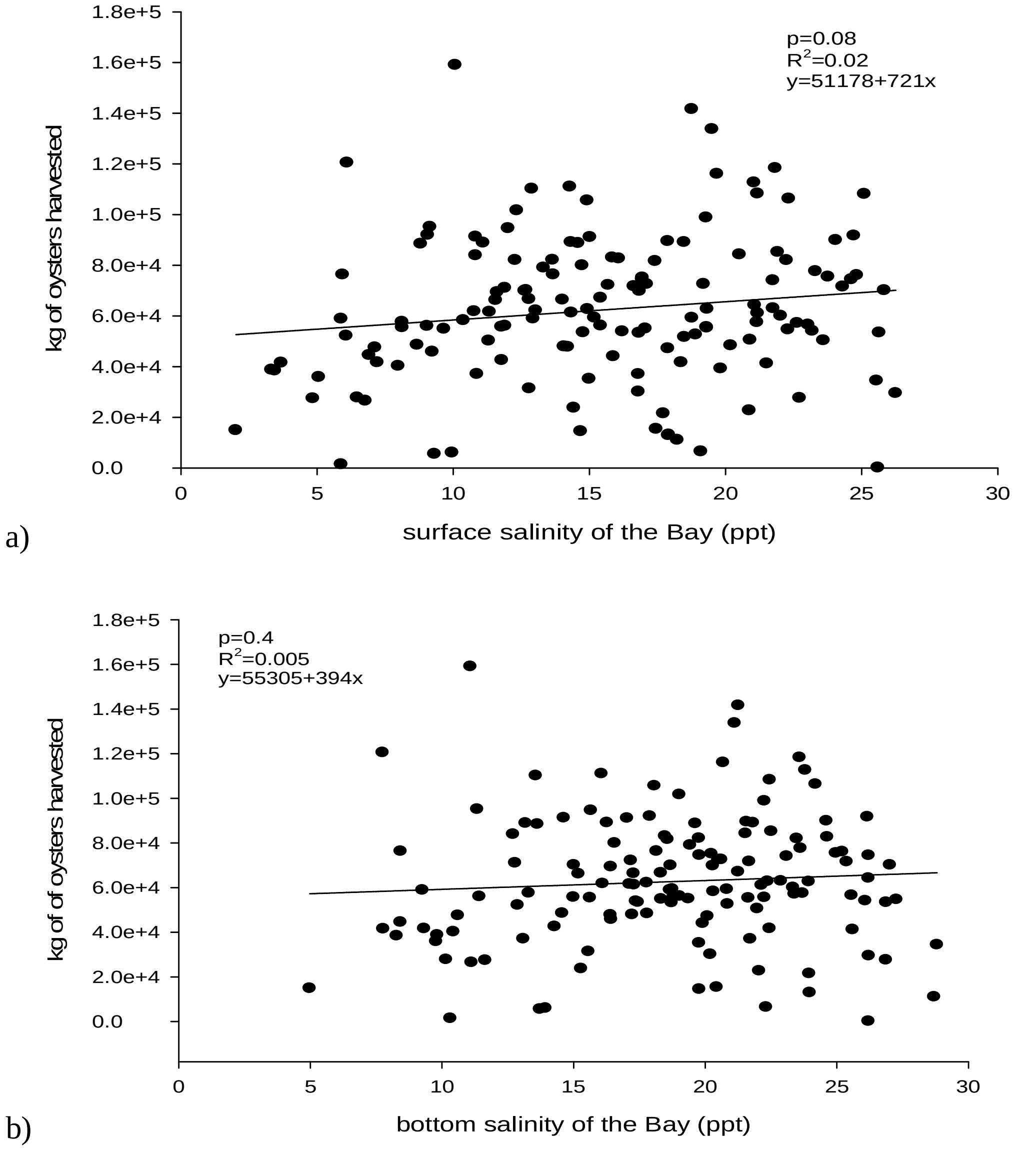


Figure 15. Relationship between monthly average a) surface and b) bottom salinity of the Apalachicola Bay and kilograms (kg) of oysters harvested monthly.

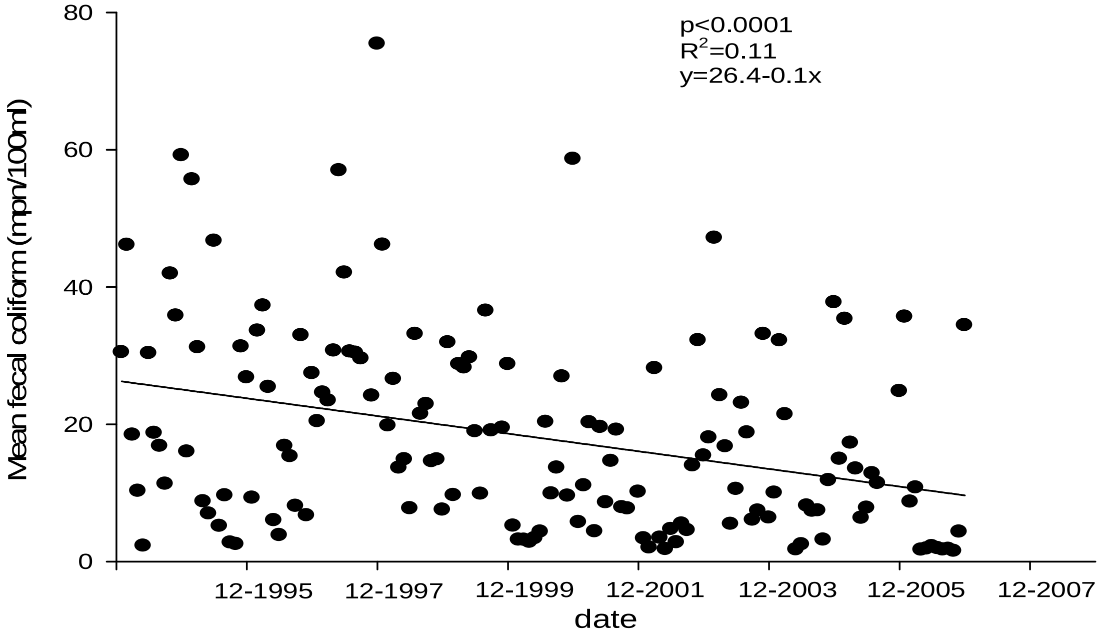


Figure 16. Relationship of monthly mean fecal coliform (mpn/100 ml) over time (1994-2006) for the Apalachicola Bay.

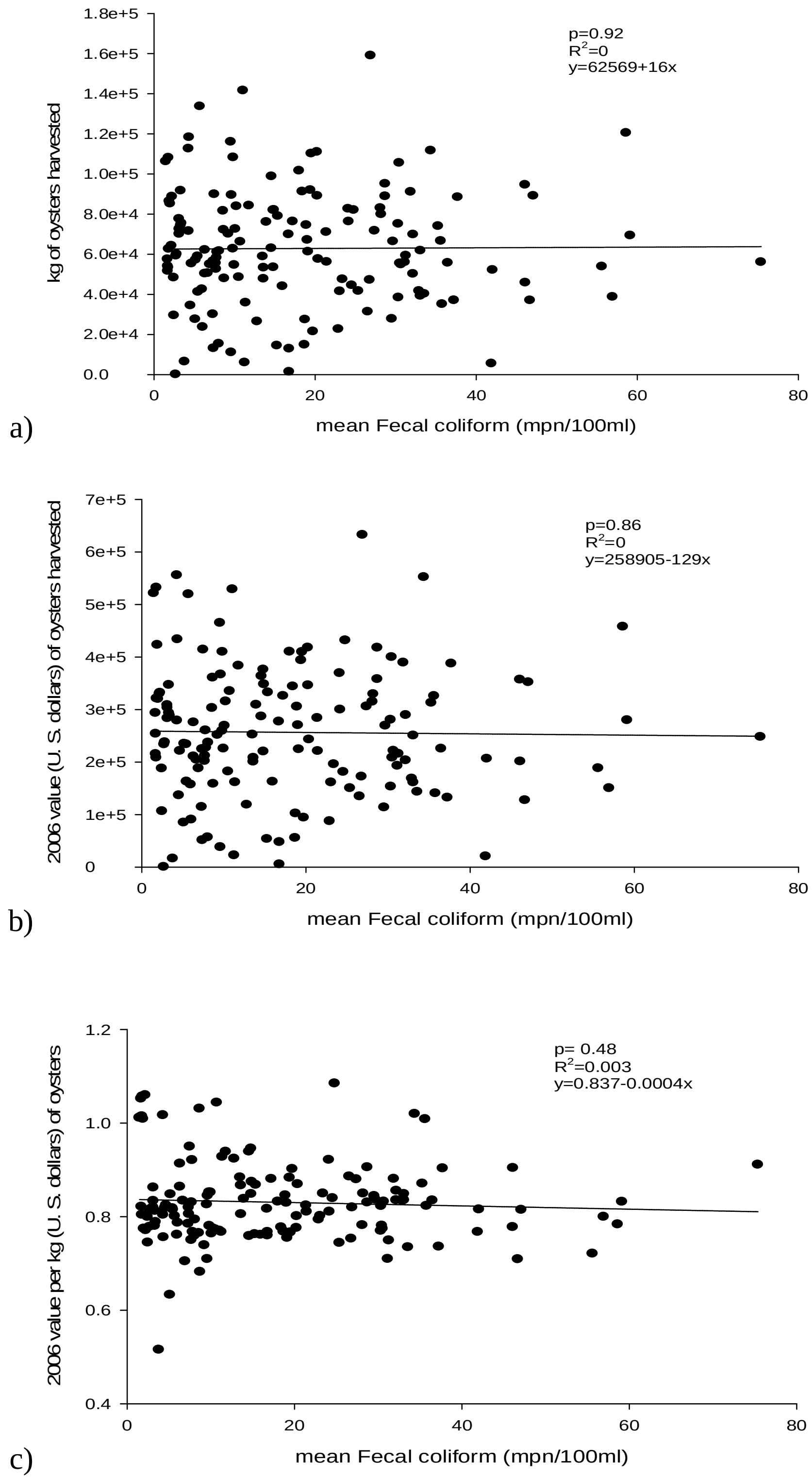


Figure 17. Monthly mean Fecal coliform (mpn/ 100ml) of the Apalachicola Bay and a) kilograms (kg) of oysters harvested by month, b) value of monthly harvest corrected to 2006 dollar, and c) the 2006 dollar value per kg of oysters harvested.

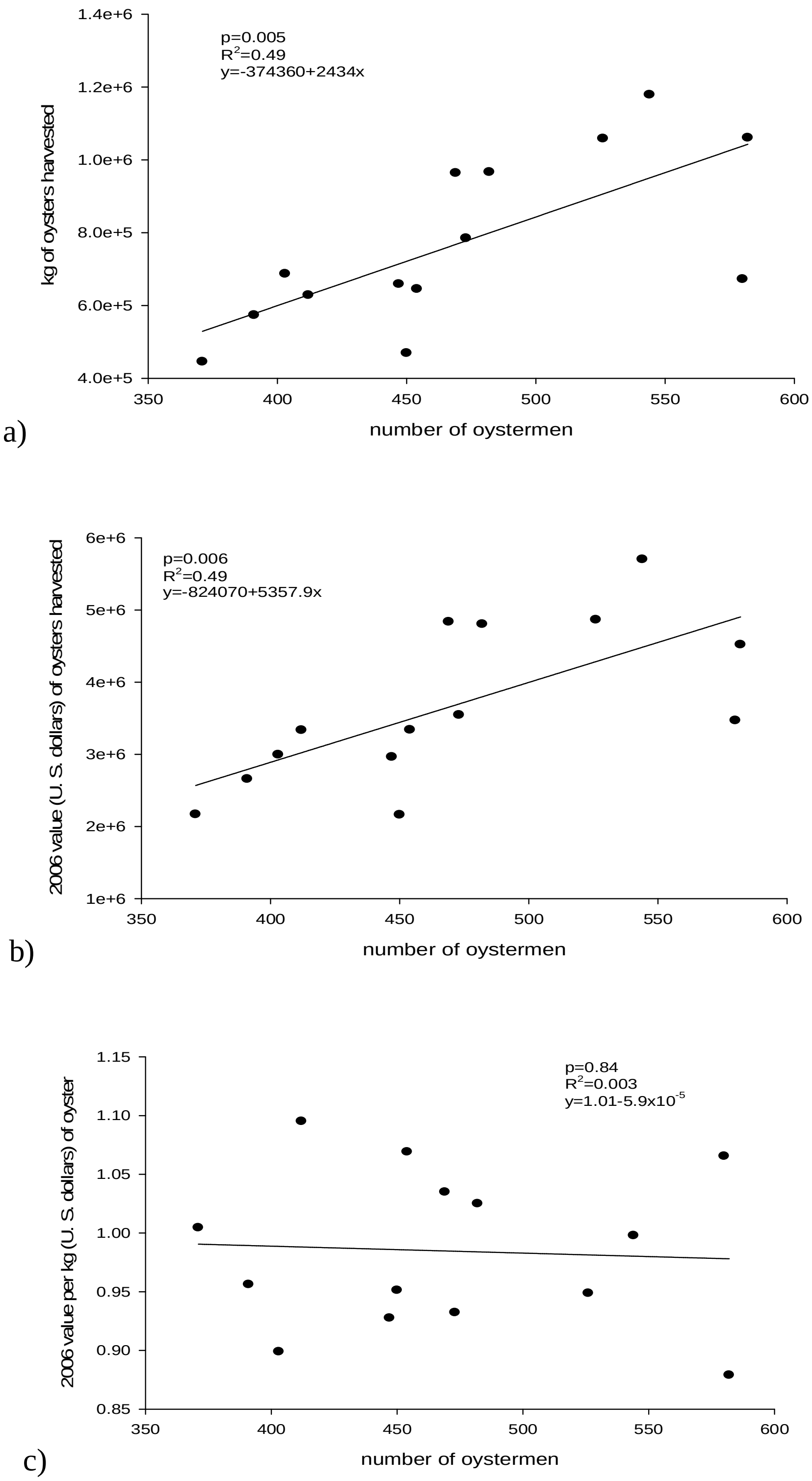


Figure 18. Relationship between the number of licensed oystermen harvesting in Apalachicola Bay by year and a) yearly total kilogram (kg) of oysters harvested, b) yearly 2006 value, and c) the average annual value per kg of oyster (in 2006 U.S. dollars).

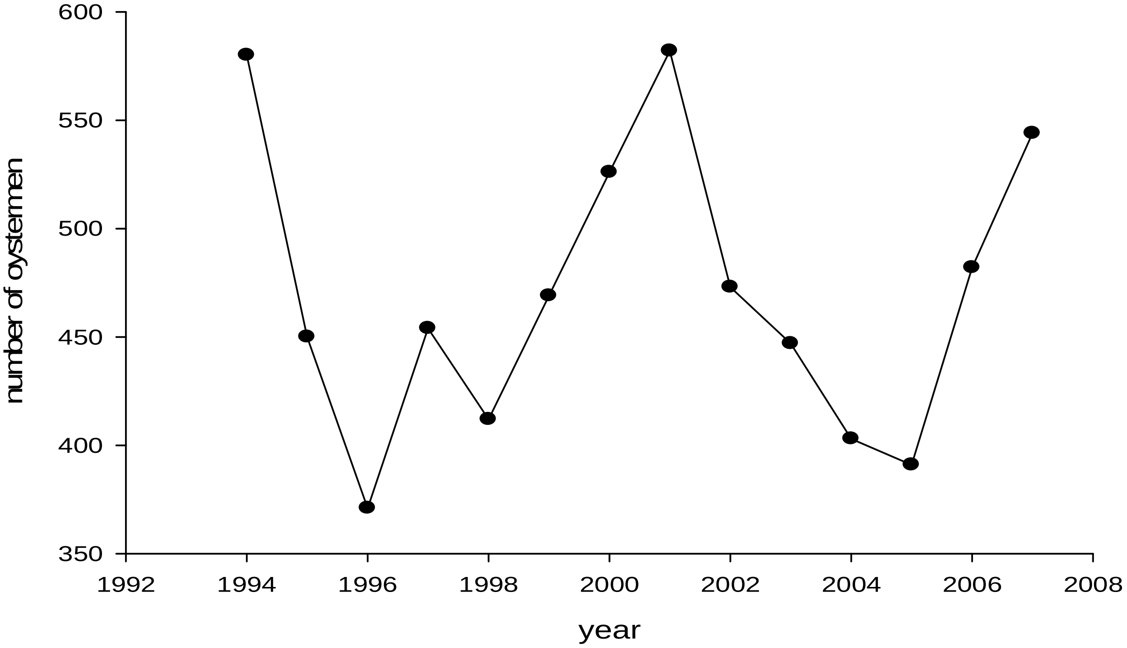


Figure 19. Annual number of licensed oystermen harvesting in Apalachicola Bay 1994-2006.

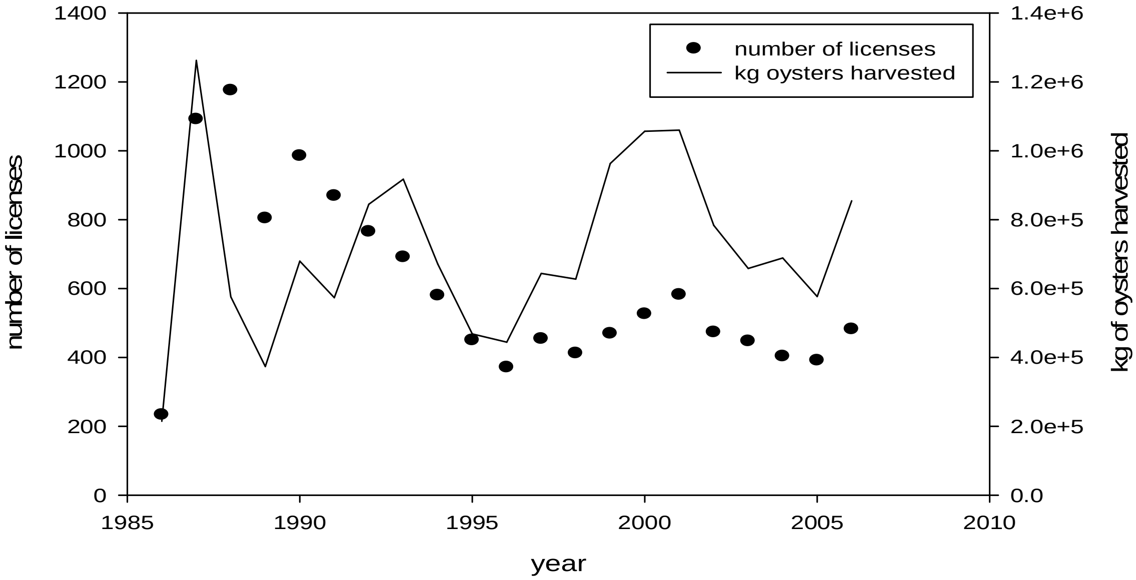


Figure 20. Comparison of the annual number of oyster licenses with kilograms (kg) of oysters harvested in Apalachicola Bay.

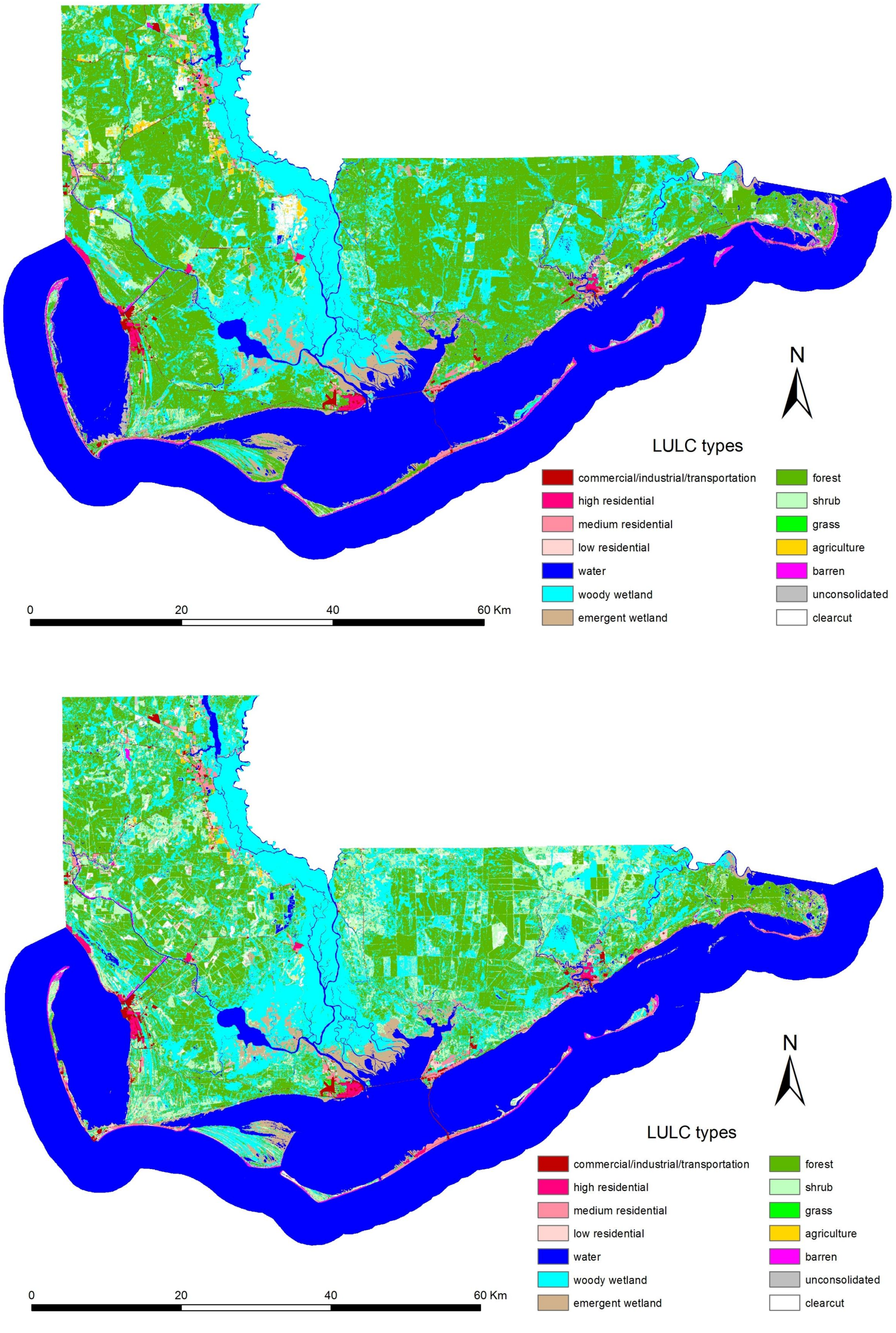


Figure 21. Land use land cover classification for a) 1995 and b) 2005 for Gulf and Franklin counties in Florida.

CHAPTER V

SUMMARY AND CONCLUSIONS

Study Objectives

The overall goals of this research were: 1) to determine how increasing abundance of Chinese privet influenced decomposition rates; 2) to quantify alterations in biogeochemical processes and nutrient cycling in riparian forests in west Georgia across a gradient of Chinese privet abundance; and 3) to assess the economic impact of declining water quality and quantity on Apalachicola Bay, Florida closures in relation to oyster harvests.

Synthesis

Chinese privet. Overall, results suggest that Chinese privet has an influence on biogeochemical cycles in riparian forests in west Georgia. The leaf litter of Chinese privet had higher quality compared to native species because of its low lignin concentrations and high N concentrations. In the controlled study, decomposition rates had a positive relationship with the percent of Chinese privet in litter bags. Faster decomposition rates imply that Chinese privet may accelerate carbon cycling. As Chinese privet becomes more abundant in riparian forests it may decrease carbon storage in steady state forest floors. However, in this study, forest floor nutrient dynamics did not vary significantly across sites with different percentages of Chinese privet in the understory, which may indicate that Chinese privet was not a large proportion of litter in samples, possibly due to timing of collection.

Chinese privet has a different phenology than most native riparian species since it is semi-evergreen. The majority of its leaves senesce in late winter and early spring which influenced changes in the timing and quantity of nutrients on a site, as a result of its altered leaf nutrient composition in comparison to native species. Therefore, the microclimate to which senesced Chinese privet leaves are initially subjected is likely to be warmer and wetter than that associated with native litter in the fall. Not only was timing of litterfall altered, but N composition of litterfall was increased. Litterfall on sites with >30% Chinese privet had higher N concentrations in spring and summer than uninvaded sites. However, P concentrations were higher year round for uninvaded sites. Therefore, in sites that have more than 30% Chinese privet, litterfall exhibited different nutrient ratios in comparison to uninvaded sites suggesting that Chinese privet may have different nutrient requirements in comparison to native species. N:P ratios ranged from 6.9 to 9.3 on sites with Chinese privet and 5.2 to 6.7 in uninvaded sites across all seasons, yet C:N ratios were narrower for spring and summer on sites with >30% Chinese privet. Chinese privet had significantly lower N resorption efficiencies and higher proficiencies compared to sweetgum. In conclusion, nutrient ratios further suggest that N was limited on sites in west Georgia. However, sites with Chinese privet reflected reduced N-limitation, possibly resulting from the high amount of N in senesced Chinese privet leaves.

Not only do invasive plants influence nutrient cycling in riparian forests, land use also had an influence on nutrient circulation patterns in quantified by N nutrient use efficiency (NUE) and N content in litterfall. Urban sites had altered N dynamics because of increased litterfall productivity and N concentrations in urban sites. Urban sites also had low N-NUE the first year of the study, when stream was in contact with its floodplain, possibly indicating lower efficiency compared to the other sites in non-drought years. Lower efficiency would suggest that nutrient limitation was not as severe in the urban sites possibly due to increased stream N. It is possible for there to be a synergistic interaction between land use change and Chinese privet resulting of Chinese privet's ability to establish in disturbed areas especially in urban settings which could severely alter biogeochemical cycles.

Macronutrients in soil and litterfall had significant relationships with respect to Chinese privet abundance. Severely invaded sites had low Ca-NUE and high soil Ca which suggests an adequate supply of Ca, because productivity per amount of Ca available was high. Magnesium was highest in soil of the severely invaded sites; however, Mg-NUE was lowest in uninvaded sites. This may indicate that Chinese privet has a greater Mg requirement than some native species.

Chinese privet also influenced microbial biomass and N-mineralization. Again, the seasonality of Chinese privet litterfall may have increased N-mineralization rates on Chinese privet sites since they were higher in the summer. On sites with >80% Chinese privet, there was a trend of increased microbial N in spring and summer. It can be assumed that Chinese privet has been present longer in the sites where it is more abundant. These sites also had Chinese privet with larger stems, which would mean that Chinese privet has been influencing those systems for a greater length of time. There may be a lag time after privet invasion before changes in soil properties are manifested.

The duration and dominance requirements for Chinese privet to initialize change in the biogeochemistry of riparian sites are not yet known and could be analyzed in a future study.

The higher litter quality of Chinese privet compared to that of some native species may explain increases in decomposition rates in the studied riparian forests of west Georgia which may increase C turnover. Altered decomposition rates may be further influenced by privet-induced changes in soil processes with increased microbial biomass and N mineralization in spring and summer which could further speed up decomposition rates. Also, soil nutrients in these forests may be altered by the species' presence as in soil Ca and Mg. As is the case with many invasive species, these data suggested that Chinese privet altered biogeochemical cycles in riparian forests of central Georgia as it became more abundant.

Apalachicola oysters. Conversion of land from forests to impervious surfaces during 1995–2005 in Gulf and Franklin counties, which border Apalachicola Bay, was not related to the frequency or duration of Bay closures for oyster harvests. However, the extensive urbanization that has occurred within the entire river basin may influence water quality in the Bay, but this was not investigated in this study.

Oyster harvest and Bay closings were examined to determine which environmental factor was of greater influence on the quantity of oyster harvest. The status of each oyster harvesting area in the Bay is determined by an equation calculated by Shellfish Environmental Assessment Section (SEAS) that relates fecal coliform (FC) contamination to discharge and precipitation. At times of high discharge or precipitation, areas are closed based on predicted elevated FC abundance. Consequently, whether closures are justified or not depends on the accuracy of this equation. For example, if the relationship is highly variable, land use conversion could cause actual FC contamination to be higher than predicted for a constant discharge and, as a result, harvesting may be allowed in contaminated waters. Frequent validation of this equation is necessary for accurate classification of the harvesting areas. Closures are based on elevated FC levels that are positively associated with high discharge from the Apalachicola River and large quantities of precipitation.

Oyster harvest quantities were most influenced by river discharge. Low discharge of the river corresponded with increased surface salinity and increased harvest quantity. Under low discharge conditions, a greater proportion of the Bay remains open and harvests are larger. Furthermore, during low flow there was a small proportion of the Bay that was closed because predictions using the SEAS equation and measured values of FC contamination declined with decreased overland flow and corresponding low river discharge. Therefore, it is logical that a greater majority of the Bay would be open with low river discharge and harvests can be larger.

The economic influence of harvesting Apalachicola oysters was examined in this study. For the period of study from 1994-2006, Apalachicola oysters represented 3.6-7% of the total oyster harvest in the U.S., and provided 95.3-98.7% of the oysters to the Florida industry. Furthermore, harvest area closures caused unrealized values of $43,375 when 0.1-25% of the Bay was closed for a month, and unrealized values increased as a greater proportion of the Bay was closed. If larger harvesting areas are closed or longer periods of closure are imposed, hundreds of thousands of dollars may be unrealized monthly.

Water quantity had the greatest influence on oyster harvests of all the factors studied because it is the basis for FC predictions and, ultimately, Bay closures. Although lower discharge was related to increased harvest quantity, extended high salinity conditions may eventually decrease harvests because of increased predation and disease brought on by higher salinities. Oysters remain important to the economy of Franklin and Gulf counties, providing 1.5 to 4.8 million dollars annually, and should be considered when making decisions that will influence runoff into the Bay and discharge of the Apalachicola River.