

IMPLICATIONS OF PLANT DIVERSITY AND SOIL CHEMICAL PROPERTIES
FOR COGONGRASS (*Imperata cylindrica*) INVASION IN NORTHWEST FLORIDA

By

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A THESIS PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

2005

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by

Alexandra R. Collins

I dedicate this thesis to my grandfather, Edwin Frank Collins.

ACKNOWLEDGMENTS

I would like to sincerely thank my advisor and committee chair, Dr. Shibu Jose, for his numerous ideas and guidance throughout my research. I wish to express my sincere appreciation to my committee members, Drs. Jack Putz, Barry Brecke, Deborah Miller and Greg MacDonald, who despite being separated geographically have provided me with valuable insight into the field of biological invasions and community ecology.

I would like to thank my parents, Holly Nicol and Paul Collins, for being constant sources of inspiration throughout my educational career. Their thoughtful phone calls, cards and words of wisdom have been a wonderful source of encouragement throughout my time at the University of Florida. I would also like to thank my sweet little dog Lizzie whose picture next to my computer was a welcome distraction while writing this thesis.

I am grateful to several members of the West Florida Research and Education Center: Doug Hatfield and Joe Nelson for their constant help on the farm, Leah McCue for all of her help in the field and being a great friend, Rex Lawson for valuable advice and lab space and Jeremy Monnot and Cathy Hardin for their help in the field and willingness to work at all hours and in all weather conditions. I am sincerely thankful to Craig Ramsey for his insight and support throughout my thesis. Staff at Blackwater River State Forest, notably Tom Errington and Tom Cathy, and the staff at International Paper were incredibly helpful in finding field sites to carry out this research.

Friends and fellow graduate students were tremendous sources of encouragement and inspiration as I completed my thesis. I am sincerely grateful to my Milton crew

Pedram Daneshgar, Nicholas Pool, Kara Napolitano, Eric Holzmueller, Josiah Raymer and Jeff Kelly for some wonderful memories and lasting friendships. Fellow graduate and undergraduate students Julie Clingerman, Trina Hofreiter, Cara Rockwell, Keila Altidor and David Suza have been tremendously supportive throughout my time at the University of Florida. I would also like to thank the University of Florida Gator Synchro Team, most notably Rebecca Guerra, Katie Rozofsky, Crystal Amsinger, Jennifer Amsinger, Jamie Freshour, Meredith Cooke, Megan Becker, Maggie Baker, Stephanie Joyce, Nique Long, Nikki Berlin and Betsy Caza, for their constant support in all aspects of my life and providing me with memories that will last forever. Finally, I could not have completed this thesis without constant support and cheerleading from my friends back at home, Katie Thomas, Meghan McClenaghan, Sarah Ueland and Shay Wallin.

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May 2005

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Major Department: Forest Resources and Conservation

In the 1950s Charles Elton hypothesized that more diverse communities should be less susceptible to invasion by exotic species (biodiversity-invasibility hypothesis). The biodiversity-invasibility hypothesis postulates that species-rich communities are less vulnerable to invasion because vacant niches are less common and the intensity of interspecific competition is more severe.

Field studies were conducted at two sites, a logged site and an unlogged site in Santa Rosa County, Florida, U.S.A, to test Elton's hypothesis using cogongrass (*Imperata cylindrica*), a nonindigenous grass invading large areas of the Southeastern United States. The effects of cogongrass invasion on soil chemical properties were also investigated. The logged site, owned by International Paper Company, was under 17-year-old loblolly pine prior to clear cutting. The unlogged site, a longleaf pine forest, was at the Blackwater River State Forest. Both the logged site and unlogged site showed no significant relationship between the rate of cogongrass spread and native plant species

richness, functional richness, and cover of the invaded community. Increased species or functional richness may increase the use of resources; however, the extensive rhizome/root network possessed by cogongrass and its ability to thrive under shade may allow for its persistence in a diverse community. Analysis of soil samples, taken pair wise (cogongrass invaded and non-invaded areas) at both sites, showed significant differences in soil NO_3^- -N, K^+ and pH. Significantly lower levels of NO_3^- -N and K^+ were observed in cogongrass patches compared to the surrounding native vegetation. Lower levels of these nutrients may be attributed to the extreme ability of cogongrass to extract available resources from the area in which it is invading. The soil of the cogongrass patch was more acidic than that of the surrounding native vegetation. Although we do not have direct evidence of any mechanisms responsible for lowering soil pH in cogongrass invaded patches, allelopathy or the preferential uptake of ammonium seems to be plausible mechanisms.

The results from both the logged and unlogged sites do not support the general hypothesis of Elton that invasion resistance and compositional stability increase with diversity. Based on the results of all of the research reported within, biodiversity does not appear to be an important factor for cogongrass invasion in Northwest Florida. Extrinsic factors in this study prevent the ability to draw a defined causal relationship between native plant diversity and invasibility. Underlying reasons for why no relationship was observed may be simply due to the tremendous competitive ability of cogongrass or the narrow range of species richness, functional richness and cover observed in our study.

CHAPTER 1 INTRODUCTION

The invasion of habitats by non-native species is a global problem with serious consequences for ecological, economic and social systems (Pimental et al. 2000). Millions of acres of forestland in the Southeastern United States are increasingly being occupied by alien invasive plants, threatening their ecological and economic integrity. Empirical and theoretical studies of the mechanism of invasions have led to the hypothesis that high diversity may increase the resistance of a community to invasion (Elton 1958; Prieur-Richard et al. 2000). This thesis examines the ecological implications of species diversity on *Imperata cylindrica* (hereafter referred to as cogongrass) invasion in Northwest Florida. Cogongrass is an exotic non-native species and is considered to be one of the ten most troublesome weeds in the world (MacDonald 2004).

Exotic Invasive Plants

Invasive species pose many threats to native species in ecosystems worldwide. Non-indigenous harmful plants hinder the maintenance and restoration of natural ecosystems (Mack et al. 2000). Most non-indigenous invasive plants are undesirable in native communities because they exclude native plants, form monocultures and change ecosystem functions. Ecosystem functions may include but are not limited to biogeochemical activities, community respiration, nutrient cycling, nutrient retention, and decomposition. The invasion of many exotic plant species results in native species decline and ecosystem degradation (Wilcove and Chen 1998).

The globalization of earth's biota is transforming local and regional floras and faunas. Both intentional and accidental introductions of many species are altering community composition and ecology of long-established biological communities (Davis 2003). Although not all introduced plants become invasive, many plants may escape cultivation and become agricultural pests, infest lawns as weeds, displace native plant species, reduce wildlife habitat, and alter ecosystem processes. The characteristics and effects of exotic invasive species have received increasing attention from ecologists, conservationists and land managers. There has been an increase in the level of non-native plant species colonized natural areas, potentially threatening diversity and interactions of native species, have been recognized and have become the subject of ecological dialogue and experimentation. The total impact of an invader is argued to include three fundamental dimensions: range, abundance and the per-capita or per-biomass effect of the invader in the invaded community (Parker et al. 1999). The actual invasion of an environment by new species is said to be influenced by an additional three factors: the number of propagules entering the new environment (propagule pressure), the characteristics of the new species, and the susceptibility of the environment to invasion by new species (invasibility) (Lonsdale 1999; Davis et al. 2000). The most consistent correlates of invasibility are disturbance and propagule supply. Disturbances have been shown to favor plant invasions (Prieur-Richard and Lavorel 2000). Disturbances simultaneously increase resource availability and decrease competition from resident species. Frequent disturbance facilitates the colonization of ruderal species that may have greater competitive abilities than natives. Cogongrass seedlings are described as R-strategists (ruderal) (Grime 1977) and are able to invade open patches in disturbed

habitats. The amount of bare ground created by soil disturbances is correlated with abundances of invading species (Burke and Grime 1996).

Invasibility is an emergent property of an environment, the outcome of several factors, including the region's climate, the environment's disturbance regime, and the competitive abilities of the resident species (Lonsdale 1999). For example, modifications of fire regimes favor the recruitment of exotics with more tolerant life histories than many natives, and also provide both bare ground and nutrient pulses (D'Antonio and Vitousek 1992). Invasions can affect native ecosystems by changing fuel properties, which can in turn affect fire behavior and, ultimately, alter fire regime characteristics such as frequency, intensity, extent, type, and seasonality of fire (Brooks et al. 2004).

Characteristics of successful invaders often include: broad ecological requirements and tolerances, sometimes reflected in large geographical ranges (Rejmanek 1996), r-selected life histories (Tominaga 2003); associations with disturbed or anthropogenic habitats; and origins from large continents with diverse biota (Elton 1958).

Characteristics of invaded environments often include: geographical and historical isolation; low diversity of native species (Elton 1958); high levels of natural disturbance or human activities; and absence of co-adapted enemies, including competitors, predators, herbivores, parasites and diseases (Davis et al. 2000). One of the few generalizations that can be made about invasive species is that the greatest impacts often occur when a nonindigenous species performs an entirely novel function in the recipient community (Simberloff 1991). Although many hypotheses have been proposed to explain why some communities are more susceptible to invasion than others, results from field

studies have been inconsistent and no general theory of community invasibility has yet emerged (Davis et al. 2000).

Diversity-Invasibility Hypothesis

The question as to why some ecosystems are more vulnerable to invasion than others is under constant debate. There are numerous factors that influence a community's susceptibility to invasion including the composition and diversity of resident species. One of the earliest theories relating biodiversity and invasibility was Elton's hypothesis, which states that lower resident diversity favors invasion (diversity-invasibility hypothesis; Elton 1958). Empirical studies have shown conflicting patterns of relationship between species diversity of resident plant communities and their invasibility by external species. Results have shown positive (Palmer and Maurer 1997; Levine et al 2002), negative (Tilman 1997; Hector et al. 2001; Kennedy et al. 2002) and no relationships (Lavorel et al. 1999) between native plant species diversity and invasibility. Fluctuations in resource availability because of disturbance, herbivory and eutrophication were identified as key factors controlling community invasibility by nonindigenous plants (Davis et al. 2000). The most likely explanation for the conflicting results is the covariance between extrinsic factors (i.e., disturbance, grazing, nutrient levels, biomass and resident diversity) in observational studies (Naeem et al. 2000).

It is hypothesized that more diverse communities use resources more completely and are therefore more resistant to invasion (Tilman 1999). Resource-use complementarity is often proposed as the mechanism responsible for the negative impact of diversity on invasibility. Invasibility of a site should depend on the availability of the resources that limit the growth of the invading species. Because levels of limiting resource are generally lower in more diverse ecosystems within the same habitat (Tilman

et al. 1996), fewer potential invaders should be able to become established in more diverse ecosystems. Resource partitioning also leads to fewer resources (mainly light and nutrients) being made available for invaders. Biotic resistance consists of negative impacts by the resident community on the invading organism, usually through predation or competition, and is often said to increase with species richness of the recipient community (Simberloff 1986). Elevated resource levels favor fast-growing species and can lead to invasion or dominance of one species (Huenneke et al. 1990).

It is also hypothesized that diverse communities are more likely to contain competitors that can successfully outcompete the exotic (Pimm 1991). Conventional wisdom was that species-rich communities were less invasible because vacant niches were less common and the intensity of interspecific competition was more severe (Robinson et al. 1995). In particular, species-packing models (e.g., MacArthur 1970) predict that niche space becomes progressively more utilized as more species are added to a community, leaving fewer opportunities for additional species to invade (Hector et al. 2001).

Recent studies have begun to investigate how the scale on which an experiment is conducted may contribute to either a negative or a positive relationship between biodiversity and invasibility. The diversity-invasibility hypothesis is often supported by both theory and experimental studies conducted at small scales (Kennedy et al. 2002). However, there is also evidence for a positive relationship when measured at regional scales (Stohlgren et al. 1999). Brown and Peet (2003) found a positive relationship between species diversity and exotic invasion in riparian areas at large scales (100 m^2), which graded into a negative relationship at small scales (0.01 m^2).

Disentangling the relative contributions of sampling, niche-complementarity, and other potential mechanisms responsible for the observed diversity effects in diversity-gradient experiments requires further experimentation (Kennedy et al. 2002). Ecologists are struggling to develop strategies to quantify the biological diversity of landscapes and regions and to link vegetation analyses across scales (Stohlgren 1997).

Functional Diversity

The issue of whether species richness or species identity is more important in determining system-level function in biodiversity experiments is controversial (Crawley et al. 1999). Functional diversity, the number of functional groups with different behaviors for a particular process, is receiving a renewed interest because major thresholds in ecosystem processes may be related to the presence or absence of particular functional groups (Hooper 1998, Prieur-Richard et al. 2000). Functional diversity measures the extent of complementarity among species' trait values (in the same way that phylogenetic diversity is directly related to uniquely evolved characters among species) by estimating the dispersion of species in trait space (Petchey and Gaston 2002). Results from several studies have shown that species identity matters more than species richness in determining both the number of invading species and their total biomass (Crawley et al. 1999, Dukes 2002). In most natural communities, both species richness and identity matter, with the relative importance determined by resource supply, substrate heterogeneity, the size of the local and regional species pools, and the scale of the experiment (Crawley et al. 1999).

Functional diversity is an important component of biodiversity, yet in comparison to taxonomic diversity, methods of quantifying functional diversity are less developed

(Petchey and Gaston 2002). There is no simple or standardized measure of functional diversity (Diaz and Cabido 2001, Tilman 2001). The actual functional groups used depend on the community type. For example, in a study conducted by Dukes (2002), in the San Francisco Bay Area, species used were classified into one of four functional groups (annual grasses, perennial grasses, early-season forbs, and late season forbs) while Prieur-Richard et al. (2000) in a study of invasion of Mediterranean old fields by *Conyza bonariensis* and *Conyza Canadensis* classified the native species used into one of three functional groups (legumes, grasses, asteraceae). This parameter has not been significantly examined and future work should focus on separating the effects of species richness and functional diversity on invasibility.

Cogongrass Taxonomy and Distribution

Imperata cylindrica (L.) Beauv. (family Poaceae, subfamily Panicoideae, tribe Andropogoneae, subtribe Andropogoneae) originated in Southeast Asia and occurs throughout the tropical and warmer regions of the world, from Japan to Southern China, throughout the Pacific islands, Australia, India, East Africa, and Southeastern United States (Holm et al. 1977).

Cogongrass was introduced by accident in the U.S., to Alabama, as a packing material in boxes from Japan in 1912 (Dickens 1974). Cogongrass was then purposefully brought to Mississippi as a potential forage in 1921 (Dickens and Buchanan 1975) but its unpalatability due to its high silica content prevented its use as a long-term forage (Dozier et al. 1998). Cogongrass was also used to stabilize soil along roadways by state departments of transportation and spread throughout the Southeastern United States by rhizome-infested soil during maintenance work and the construction of railroads (Jose et al. 2002). Currently, cogongrass is on the Federal Noxious Weed List, which prohibits

new plantings. It is also included in the Florida Department of Agriculture and Consumer Service's Noxious Weed List (Florida Statutes, Chapter 5B-57.007, 1993 revision) and the Florida Exotic Pest Council's 2003 invasive plant list.

Cogongrass is reportedly established on over 500 million hectares of plantation and agricultural land worldwide (Figure 1-1) (Holm et al. 1977). In the United States cogongrass occurs in Florida, Mississippi, Louisiana, South Carolina, and Texas (Figure 1-2). At least 100,000 ha are infested in Alabama, Florida, and Mississippi (Schmitz and Brown 1994).

Cogongrass Biology

Cogongrass is an aggressive, rhizomatous, C₄ grass found mainly in tropical and subtropical regions with annual rainfall between 750 and 5000 mm (Bryson and Carter 1993). Cogongrass is a perennial grass with basal leaf blades that can be up to 1.5 m tall and 2 cm wide (Lippincott 1997). Leaf blades have a noticeably off-center whitish mid-vein and scabrous margins. The serrated margins of the leaves accumulate silicates, which deter herbivores (Dozier et al. 1998).

Cogongrass rhizomes can comprise over 60% of the total plant biomass. The large below-ground rhizome network leads to a low shoot-to-root/rhizome ratio and contributes to cogongrass rapid regrowth after burning and cutting (Sajise 1976; Ramsey et al. 2003; MacDonald 2004). Rhizomes are very resistant to heat (from fires) and breakage (from soil disturbance) and may penetrate the soil 1.2 m deep but generally occur in the top 0.15 m in heavy clay soils and the top 0.4 m of sandy soils (Holm et al. 1977). Rhizomes are white and tough with short internodes and possess several anatomical features, such as cataphylls (scale leaves) and sclerenchymous fibers, that help resist breakage when the rhizomes are disturbed.

Cogongrass is able to reproduce by both sexual and asexual reproduction.

Cogongrass is a prolific seed producer with over 3000 seeds per plant and seeds are capable of dispersal ranging from 15 m to 100 m. First flowering occurs within one year of germination and seeds germinate soon after ripening. No seed dormancy has been observed and seeds are highly germinable in natural populations. Seeds less than three months old have the highest viability, with rapid decline in seed viability over time and a complete loss of viability after one year (Shilling et al. 1997). Although seed production has been reported to be high, seed as a major form of spread is questionable, particularly in the U.S. (Willard et al. 1997). Seed production from populations in Florida was shown to be self-incompatible and only cross-pollination from geographically isolated, heterogeneous populations produced viable seeds (McDonald et al. 1995,1996).

Cogongrass can invade a wide variety of habitats, soil types and climates. It has colonized deserts, sand dunes, grasslands, forests, river margins, and swamps. Cogongrass is tolerant of variety of soil conditions, but grows best in acidic pH, low fertility and low organic matter soils (MacDonald 2004). Within its native range cogongrass is mostly limited by extreme aridity (Hubbard et al. 1944).

Cogongrass thrives in highly disturbed areas such as roadsides and reclaimed mine areas (Bryson and Carter 1993). Dozier et al. (1998) indicated that seedling establishment is favored in areas of limited competition, such as disturbed sites, and further suggested that seedlings are unlikely to establish in areas with greater than 75% sod cover. However, cogongrass can also occur in areas of fewer disturbances such as pine and hardwood forests (Willard et al. 1997). Ramsey et al. (2003) showed that cogongrass has

a light compensation point of 32 to 35 $\mu\text{mol m}^{-2}\text{s}^{-1}$, indicating the ability to survive in the understory.

Ecological Importance

The negative ecological impacts of cogongrass invasion far outnumber the positive ones. Cogongrass has little useful qualities except for thatch, short-term forage production, and soil stabilization (Dozier et al. 1998).

Cogongrass invasion may change the structure and function of the ecosystem. Like other exotic species, invasion may alter soil chemistry, nutrient ratios, hydrology, and disturbance regimes. Cogongrass exerts intense competition for light, water, and nutrients (Lippincott 1997). Cogongrass is able to persist through several survival strategies including an extensive rhizome network, adaptation to poor soils, drought tolerance, prolific wind-disseminated seed production, fire adaptability and high genetic plasticity (MacDonald 2004).

Cogongrass forms dense, and persistent stands that expand rapidly and displace native vegetation. Above ground biomass and increased root competition prevents recruitment of other plants and changes the properties of the litter and upper soil layers (Lippincott 1997). Koger and Bryson (2004) tested the effects of cogongrass foliage and root residue extracts on germination of radicle and coleoptile growth on various grass and broadleaf species in laboratory experiments. Cogongrass residue (foliage and root) extracts at concentrations as low as 0.5% inhibited germination and seedling growth of *Cynodon dactylon* and *Lolium perenne*. Germination of *Cynodon dactylon* and *Lolium multiflorum* was reduced by as much as 62% and radicle and coleoptile growth by as much as 96% at the highest extract concentrations. Foliage and root residue extracts reduced germination of *Echinochloa crus-galli*, *Brachiaria ramosa*, and *Sida spinosa* 52

to 64% and seedling growth by as much as 96%. Results from this study indicate that cogongrass may contain allelopathic substance(s) that contribute to its extreme invasive and competitive ability. In addition, Eussen and Soerjani (1975) and Eussen (1979) in a series of experiments showed that cogongrass suppressed the growth of tomato and cucumber and that the factors involved were more active at lower pH (Eussen and Wirjahardja 1973).

Cogongrass is also a threat to ecosystems maintained by frequent low-intensity fire. Dense stands of cogongrass change fire regimes and fires become more intense and more frequent. Sandhill, a pyrogenic pine savanna ecosystem, had significantly greater fine-fuel loads, horizontal continuity, and vertical distribution compared to indigenous sandhill grasses when invaded with cogongrass. The increase in horizontal continuity contributed to higher fire maximum temperatures at greater heights with fire temperatures reaching 450°C at heights 1.5 m above ground (Lippincott 2000). These changes in fire regime due to cogongrass invasion cause increased damage and death to normally fire tolerant seedling and juvenile native species.

Soil Ecology

Although it is acknowledged that invasions by exotic plant species represent a major threat to biodiversity and ecosystem stability, relatively little attention has been paid to the potential impacts of these invasions on nutrient cycling processes in the soil. Plant introductions of exotics have the potential to change many components of the carbon, nitrogen, water and other cycles of an ecosystem (Ehrenfeld 2003). Studies have shown that invasive plant species frequently increase biomass and net primary productivity, increase N availability, alter N fixation rates, and produce litter with higher decomposition rates than co-occurring natives (Ehrenfeld 2003). The ability to alter these

properties is most likely attributed to the differences from native species in biomass and productivity, tissue chemistry, plant morphology, and phenology.

Differences in soil ecology are valuable indications of the effect of species richness on invasion dynamics. Studies have been conducted on various abiotic and biotic components of soil ecology across the invasion area of nonindigenous plants. A study conducted by Duda (2003) tested nutrient levels (NO_3 , P, K, Na) among the native, ecotone and exotic derived soils of the exotic annual chenopod, *Halogeton glomeratus* at the Desert Experimental Range in western Utah. *H. glomeratus* monocultures that had first been observed in 1970 were sampled and found that *H. glomeratus* invasion altered soil chemistry and soil ecology, possibly creating conditions that favor exotics over native species.

Research Hypothesis

This study was designed to examine how native species richness and functional diversity affect cogongrass invasion in Northwest Florida. Field studies were performed to examine the following objectives and corresponding hypotheses:

- Objective 1: Determine how increased plant species richness affects cogongrass rate of spread.

Hypothesis 1: Diverse communities use resources more completely and are therefore more resistant to invasion by cogongrass.

- Objective 2: Determine how increased functional richness affects cogongrass rate spread.

Hypothesis: Increased diversity of functional groups will make the site less vulnerable to cogongrass invasion by increasing competition for limiting resources.

- Objective 3: Determine how cogongrass invasion affects soil chemical properties of invaded areas compared to non-invaded areas.

Hypothesis: Native communities have higher nutrient status than cogongrass patches because cogongrass is capable of extracting nutrients from the soil more efficiently.

The results of experiments carried out to test these hypotheses are presented in the two subsequent chapters. In the final chapter, a summary of these findings is presented to predict the effect of native species richness on cogongrass invasion and to discuss the advantages and disadvantages of this methodology in predicting ecosystem change caused by nonindigenous species invasion.

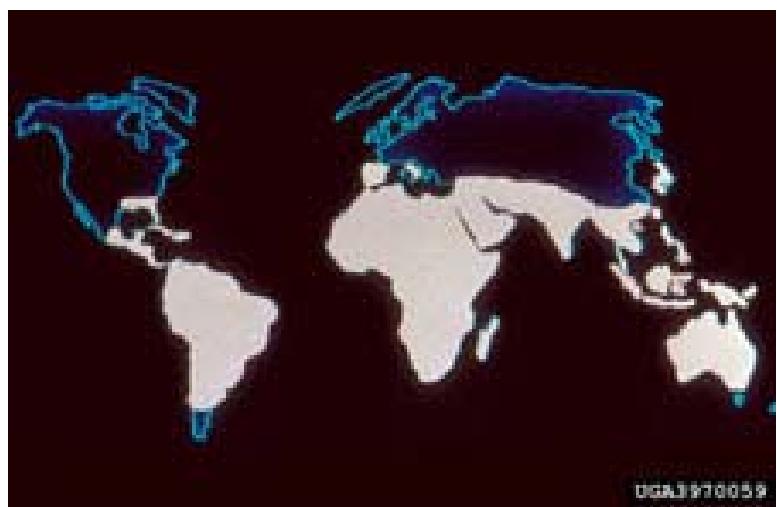


Figure1-1 The global distribution of *Imperata cylindrica*, depicted by areas in white.
(Based on information from Holm et al. 1977)



Figure 1-2 The general distribution of *Imperata cylindrica* in the United States (Based on information from Holm et al. 1977)

CHAPTER 2

IMPLICATIONS OF SPECIES RICHNESS AND FUNCTIONAL DIVERSITY ON COGONGRASS INVASION

Introduction

Charles Elton hypothesized that invasion resistance and compositional stability increase with diversity (Elton 1958). The renewed debate about the relationship between ecological diversity and ecosystem stability offers the opportunity to investigate which characteristics of plant communities contribute to their invasibility. Empirical studies have shown conflicting patterns of relationship between species diversity of resident plant communities and their invasibility by introduced species. Recent observational and experimental studies have shown both positive (McIntyre et al. 1988; Robinson et al. 1995; Palmer and Maurer 1997) and negative (Tilman 1997; McGrady-Steed et al. 1997; Knops et al. 1999) relationships between species richness in the community and the number of invading species while other studies have shown no relationship at all (Crawley et al. 1999).

The conflicting conclusions of various studies have led many researchers to question the predictability of Elton's hypothesis. Although comparative syntheses of a wide range of invasive species can identify a large number of attributes that correlate with invasiveness, little generality has been possible (Rejmanek 1996). The variability that has been seen among studies may be because many factors covary with species richness. For example, disturbance, resident cover and biomass, propagule pressure and

climate may vary with species richness and these variables have not been explicitly accounted for in previous studies (Von Holle 2005).

Biological invasion is a widespread, but poorly understood phenomenon. Elton's hypothesis, supported by theory, experiment, and anecdotal evidence, suggests that an important determinant of invasion success is resident biodiversity, arguing that high diversity increases the competitive environment of communities and makes them more difficult to invade (Naeem et al. 2000). Several mechanisms have been proposed to explain why diverse communities are less susceptible to invasion. First, invasions can be favored by the existence of empty ecological niches that are open to colonization by non-native species in the absence of suitable competitors (Elton 1958; Prieur-Richard et al. 2000). Second, theoreticians have suggested that diverse systems should be difficult to invade because newly arrived species are more likely to find a competitor that precludes their success (Dukes 2002). Third, diverse communities are more likely to use resources more completely and therefore limiting the ability of exotics to establish (Tilman 1999; Hooper and Vitousek 1998). A new species (whether native or exotic) must both survive and attain a positive rate of increase while living on the resources left unconsumed by the resident species (Seabloom et al. 2003). Thus, the mechanism governing community assembly, exotic invasion, and restoration may depend on the levels to which various species can reduce limiting resources. Fourth, interactions with other trophic levels, for example herbivore pressure, may preclude establishment and invasion of exotic species (Lodge 1993). Diversity among trophic levels, including the diversity of resident native plants, may be an important mechanism in determining community resistance to invasion.

Current debate has also focused on whether it is species diversity or functional diversity that contributes to the invasibility of a community. Contemporary biodiversity research has recently concerned itself with ecosystem functioning and functional traits. Emphasis, in the past, has been on taxonomic diversity, i.e. the richness (number of species) and evenness (relative abundance) of assemblages, cumulative phylogenetic distance among species and spatial and temporal patterns in the distribution of species within a biota (Naeem and Wright 2003). The debate lies in the idea that the functioning of an ecosystem may not be governed solely by the phylogenetic content of its biota, but instead in combination with the functional traits of individuals, and their biological activity. Functional diversity, the number of functional groups with different behaviors for a particular process, is receiving a renewed interest because major thresholds in ecosystem processes may be related to the presence or absence of particular functional groups (Hooper 1998; Prieur-Richard and Lavorel 2000). For example, Dukes (2001) found that high functional diversity reduced the success of *Centaurea solstitialis* in grassland microcosms when resident plant species were classified in to one of four functional groups: annual grasses, perennial bunchgrasses, early-season annual forbs, and late-season annual forbs. Results have shown that species identity matters more than species richness in determining both the number of invading species and the total biomass of invaders (Crawley et al. 1999; Dukes 2002).

Cogongrass, the seventh worst weed in the world, has invaded a variety of ecosystems in the southern United States, from highly xeric uplands to fully shaded mesic sites (MacDonald 2004). Cogongrass is able to invade areas by both sexual reproduction by seed and asexual reproduction through rhizomes. Although it was once thought that

flowering was rare and that flowers produced in response to stress would rarely produce seeds (Eussen 1980), more recent work indicates that cogongrass is a prolific producer of viable wind-blown seeds. Sexually produced seed are the only propagules capable of natural long-distance dispersal (Dozier et al. 1998). Aerodynamic properties of the spikelet clumps allow for long distance dispersal of up to 15 m (Hubbard et al 1944) with each plant producing up to 3000 seeds in hair covered spikelets.

Vegetative reproduction is believed to be the primary means of local spread (Dozier et al. 1998). Cogongrass tends to emerge in a clumped pattern and quickly forms dense monocultures that cover vast areas (Figure 2-1). Cogongrass rhizomes are white and tough with shortened internodes (MacDonald 2004) (Figure 2-2). The sharp apical ends of cogongrass may cause physical damage to the roots of surrounding vegetation therefore increasing its competitive ability (Dozier et al. 1998). Cogongrass allocates a large proportion of its photosynthate to the rhizomes. Rhizomes can give rise to shoots at every node. Eussen (1980) reported the production of 350 above-ground shoots from rhizomes, covering an area of 4 m^2 in 11 weeks.

The objective of this study was to determine how surrounding vegetation affects cogongrass invasion at both a disturbed and an undisturbed site. Elton's hypothesis predicts that as species richness of the community increases, the rate of invasion decreases. Therefore, one would expect to observe a negative relationship between plant species richness and invasibility (Elton 1958). The study also examined how vegetative cover and functional diversity affected the rate of invasion. We hypothesized that as vegetation cover (closely correlated with biomass) and functional diversity increased the rate of cogongrass invasion would decrease.

Methods

Field studies were conducted in a logged site and an unlogged site in Santa Rosa County, Northwest Florida, U.S.A. The logged site, owned by International Paper Company ($30^{\circ}50'N$. $87^{\circ}10'W$), was a cutover site that was under 17-year-old loblolly pine prior to clear cutting in 2001. The unlogged site was in Blackwater River State Forest, which is one of the largest contiguous longleaf pine ecosystems in the Southeast ($30^{\circ}50'N$, $86^{\circ}50'W$). Four patches of cogongrass were randomly chosen from each site (8 patches total). Both sites differed in soil series (Table 2-1).

Rate of Cogongrass Invasion

In June of 2003, up to 20 4 m x 1 m plots were established at random surrounding each of the four cogongrass patches at each site (total of eight patches and 142 plots) (Figure 2-3). Plots were marked with metal stakes around the perimeter of each patch. Plots were established so that approximately 1 m^2 of the plot was initially cogongrass dominated and 3 m^2 was native vegetation. Flags were used to mark the foliar cogongrass edge. Plots were monitored at six-month intervals to assess the rate of spread. The first census was on June 14 and 15, 2003; the second on November 23 and 24, 2003; and the third on June 19 and 20, 2004. At each six-month interval the advancing front was marked with flags. The distance of the flags along both the width and length of the plot was measured to yield plot co-ordinates. Plot co-ordinates of the flags in each plot were used to create a polygon and calculate the area and the rate of spread at each six-month interval. Rate of spread was calculated using polygon analysis in ArcView 3.2 (Environmental Systems Research Institute, Inc.).

Vegetation Sampling

Vegetation surveys were conducted in all plots; one in the summer of 2003 (June 14,15) and the other in the winter of 2003 (November 24,25). Surveys were conducted at each 4m x 1 m plot using sliding plots of 1 m² directly adjacent to the advancing edge of the cogongrass patch (Figure 2-4). This sampling design caused some vegetation to be sampled twice if the cogongrass patch had not invaded more than 1 m² in the six-month interval. The 1 m² area sampled extended from the plots that were established in June of 2003 to measure rate of cogongrass spread. Percent cover of each species and overall species richness were recorded in each 1 m² plot. Using the information gathered from the vegetation surveys, each species was grouped according to one of six designated functional groups: trees, shrubs, annual forbs, perennial forbs, vines, and grasses (Table 2-2).

The Shannon-Weiner diversity index (H), a commonly used index that characterizes species diversity in a community, was calculated for each plot using the following equation:

$$H = -\sum_{i=1}^s p_i \ln p_i$$

where i is the proportion of species relative to the total number of species (p_i).

Statistical Analysis

Rate of spread data was summed over the two observational intervals to yield an annual rate. Plant species richness and functional richness were averaged over the two observation intervals. Each patch was averaged to yield a per year rate of spread, species richness value, functional richness value and an average per-plot percent cover value. Each patch was considered a separate replication and each plot in the patch was a subplot descriptor. Stepwise multiple linear regressions of the data were done using SAS (PROC

REG), where the independent variables (total percent cover, species richness and functional diversity) were the continuous predictors and annual cogongrass rate of spread was the response. The adjusted mean square was also calculated along with the r^2 values by adjusting both the numerator and the denominator by their respective degrees of freedom. Treatment effects were considered significant at $\alpha= 0.10$. Tests of intercorrelation were done using the Pearson Correlation Coefficient to show correlations among all independent variables (SAS PROC CORR) (SAS 2002).

Results

The number of native species was variable across plots, ranging from two to thirteen species per plot for the logged site and zero to thirteen species per plot for the unlogged site. The most dominant species at the logged site were *Andropogon virginicus*, *Diodia teres*, *Gnaphalium obtusifolium*, *Panicum aciculare*, *Polypremum procumbens*, *Rubus cuneifolius*, and *Rumex hastatulus*. The most dominant species at the unlogged site were *Andropogon virginicus*, *Aristida stricta*, *Conyza canadensis*, *Panicum aciculare*, *Rubus cuneifolius* and *Gelsemium sempervirens*.

At the logged site, cogongrass advanced an average of 0.50 m^2 in the first six-month survey and 1.13 m^2 in the second survey. At the unlogged site, cogongrass advanced 0.33 m^2 in the first 6-month survey and 0.81 m^2 in the second survey. The total average area advanced for the logged and unlogged site per year was 1.63 m^2 and 1.14 m^2 respectively (Table 2-3). There was no significant difference in the area advanced between the two sites ($P= 0.29$). Both logged and unlogged sites had significantly greater advancement in the second six-month survey than the first ($P<0.0001$).

There was no difference between sites for species richness ($P= 0.29$), functional richness ($P= 0.39$) and percent total cover ($P= 0.20$) (Table 2-4). Using stepwise multiple linear regressions, no significant correlation was observed between the independent variables and cogongrass spread as the response (Table 2-5). Species accounted for 11% of the variation observed in the model while functional richness and cover only accounted for 0.0013% and 0.030%, respectively. When all three independent variables were included in the model they accounted for 36% of the variation. No significant correlation was observed when linear regressions were performed between cogongrass area advanced per year and species richness ($r^2= 0.11$, $P = 0.24$), functional richness ($r^2= 0.0015$, $P= 0.37$) and percent cover ($r^2= 0.030$, $P= 0.33$) (Figure 2-5, 2-6, 2-7).

Pearson's correlation coefficients showed no significant correlation between any of the independent variables when both the logged and unlogged site were combined (Table 2-6). The Shannon-Weiner index for both the logged and unlogged sites ranged from 0.84-2.37. There was no correlation between cogongrass invasion and the indices for both the logged ($r^2= 0.0071$, $P= 0.36$) and unlogged ($r^2= 0.0058$, $P= 0.47$) sites.

Discussion

There was no difference in rate of cogongrass spread between the logged and the unlogged site. This may be explained by the aggressive growth of cogongrass and its ability to invade a wide variety of habitats. Disturbance often favors invasion (Burke and Grime 1996, Hobbs and Huenneke 1992), but the relationship between invasibility and disturbance is related to disturbance type, size and intensity and can relate to a diversity of mechanisms as well as to the type of invader. The unlogged sites selected for the study were located in the longleaf pine understory; however, were also close to roads and were

used as hunting grounds. It is possible that the intensity of disturbance was greater than predicted initially for this site.

The results of this study, at both the logged and unlogged site, do not support the general hypothesis of Elton (1958). Consistent with Levine and D'Antonio (1999), but in contrast to Tilman (1997) and Stohlgren et al. (1999), results show that species richness did not offer resistance to community invasibility for cogongrass invasion in Northwest Florida. The lack of diversity effect at both the logged and unlogged sites may be due to the aggressive growth pattern of cogongrass and its tremendous ability to outcompete surrounding vegetation. Increased species richness is hypothesized to increase the use of resources; decrease the space for establishment by increasing the productivity of the community and decrease root space (Prieur-Richard et al. 2000). However, cogongrass' extensive rhizome and root network may allow for its persistence in more diverse communities regardless of nutrient levels. Cogongrass has many anatomical features that help conserve water and resist breakage including a band on sclerenchymous fibers just below the epidermis and brownish colored cataphylls (scale leaves), which form a protective sheath around the rhizome (English 1998). Cogongrass is successful in low fertility, low organic matter and acidic soils. Therefore, it is possible that nutrient limitations may not be as restrictive to cogongrass invasion and competitive processes.

No significant correlation between area advanced and percent native ground cover was observed. Percent cover was assumed to be correlated with biomass. Cogongrass invasion was predicted to decrease in response to percent total cover because of increased root competition due to greater biomass and reduced light availability. However, cogongrass rhizomes are incredibly resilient and posses both morphological and

anatomical features, which may make it a better competitor, even under dense canopy cover. The hard sharp points of cogongrass rhizomes are able to penetrate roots, bulbs and tubers of other plants leading to infection, which may explain its success in areas of high root competition (Terry et al. 1997). Finally, cogongrass has been shown to have a light compensation point of between 32 and 35 $\mu\text{ mol/ m}^2\text{ s}^{-1}$, which indicates cogongrass' ability to survive as an understory species. For this reason, cogongrass may continue to be successful in areas with increased cover and shading.

Previous studies of natural invasion patterns have been criticized for not considering the effects of other ecological components (e.g. species v. functional richness) (Lavorel et al. 1999). Hence, the relationship found between number of species and invader performance from previous studies had to be considered with care because it may have been an effect of species identities instead of species richness. This study attempted to look at both the effects of species richness and also the effect of functional diversity.

The results of this study do not support functional richness as playing an important role in community invasibility. The role of functional diversity has recently received much attention and negative relationships between functional diversity and rate of invasion have been reported (Crawley et al. 1999; Dukes 2002). In this case, the lack of observed functional diversity effect may have resulted from large amounts of species that were placed in the functional category of annual forbs and perennial forbs and the low proportion of sites occupied by different functional groups. There were also large differences in biomass between of the different functional groups, which may have led to no diversity effects being observed. The observational nature of this study prevents

sampling of a true diversity of functional groups amongst plots. Previous studies that have observed functional diversity effects have manipulated functional diversity of plots (Dukes 2002). Similar work is currently underway in which microcosm of manipulated functional richness are being used to assess how different functional groups affect cogongrass regrowth and invasion (Daneshgar and Jose, unpublished data).

Lack of control of extrinsic factors (e.g., disturbance, climate, or soil fertility) that covary with biodiversity and invasion in observational studies make it difficult to determine if findings truly support or refute Elton's hypothesis. Several experimental studies that directly manipulated diversity in plant communities suggest that inhibitory effects of diversity on invasibility can be detected when extrinsic factors are controlled experimentally (Knops et al. 1999, Levine 2000, Naeem et al. 2000, Prieur-Richard et al. 2000, Foster 2002). Nonetheless, this study suggests that within a neighborhood, diversity does not minimize community invasibility.

Conclusions

Observational studies of the relationship between community invasibility and native plant diversity have yielded conflicting results. Results from previous studies on diversity-invasibility relationship have been positive (McIntyre et al 1988; (Robinson et al. 1995, Palmer and Maurer 1997) and negative (Tilman 1997; McGrady-Steed et al. 1997; Dukes 2002; Knops et al. 1999). While it is still too early to resolve these conflicting results, the findings of this study do not lend support to Elton's hypothesis. Although this study is an observational study, which can often limit the ability to draw causal relationships, this research offers valuable insight to researchers and managers as to whether plant diversity affects cogongrass invasion and may generate important research questions for future exploration. Observational studies such as these are often

confounded by numerous extrinsic factors (e.g., disturbance, climate, or soil fertility) that cannot be controlled. Future work could look at similar relationships between species diversity and invasibility by controlling several of these extrinsic factors.

Future work may also look at larger plot sizes. Recent studies have begun to investigate how the scale that an experiment is carried out may contribute to either a negative or a positive relationship between biodiversity and invasibility. The diversity resistance hypothesis is supported by both theory and experimental studies conducted at small scales (Kennedy et al. 2002). However, there is also evidence to support that a positive relationship may exist when measured at regional scales (Stohlgren et al. 1999). Based on studies conducted by Tilman (2004) the resolution to this invasion paradox is that small nearby plots are likely to have similar within-plot spatial heterogeneity and therefore differences in their diversity would correspond to differences in the degree to which the existing species exploited that heterogeneity. At larger scales, the regional species pool should be sufficient to exploit the heterogeneity of areas with low spatial heterogeneity, but insufficient to do so in areas with the greatest spatial heterogeneity. This insufficiency would cause the most diverse regions to be the most readily invaded because the greater heterogeneity would be less fully exploited.

One limitation of this study was the narrow range of species richness, functional richness and total percent cover at the patches sampled. Future studies should consider sampling communities with a wide range of species richness as well as increasing the sample size (number of patches) monitored.

Table 2-1 Site descriptions of cogongrass patches used at International Paper (logged site) and Blackwater River State Forest (unlogged site)

	Soil Survey	Soil Classification
Logged Site		
Patch 1	Troup loamy sand (0-5 % slope)	Loamy, siliceous, thermic, Grossarenic Paleudults
	Bonifay loamy sand	Loamy, siliceous, thermic Grossarenic Plinthic Paleudults
Patch 2	Troup loamy sand	Loamy, siliceous, thermic, Grossarenic Paleudults
Patch 3	Troup loamy sand	Loamy, siliceous, thermic, Grossarenic Paleudults
Patch 4	Troup loamy sand	Loamy, siliceous, thermic, Grossarenic Paleudults
	Lakeland sand	Thermic, Typic Quartipsammments
Unlogged Site		
Patch 1	Troup sand (0-5% slope)	Loamy, siliceous, thermic, Grossarenic Paleudults
Patch 2	Dothan loamy sand (0-5% slope)	Fine-loamy, siliceous, thermic, Plinthic Kandiudults
	Dothan loamy sand (2-5% slope)	Fine-loamy, siliceous, thermic, Plinthic Kandiudults
Patch 3	Troup loamy sand (0-5% slope)	Loamy, siliceous, thermic, Grossarenic Paleudults
Patch 4	Dothan loamy sand	Fine-loamy, siliceous, thermic, Plinthic Kandiudults
	Fuquay loamy fine sand (5-8 % slope)	Loamy, siliceous, thermic arenic, Plinthic Kandiudults.

Table 2-2. Species found at logged and unlogged

<u>Scientific Name</u>	<u>Common Name</u>	<u>Functional Group</u>	<u>Annual/Perrenial</u>
<i>Acalypha gracilens</i>	Slender threeseed mercury	Forb	A
<i>Acer rubrum</i>	Red maple	Tree	P
<i>Agalinus fasciculata</i>	Beach false foxglove	Forb	P
<i>Ambrosia artemisifolia</i>	Annual ragweed	Forb	A
<i>Ampelopsis arborea</i>	Peppervine	Vine	P
<i>Andropogon virginicus</i>	Broomsedge	Grass	P
<i>Aristida beyrichiana</i>	Beyrich threeawn	Grass	P
<i>Aristida stricta</i>	Pineland threeawn	Grass	P
<i>Andropogon gyrans</i>	Elliott's bluestem	Grass	P
<i>Bonamia grandiflora</i>	Florida lady's nightcap	Vine	P
<i>Brachiaria platyphylla</i>	Broadleaf signal grass	Grass	A
<i>Carphephorus paniculatus</i>	Herbert hairy chaffhead	Forb	P
<i>Carphephorus odoratissimus</i>	Herbert vanilla leaf	Forb	P
<i>Ceanothus americanus</i>	New Jersey tea	Shrub	P
<i>Chamaecrista fasciculata</i>	Sleeping plant	Forb	A
<i>Chrysobalanus oblongifolius</i>	Gopher apple	Shrub	P
<i>Chrysopsis</i>	Florida goldenaster	Forb	P
<i>Conyza Canadensis</i>	Canadian horseweed	Forb	A
<i>Cyperus Retrorsus</i>	Pine barren flatsedge	Grass	P
<i>Dichanthelium clandestinum</i>	Deer tongue	Grass	P
<i>Diodia teres</i>	Poorjoe	Forb	A
<i>Desmodium†</i>		Forb	P
<i>Diospyros virginiana</i>	Common persimmon	Tree	P
<i>Elephantopus elatus</i>	Tall elephantsfoot	Forb	P

Table 2-2. Continued

<u>Scientific Name</u>	<u>Common Name</u>	<u>Functional Group</u>	<u>Annual/Perrenial</u>
<i>Erechtites hieracifolia</i>	Fireweed	Forb	A
<i>Eupatorium capillifolium</i>	Dogfennel	Forb	P
<i>Euphorbia floridana</i>	Greater Florida spurge	Forb	P
<i>Euthamia caroliniana</i>	Slender goldentop	Forb	P
<i>Gelsemium sempervirens</i>	Yellow jessamine	Vine	P
<i>Gnaphalium obtusifolium</i>	Rabbitabacco	Forb	A
<i>Hedyotis procumbens</i>	Roundleaf bluet	Forb	P
<i>Helianthus radula</i>	Rayless sunflower	Forb	P
<i>Heterotheca subaxillaris</i>	Camphorweed	Forb	A
<i>Hypericum perforatum</i>	Saint Johnswort	Forb	P
<i>Haplopappus divaricatus</i>	Scratch daisy	Forb	A
<i>Ilex glabra</i>	Gallberry	Shrub	P
<i>Ilex opaca</i>	American Holly	Tree	P
<i>Ilex vomitoria</i>	Yaupon	Shrub	P
<i>Ipomoea pandurata</i>	Man of the earth	Vine	P
<i>Lespedeza capitata</i>	Roundhead lespedeza	Forb	P
<i>Lespedeza hirta</i>	Hairy lespedeza	Forb	P
<i>Lespedeza striata</i>	Japanese clover	Forb	A
<i>Lonicera japonica</i>	Japanese honeysuckle	Vine	P
<i>Ludwigia maritima</i>	Harper seaside primrose willow	Forb	P
<i>Oenothera laciniata</i>	Cutleaf evening primose	Forb	P
<i>Oxalis delinii</i>	Woodsorrel	Forb	P
<i>Panicum†</i>	Panicum	Grass	G
<i>Panicum aciculare</i>	Needle leaf rosette grass	Grass	P
<i>Paronychia baldwinii</i>	Baldwin's nailwort	Forb	P

Table 2-2. Continued

<u>Scientific Name</u>	<u>Common Name</u>	<u>Functional Group</u>	<u>Annual/Perrenial</u>
<i>Parthenocissus quinquefolia</i>	Virginia creeper	Vine	P
<i>Penstemon multiflorus</i>	Many flower beardtongue	Forb	P
<i>Physalis walteri</i>	Walter's groundcherry	Forb	P
<i>Pinus palustris</i>	Longleaf pine	Tree	P
<i>Pinus taeda</i>	Loblolly pine	Tree	P
<i>Pityopsis graminifolia</i>	Narrowleaf silkglass	Forb	P
<i>Polygonella gracilis</i>	Tall jointweed	Forb	A
<i>Polypremum procumbens</i>	Juniper leaf	Forb	P
<i>Pteridium aquilinum</i>	Brackenfern	Forb	P
<i>Quercus pumila</i>	Running oak	Shrub	P
<i>Rhexia mariana</i>	Maryland meadowbeauty	Forb	P
<i>Rhus copallina</i>	Winged sumac	Shrub	P
<i>Rhynchospora†</i>	Rush	Grass	P
<i>Richardia†</i>		Forb	P
<i>Rubus argutus</i>	Sawtooth blackberry	Shrub	P
<i>Rubus cuneifolius</i>	Sand blackberry	Shrub	P
<i>Rumex hastatulus</i>	Heartwing sorrel	Forb	P
<i>Smilax bona-nox</i>	Saw greenbriar	Vine	P
<i>Solidago odora</i>	Goldenrod	Forb	P
<i>Solidago rugosa</i>	Wrinkleleaf goldenrod	Forb	P
<i>Strophostyles helvula</i>	Trailing fuzzybean	Forb	A
<i>Toxicodendron radicans</i>	Eastern poison ivy	Vine	P
<i>Tragia urens</i>	Wavyleaf noseburn	Forb	P
<i>Trichostema dichotomum</i>	Forked bluecurls	Forb	A
<i>Vaccinium corymbosum</i>	Highbush blueberry	Shrub	P

Table 2-2. Continued

<u>Scientific Name</u>	<u>Common Name</u>	<u>Functional Group</u>	<u>Annual/Perrenial</u>
<i>Vaccinium darowii</i>	Darrow's blueberry	Shrub	P
<i>Vitis rotundifolia</i>	Muscadine grape	Vine	P
<i>Wahlenbergia marginata</i>	Southern rockbell	Forb	P

† Indicate species that could not be more specifically identified

Table 2-3 Area advanced in 2 six-month intervals (mean \pm 1 SE)

	Area Advanced (m^2)					
	First Survey (May-October)	N	Second Survey (October-May)	N	Per Year	
Sites						
Logged	0.50 ± 0.021	4	1.13 ± 0.095	4	1.63 ± 0.11	
Unlogged	0.33 ± 0.10	4	0.81 ± 0.18	4	1.14 ± 0.27	

Table 2-4 Average values for the three independent continuous variables at both the logged and unlogged site.

	Logged Site	Unlogged Site	P
Species Richness/ m ²	7.02±0.23	6.07±0.18	0.29
Functional Rich./ m ²	3.48±0.069	3.18±0.10	0.39
Percent Cover / m ²	45.92±1.63	46.67±1.79	0.20

Table 2-5 Stepwise multiple linear regression summary table of results for the 3 independent variables total percent cover, species richness, and functional richness) with cogongrass annual spread as the response for the logged site and unlogged site combined. Effects were considered significant at $\alpha = 0.1$. Where, Cover = the total percent cover per plot, Species = the total species richness per plot and, Func. = the total functional diversity per plot.

Variables in model	Adjusted r ²	r ²
Species	-0.035	0.11
Func.	-0.17	0.0013
Cover	-0.13	0.030
Species Cover	-0.15	0.17
Species Func.	-0.20	0.14
Func. Cover	-0.36	0.031
Species Func. Cover	-0.15	0.36

Table 2-6 Pearsons coefficient correlation of the three independent variables (total percent cover, species richness and functional diversity) for the logged site and unlogged site combined. None of the correlations were significant.

	% Total Cover	Species Richness	Functional Diversity
% Total Cover	1.0		
Species Richness	0.21	1.0	
Functional Diversity	-0.41	0.18	1.0



Figure 2-1 Aerial photograph of cogongrass invasion at the logged site taken in 2003.
Light green patches are cogongrass invaded areas



Figure 2-2 Photograph of cogongrass extensive rhizome network. Photograph was taken at the logged site.



Figure 2-3 Photograph of a cogongrass patch used at the logged site. Flags were used to mark the cogongrass edge at each six-month interval.

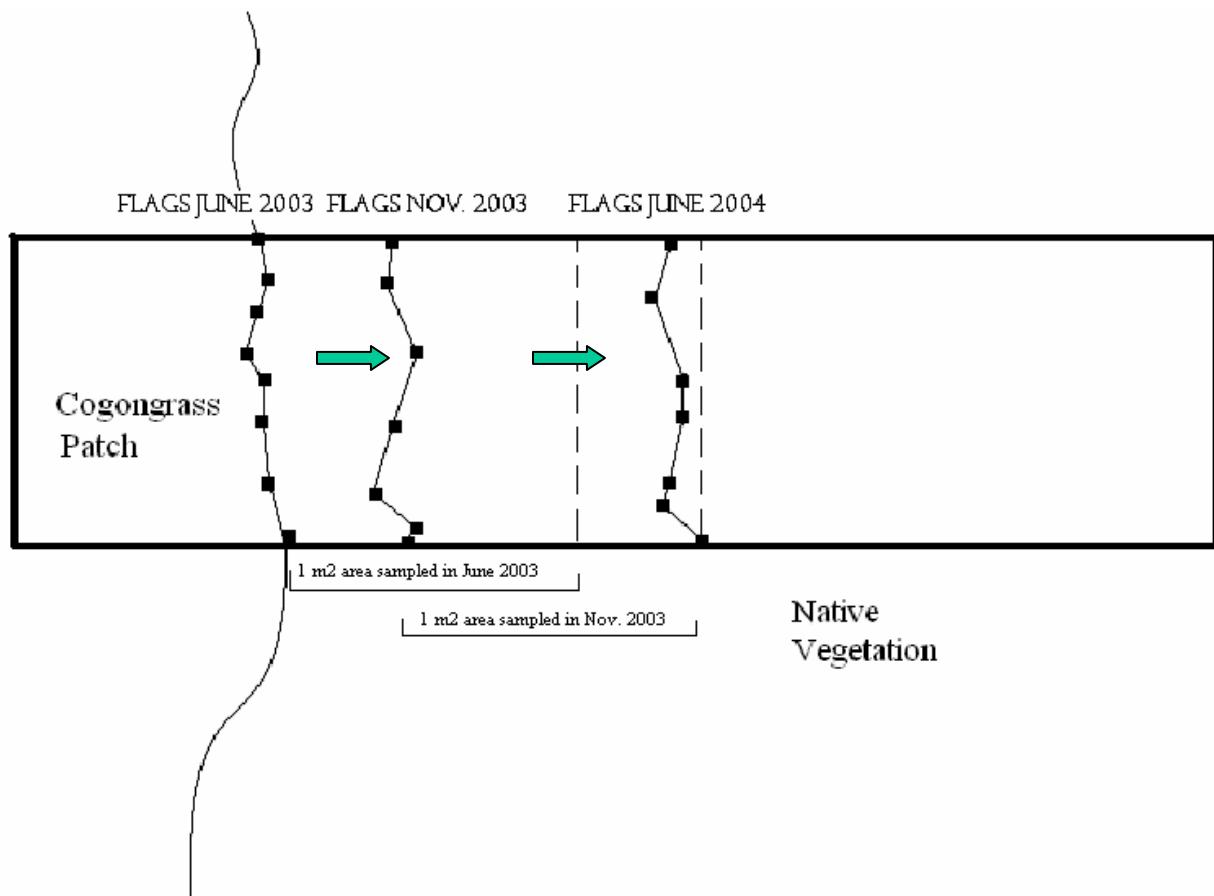


Figure 2-4 Diagram of sampling design for plots at both sites. Twenty 4 m x 1 m plots (bold boundary) were established on the perimeter of each cogongrass patch. The percent cover of each species was recorded from 1 m² sliding plots directly adjacent to the cogongrass patch. Therefore, some native areas were sampled more than once if the cogongrass patch did not invade more than 1 m² in the six month interval.

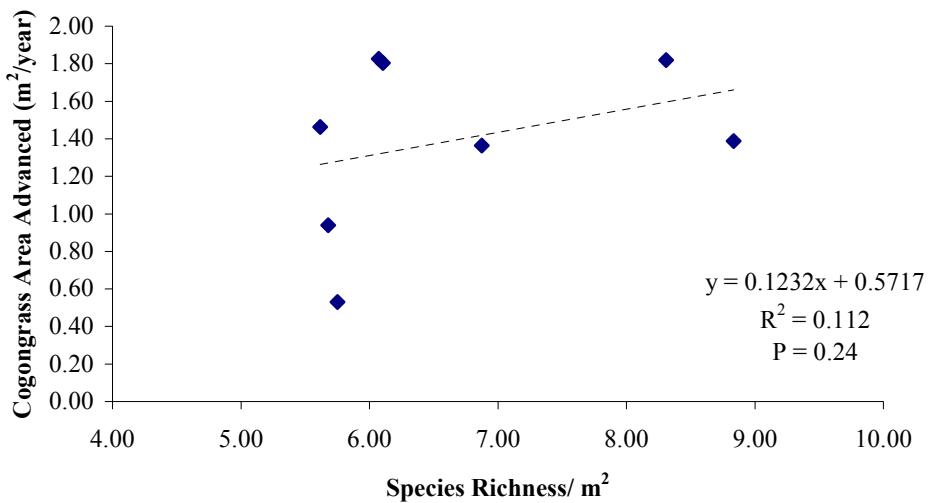


Figure 2-5 Relationship of native plant species richness and area advanced by cogongrass over the period of one year for each patch. Area advanced by cogongrass is plotted against plant species richness of the resident community for both the logged and unlogged sites ($n=8$). Dashed line represents linear regression of patch values for both logged and unlogged sites ($r^2 = 0.112$, $P = 0.24$).

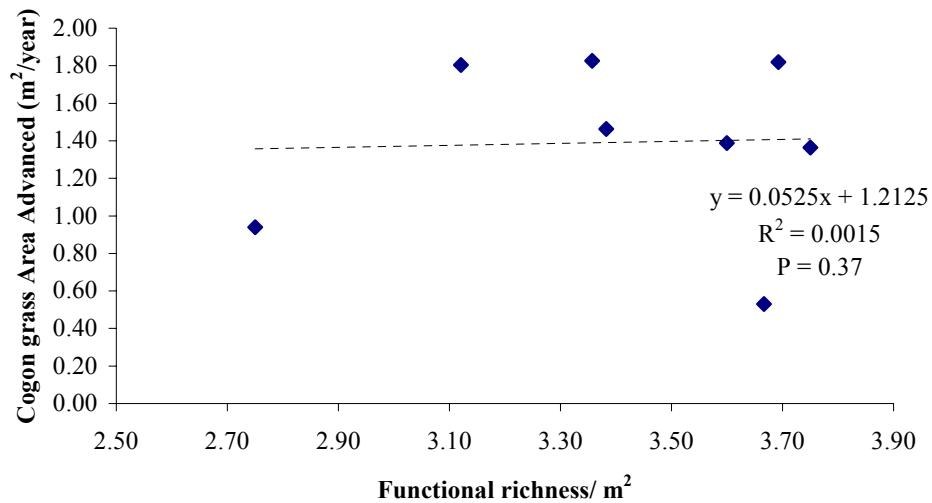


Figure 2-6 Relationship of native plant functional richness and area advanced by cogongrass over the period of one year for each patch. Area advanced by cogongrass is plotted against plant functional richness of the resident community for both the logged and unlogged sites ($n=8$). Dashed line represents linear regression of patch values for both logged and unlogged sites ($r^2=0.0015$, $P = 0.37$).

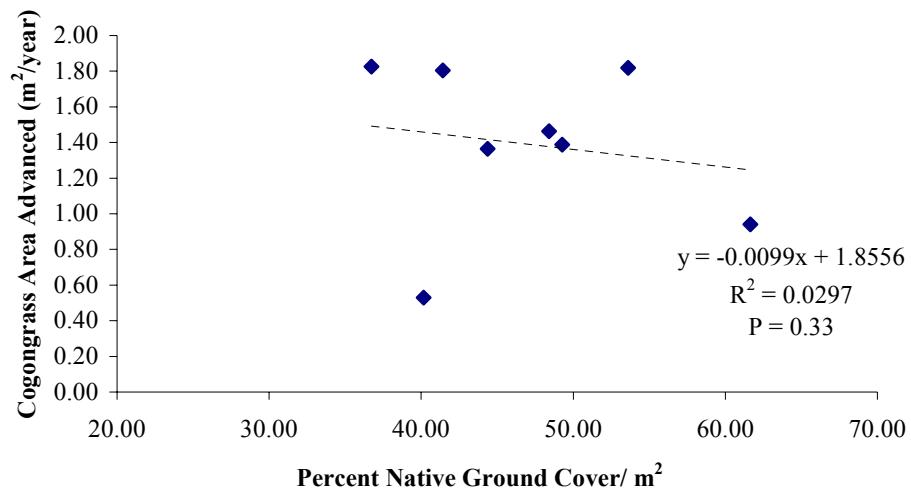


Figure 2-7 Relationship of percent native ground cover and area advanced by cogongrass over the period of one year for each patch. Area advanced by cogongrass is plotted against percent native ground cover of the resident community for both the logged and unlogged sites ($n=8$). Dashed line represents linear regression of patch values for both logged and unlogged sites ($r^2 = 0.0297$, $P = 0.33$).

CHAPTER 3

COGONGRASS INVASION ALTERS SOIL CHEMICAL PROPERTIES OF NATURAL AND PLANTED FORESTLANDS

Introduction

Invasions by exotics are changing large areas of North American ecosystems, but their biogeochemical impacts are not well characterized (Hook et al. 2004). Past research has shown that introduction of a new plant species, such as an exotic invasive, has the potential to change many components of the carbon (C), nitrogen (N), water, and other cycles of an ecosystem (Duda et al. 2003; Ehrenfeld 2003). Altered soils may be the driving mechanism that provides a suitable environment to facilitate future invasions and decrease native biodiversity. These consequences may, in turn, have impacts on the invasibility of an ecosystems and the invasiveness of the exotic species.

Exotic plants alter soil nutrient dynamics by differing from native species in biomass and productivity, tissue chemistry, symbiotic associates, plant morphology, and phenology. Available data suggest that invasive plants frequently increase biomass and net primary productivity, alter nutrient availability, and produce litter with higher decomposition rates than co-occurring native species (Ehrenfeld 2003). Differences in litter mass or the litter decomposition is often, but are not always, accompanied by changes in organic matter. For example, Windham (1999) found that despite having large differences in standing crop biomass and litter dynamics, there was no difference in soil organic matter content in *Phragmites*- invaded compared to non-invaded *Spartina patens* marshes.

Plant invasions do not result in consistent changes in soil properties, even for the same invasive species. For example, a recent study by Hook et al. (2004) indicated that *Centaurea maculosa*, a perennial Eurasian forb, might increase or decrease soil C and N pools in native grasslands in Montana, U.S.A. Available data suggest a number of trends with respect to soil nutrients and plant invasions. Invasions have been associated with increases (Rutherford et al. 1986; Stock et al. 1995; Witkowski 1991; Vitousek and Walker 1989), decreases (Feller 1983; Versfeld 1986) or no change in soil N (Belnap et al. 2001). Howard et al. (2004) surveyed 44 sites in southeastern New York to examine the relationships between plant community characteristics, soil characteristics, and invasions by a number of exotic invasive plant species. Their study indicated that soil nitrogen mineralization and nitrification rates were strongly related to the degree of site invasion. Across the broad environmental gradients and community types, invasive species were more commonly found in communities associated with higher resource levels.

Exotic plant invasions have also shown to have an effect on a variety of other elements including P, K, Ca, and Mg. Decreases in soil extractable pools may be associated with high uptake rates of these elements, which is driven by a large biomass or high tissue nutrient concentrations of the exotic species. For example, studies conducted by Suding et al. (2004) showed that reduction of soil P weakened the ability of *Centaurea diffusa*, an exotic invasive, to tolerate neighbor competition proportionately more than other native species in grazed mixed-grassprairie. Consequently, under low P conditions, *C. diffusa* lost its competitive advantage and tolerated neighbor competition similarly to other native species.

Potassium is usually the most abundant of the major nutrient elements in soil. The total K content of soils varies from <0.01% to about 4% and is commonly about 1% (Blake et al. 1999). When K levels were manipulated in a mid-elevation *Trachypogon* savanna in Venezuela, *Melinis minutiflora*, an invasive African grass, greatly increased seedling biomass (Barger et al. 2003). This effect was greatly enhanced when neighbor competition was reduced (e. g. clipping). The significant enhancement of *Melinis* seedling growth with K addition suggests that low soil nutrients and the presence of native savanna species are important factors in the ability of native savanna to resist *Melinis* establishment. In contrast, Howard et al. (2004) found a strong positive relationship between degree of site invasion and soil C, P and Mg for a variety of invading species studies with a broad range of environmental gradients and community types in New York.

Changes in soil pH have also been reported to result from a variety of exotic plant invasions. Conflicting results of increases (Ehrenfeld 2001; Kourtev et al. 1998; Kourtev et al. 1999), decreases (Boswell and Espie 1998; Scott et al. 2001) or no change in response to invasion have been reported. Studies of two newly invading exotic plant species in hardwood forests of New Jersey, *Berberis thunbergii* and *Microstegium vimineum*, found that soil pH in invaded areas were significantly higher than in the non-invaded areas, and the litter and organic horizons were thinner (Kourtev et al. 1998). In contrast, studies conducted by Scott et al. (2001) found that *Hieracium* species, invading New Zealand's tussock grasslands, increased total soil C and N and lowered soil pH and mineral N relative to the adjacent herb-field vegetation.

The present study examined soil chemical properties in areas invaded by a non-native invasive species, *Imperata cylindrica* (hereafter cogongrass). As an opportunistic C₄ perennial grass, cogongrass possess characteristics that make it more competitive compared to native species. Cogongrass can colonize disturbed or undisturbed areas from a large number of seeds and also from an extensive belowground rhizome network. It forms dense monospecific stands that competes with and displaces native species. Congongrass also has allelopathic properties, which may add to its ability to outcompete other species (Eussen and Soerjani 1975).

The successful invasion of cogongrass in many areas can also be attributed to its ability to tolerate a wide range of soil conditions. The habitats where cogongrass invades are diverse, ranging from the coarse sands of shorelines; the fine sands or sandy loams of swamps and river margins, to the clay soils of reclaimed phosphate settling ponds. Cogongrass has extremely efficient nutrient uptake (Saxena and Ramakrishnan 1983) and associations with mycorrhizae, which may help explain its competitiveness on unfertile soils (Brook 1989). Brewer and Cralle (2003) suggested that cogongrass is a better competitor for phosphorus than are native pine-savanna plants, especially legumes, and that short-lived, high-level pulses of phosphorus addition reduce this competitive advantage without negatively affecting native plant diversity. Species richness of native plants was negatively correlated with final aboveground biomass of cogongrass in control and P-fertilized plots.

The objective of our study was to determine whether cogongrass would alter soil chemical properties of invaded patches. The first hypothesis was that soil organic matter would increase in invaded areas because of the higher biomass of cogongrass in

comparison to the native flora. Second, that soil nutrients ($\text{NO}_3\text{-N}$, P, K, Ca, and Mg) would decline in cogongrass-invaded patches because of its extensive rhizome/root network and rapid accumulation of aboveground biomass. Third, that root exudates into the rhizosphere would make the soil more acidic in invaded areas.

Materials and Methods

Field studies were conducted at two sites in Santa Rosa County, Northwest Florida, U.S.A.; a logged site and an unlogged site. The logged site, owned by International Paper Company ($30^{\circ}50'N$, $87^{\circ}10'W$), was a cutover site that was under 17-year-old loblolly pine prior to clear cutting. The unlogged site in Blackwater River state forest, is one of the largest contiguous longleaf pine forest tracts in the Southeast ($30^{\circ}50'N$, $86^{\circ}50'W$). Four patches of cogongrass were randomly chosen from each site. Two soil surveys were conducted one in the spring of 2004 and the other in the fall of 2004.

Soil Sampling

Soil samples were collected from rectangular plots (4 m x 1 m) established at random around the perimeter of each patch at both sites. Two composite samples of 10 soil cores (15 cm deep) each were extracted pair wise from a total of 75 plots in the native and cogongrass monoculture areas using a soil auger. All soil composites were analyzed for organic matter, $\text{NO}_3\text{-N}$, P, K, Ca, Mg and soil pH. Soil organic matter was determined by loss on ignition (500°C) (Storer 1984). Soil samples were sieved through a 2 mm sieve prior to extractions for elemental analysis. Soil $\text{NO}_3\text{-N}$ was determined by extracting 20 g subsamples with 100 ml 1 M KCl. The extractant was gravity filtered and then frozen in 20 ml scintillation vials until analysis by Analytical Research Laboratory of the University of Florida (ARL-UF) using an Alpkem Flow Solution IV semi-automated spectrophotometer. P, K, Ca and Mg were also analyzed (EPA method 200.7)

by ARL-UF using an inductively coupled plasma-atomic emissions spectrometer following extraction of 5 g subsamples with 20 ml Mehlich-1 extractant solution.

Soil acidity was measured in a 1:2 soil/water solution (Kalra 1995). Soil texture was determined based on a soil composite sample from each site (Waters Agricultural Laboratories Inc., Georgia, U.S.A) (Appendix A).

Statistical Analysis

Each patch was considered to be a replicate (total of 8 patches) and plots as subplot descriptors. Soil organic matter, NO₃-N, P, K, Ca, Mg and soil pH , between invaded and native patches, was analyzed using a mixed linear model, which took into account the within plot variation (pair-wise sampling) and also the between patch variation using analysis of variance (SAS PROC MIXED) (SAS 2002). Treatment effects were considered significant at $\alpha= 0.10$.

Results

Soil Organic Matter

There were no differences in soil organic matter (0-15 cm) between logged and unlogged sites ($P= 0.68$). Soil organic matter content was also the same between invaded and non-invaded areas at both sites (3.05 % invaded and 2.88 % native; $P= 0.46$).

Nutrient Pool

NO₃-N was significantly lower at logged site compared to the unlogged site ($P= 0.019$). Average soil NO₃-N at the logged site was 0.1676 mg/L whereas it was 0.1751 mg/L at the unlogged site. NO₃-N levels of the invaded patches were 2.7% lower than native areas for the first soil survey ($P= 0.010$) (Figure 3-1). The second soil survey (fall) showed a significant difference in NO₃-N between sites ($P= 0.10$), but did not show a significant difference between native and cogongrass infested areas ($P= 0.60$).

The amount of available P did not differ between the native and cogongrass patches in both summer ($P= 0.30$) and fall ($P= 0.53$) samplings. There was also no significant difference between the two sample sites for both soil surveys ($P= 0.12$ for summer and $P= 0.12$ for fall). Similarly, there was no significant site difference in available K for both sampling dates ($P= 0.75$, $P= 0.95$). However, in summer, soil available K was 6% lower ($P= 0.0001$) in cogongrass patches compared to native patches. The fall sampling yielded similar results with 4.9 % less K in the cogongrass patches ($P=0.038$) (Figure 3-2) compared to native areas.

Although there was no significant difference between the invaded and control patches for available Mg during the summer sampling ($P= 0.71$), the fall sampling showed significant reduction in the native areas ($P= 0.067$) (Figure 3-1). There was no significant difference in Mg concentration between the two sites ($P= 0.31$) for any of the sampling dates (Figure 3-2).

Both sampling dates showed significantly less available Ca at the undisturbed site compared to the disturbed sites ($P= 0.033$ for summer, $P= 0.031$ for fall). However, Ca concentration did not differ between the invaded and native patches for both samplings.

Soil pH

Soil pH was lower in the cogongrass patches compared to the native patches for the summer (5.02 for cogongrass and 5.11 for native) and fall (4.40 for cogongrass and 4.62 for native) sampling (Table 3-1). However, there was no difference between the two sites for both samplings.

Discussion

Despite the extensive rhizome network and increased above ground biomass in cogongrass invaded areas (Ramsey et al. 2003), no difference in soil organic matter was

observed between the invaded and native patches sampled. Differences in litterfall mass interact with differences in the litter decomposition rate to affect the net flux of C into the soil. The slow decomposition rate of cogongrass litter may ultimately be the reason for no observed difference in soil organic matter between treatments. This is supported by research of Hartemink and O'Sullivan (2001) who tested the decomposition and nutrient release patterns of cogongrass in the humid lowlands of Papua New Guinea. These authors determined that cogongrass leaf litter decomposed much slower and half-life values exceeded the period of observation. The differences among decomposition patterns were best explained by the lignin+polyphenol:N ratio, which was highest for cogongrass (24.7).

There are several reasons to believe that cogongrass played a role in lowering soil NO₃-N in the invaded patches. All patches were similar with regard to soil texture, color and disturbance history at each site. The lower NO₃-N availability found in invaded patches may have resulted from cogongrass' aggressive growth pattern, extensive rhizome network and longer growing season. A companion study by Daneshgar et al. (2005) at the logged site showed that belowground biomass of cogongrass was ten times greater than that of native vegetation. Lower NO₃-N levels in cogongrass patches may be the result of efficient nutrient uptake by the dense root/rhizome systems. Cogongrass is also known to have mycorrhizal associations, which may also explain the lower nitrate availability in invaded patches (Brook 1989). Mycorrhizae improve nutrient availability to host plants and alter their morphology, physiology, and competitive ability (Bray et al. 2003). As a result of lowering nutrient levels, specifically N, cogongrass may also be able to impede colonization and survival of native species, and facilitate its own persistence.

Lower nitrate levels may also indicate lower ammonium and reduced nitrification; however, these variables were not tested.

Differences in soil NO₃-N among soil surveys is attributed to differences in active growth and nutrient uptake during the growing season (March 2004) compared to the slow-growth in the fall. Following active vegetative growth early on, cogongrass growth and biomass accumulation reach a plateau in late summer (Shilling et al 1997). The difference in soil NO₃-N between sampling dates, perhaps, reflects the difference in nutrient uptake patterns at different times of the year. Similar conclusions have been drawn by Wolf et al. (2004), whose study of invasion of a nitrogen-fixing non-native species, *Melilotus officinalis*, yielded a similar trend for soil nitrate. In this case, NO₃-N was significantly lower in invaded patches sampled in May and then progressively decreased in both invaded and control patches so that no significant difference between the areas was evident when sampled in August.

Other nutrients (P,K,Ca, and Mg) exhibited varying trends with respect to cogongrass invasion. There was no significant difference in soil extractable pools for P for both surveys. This was contrary to previous research that has shown levels of P and N are often related (Evans and Belnap 1999). Because our sampling scheme allowed only the newly invaded edges to be sampled, perhaps a significant relationship was not observed because of temporal constraints. Changes in soil nutrient pools may require longer periods of time to show differences to native patches. Future research could examine P differences between cogongrass patches that have been established for longer periods of time and native vegetation.

Lower levels of K were observed in invaded patches than native patches for both soil surveys. Many grass species with fine, fibrous root systems are able to exploit K held in clay interlayers and near the edges of mica and feldspar crystals of clay and silt size particles (Brady and Weil 2002). The extensive belowground rhizome network (Daneshgar et al. 2005) as well as association with mycorrhizae (Brook 1989) may account for the ability to exploit soil K more efficiently than native species. Elephant grass (*Pennisetum purpureum* Schum), has been shown to obtain K from sand-sized particles, a form usually considered unavailable to plants (Brady and Weil 2002). Potassium is known to affect cell division, formation of carbohydrates, translocation of sugars, some enzyme actions, the resistance of some plants to certain diseases, cell permeability, and several other functions (Plaster 1992). Thus, decreases in soil K in cogongrass areas could have serious implications for recruitment and growth of native plant species.

Lower pH was found in invaded patches in relation to control patches, for both soil surveys. The mechanisms for decreases in pH in response to exotic invasion have been attributed to increased nitrification, high rates of uptake of NH₄⁺, and/or changes in litter quality (more acidic, base-poor litter) (Ehrenfeld 2003). Although NH₄⁺ was not tested directly, decreases in NO₃-N were observed in cogongrass areas and lower nitrate levels may also indicate lower ammonium levels. The preferential uptake of NH₄⁺ ions from cogongrass infested areas releases H⁺ ions, resulting in a lower pH in the rhizosphere soil immediately surrounding the plant root. Differences in NH₄⁺ uptake between cogongrass and native plants could account for the differences in soil pH in such short proximity.

Although we do not have direct evidence of any mechanisms responsible for lowering soil pH in cogongrass invaded patches, past research findings may also point to allelopathy as a potential mechanism. In addition to the possibility of root exudates that are acidic, allelochemicals produced by cogongrass may also make the soil more acidic. Phenolic compounds present in foliage, roots, and rhizomes of cogongrass may be responsible for the allelopathic inhibition of germination and seedling development of other species (Inderjit and Dakshini 1991). Koger and Bryson (2003) suggest that allelopathic substance(s) provide cogongrass its extreme invasive and competitive abilities. However, the specific phenolic compounds in cogongrass tissues have not been identified and tested for allelopathic properties and any research on potential allelopathy by cogongrass is still preliminary and inconclusive.

Decrease pH in cogongrass patches may also have implications for other soil extractable pools in the long term. At low pH, the cation exchange capacity is in general lower with only the permanent charges of the 2:1 type clays and a small portion of the pH dependent charges on organic colloids, allophane and some 1:1 type clays holding exchangeable ions. Strongly acidic soils hold H⁺ and hydroxy aluminum ions tightly to the soil surface. This tight association prevents K and other elements from being closely associated with the colloidal surfaces, which reduces their susceptibility to fixation (Brady and Weil 2002). Continuous acidic conditions may eventually reduce many soil nutrient pools; greatly reducing the success of surrounding native vegetation as well as transforming ecosystem biogeochemical properties.

Conclusions

This research offers valuable insight to researchers and managers as to whether soil effects may be due to or responsible for cogongrass invasion and may generate important

research questions for future experimentation. Future research could continue to examine how cogongrass changes soil properties in the area it is invading. Further variables such as nitrogen mineralization and soil moisture would be valuable to consider. Feedback, both positive and negative, resulting from plant–soil interactions is often invoked to explain vegetation patterns (Berendse 1998; Petraitis and Latham 1999). Future research could examine how soil based feedback is acting either to accelerate the invasion of cogongrass or stabilize it once it has already invaded.

More definitive conclusions regarding these and other hypotheses await field and greenhouse experiments that clearly separate the independent effects of abiotic and biotic mechanisms determining community invasibility. Information gathered from such studies could have important implications for the restoration of native communities and revegetation with native species. Cogongrass invasion in the southeastern United States continues to be a large economic and ecological problem. Extensive study of soil processes and plant-soil feedbacks would be a valuable tool before expensive resource demanding control programs are undertaken (Zavaleta et al. 2001). More studies of a similar nature are necessary to determine whether invaders escape resource limitations of the resident community and use other resources to their competitive advantage so that they could facilitate their own invasion into an area.

Table 3-1 Mean soil pH in invaded and control patches for soil surveys in spring 2004 and fall 2004 for the logged and unlogged sites combined.

	Invaded	Control	SD	F(df _n , df _d)	P<
<hr/>					
Spring 2004 (n=8)	5.02	5.11	0.13	18.71 (1,140)	0.0001
<hr/>					
Fall 2004 (n=8)	4.40	4.62	0.49	8.38 (1, 138)	0.0044
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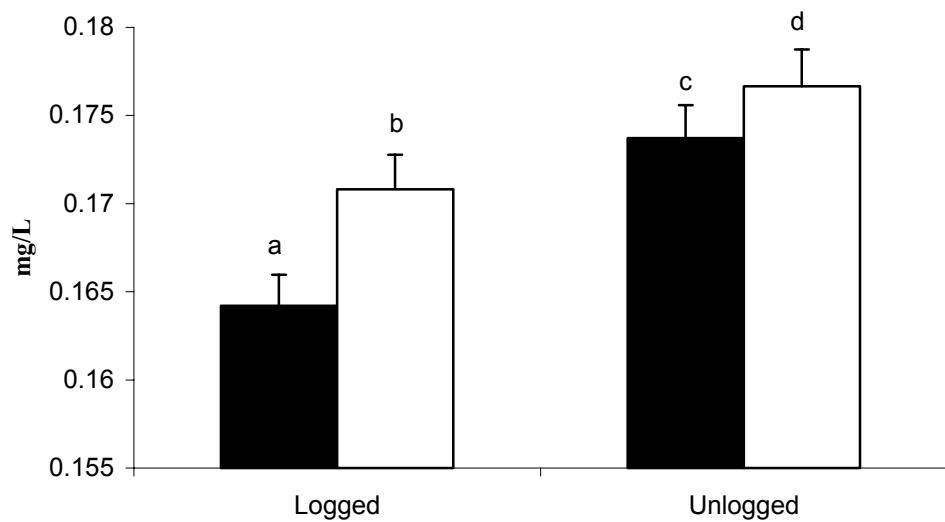


Figure 3-1 Mean concentrations (Mean + 1 SE) of available $\text{NO}_3\text{-N}$ for the logged ($n=4$) and unlogged ($n=4$) sites for the summer 2004 soil survey. Different letters indicate significant differences between cogongrass (■) and native patches (□) ($P<0.05$).

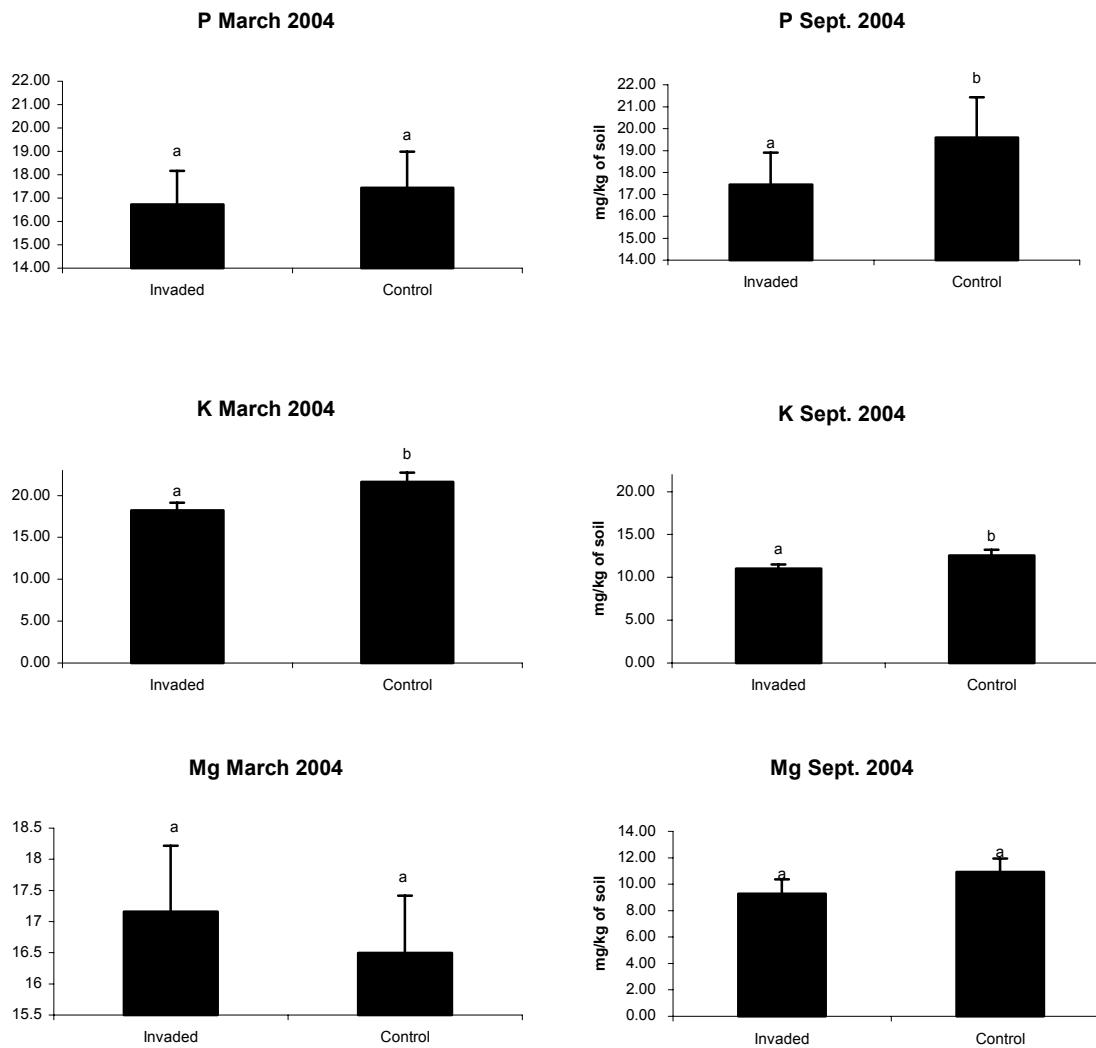


Figure 3-2 Mean concentrations (Mean + 1 SE) of available P, K, and Mg ($n = 8$) for the logged and unlogged sites for the spring and fall 2004. Different letters indicate significant differences between cogongrass and native patches ($P < 0.05$).

CHAPTER 4 SUMMARY AND CONCLUSIONS

Field studies were performed to investigate the implications of plant diversity and soil chemical properties on *Imperata cylindrica* (hereafter referred to as cogongrass) invasion in Northwest Florida ecosystems. Here, invasibility is defined as the degree to which a community is susceptible to an exotic species. There are numerous factors that influence a community's susceptibility to invasion including the composition and diversity of resident species. One of the earliest theories relating biodiversity and invasibility was hypothesized by Charles Elton. Elton predicted that lower resident diversity would favor invasion (diversity-invasibility hypothesis). The objectives of this study were: 1) determine how increased plant species richness affects cogongrass rate of spread, 2) determine how increased plant functional richness affects cogongrass rate of spread, and 3) determine how cogongrass invasion affects soil chemical properties of invaded areas compared to non-invaded areas.

There have been several proposed mechanisms as to why diverse communities are less susceptible to invasion. First, invasions can be favored by the existence of empty ecological niches which are open to colonization by non-native species in the absence of suitable competitors (Elton 1958; Prieur-Richard et al. 2000). Second, theoreticians have suggested that diverse systems should be difficult to invade because newly arrived species are more likely to find a competitor that precludes their success (Dukes 2002). Third, diverse communities are more likely to use resources more completely and therefore limiting the ability of exotics to establish (Tilman 1999; Hooper and Vitousek

1998). Fourth, interactions with other trophic levels, for example herbivore pressure, may preclude establishment and invasion of exotic species (Lodge 1993). Diversity among trophic levels may be an important mechanism in determining community resistance to invasion. In this research, I hypothesize that as species richness and functional richness increase an ecosystem may be less susceptible to cogongrass invasion. Similarly, I also predict that as cogongrass invades it will be a better competitor for light and nutrients and will deplete the resources in the area where it invades.

After thorough investigation of two field sites, a logged site and an unlogged longleaf pine site, the extreme competitive ability and resiliency of cogongrass became evident. The total per year advancement for the logged and unlogged site was 1.63 m^2 and 1.14 m^2 , respectively, indicating the ability of cogongrass to dominate large areas in a short period of time. The first study sought to investigate the effect of species richness and functional richness on cogongrass invasion. The number of native species was variable across the plots examined, ranging from two to thirteen species per plot for the logged site and zero to thirteen species per plot for the unlogged site.

Species richness, the total number of species, did not significantly affect the rate of cogongrass invasion at the logged site and the unlogged site. Increased species richness in a community may increase the productivity of the community and decrease root space available to an invading species. Cogongrass invasion did not show this relationship. The lack of diversity effect observed for cogongrass invasion is attributed to the aggressive below ground spread by rhizomes. Cogongrass rhizomes have morphological and anatomical features that make them more competitive to acquire soil nutrients. The ability of cogongrass to survive and spread on low fertility and low organic matter soils

may indicate that competition for soil nutrients in a diverse community may not be as limiting to cogongrass invasion as hypothesized.

Increased functional diversity did not significantly affect cogongrass invasion at either site. In general it is believed that, a diversity of functional groups (i.e. rooting depths, life forms, life histories etc.) may support the hypothesis that diverse areas are more likely to carry a competitor that will preclude the success of an exotic species. The lack of observed diversity effect may result from large amounts of species that were in the functional category of annual and perennial forbs and also that the proportion of sites occupied by different functional groups was low. Future work could use microcosm studies of manipulated functional richness to assess how different functional groups affect cogongrass regrowth and invasion.

No significant relationship was observed between percent native ground cover and cogongrass invasion. In previous studies reduced invasion rates in areas of high percent plant cover have been attributed to increased root competition and reduced availability of light. In the case of cogongrass, reduced light availability and rooting competition do not appear to be a significant barrier against invasion. Cogongrass is able to persist in low light conditions under the moderate shade of savannahs and the sharp rhizomes are able to cause physical injury to surrounding vegetation.

To determine how cogongrass invasion affects soil properties, two soil surveys were conducted and samples were taken pair wise from both the cogongrass monoculture and the native side of the cogongrass patch. A significant difference between treatments was observed for pH, NO₃-N and K between invaded and non-invaded areas. Significantly lower levels of NO₃-N and K were observed in the cogongrass patch

compared to the native patch. Lower levels of these nutrients may be attributed to the extreme competitive ability of cogongrass to extract available resources from the area in which it is invading. Cogongrass has an extensive belowground rhizome/root network as well as an association with mycorrhizae, which may help explain its competitiveness on infertile soils and efficient nutrient uptake. The degree of fine roots, root length and root turnover may influence root competition and lead to higher spatial variability and heterogeneity in soil resources.

The soils of the cogongrass patch were found to be significantly more acidic than that of the surrounding native vegetation. Based on the observations made in this study, cogongrass may suppress growth of surrounding species and effectively lower pH in the area it is invading through root exudates, which could include allelochemicals. Decreased pH in cogongrass patches may also have implications for other soil extractable pools in the long term. Continuous acidic conditions may eventually reduce many base ions; greatly reducing the success of surrounding native vegetation as well as transforming ecosystem biogeochemical properties.

This study provides important new insight into currently proposed hypotheses concerning community invasibility. The results, from both the logged and unlogged site of this study do not support the general hypothesis of Elton (1958) that invasion resistance and compositional stability increase with diversity. Based on the results of all of the research reported within, plant species diversity, functional richness and total percent cover of the native community do not appear to be important factors affecting the rate of cogongrass invasion in Northwest Florida. Cogongrass invasion does appear to

have a significant effect on soil extractable nutrient pools. Our results indicate that exotic invaders may modify their environment in a way to favor their own invasion.

One limitation of this study was the narrow range of species richness, functional richness and total percent cover at the patches sampled. Future studies should consider sampling communities with a wide range of species richness as well as increasing the sample size (number of patches) monitored.

APPENDIX A

SOIL TEXTURE DATA

Table A-1. Soil texture data from sites used at both clearcut sites at International Paper (logged) and sandhill sites at Blackwater River State Forest (unlogged)

Location	Depth (cm)	Texture
<u>Site 1</u>		
Patch 1,2,3	0-15	Sandy Clay Loam
	15-30	Sandy Loam
	30-45	Loamy Sand
	45-60	Loamy Sand
Patch 4	0-15	Loamy Sand
	15-30	Loamy Sand
	30-45	Sand
	45-60	Loamy Sand
<u>Site 2</u>		
Patch1	0-15	Loamy Sand
	15-30	Sand
	30-45	Loamy Sand
	45-60	Loamy Sand
Patch 2	0-15	Loamy Sand
	15-30	Loamy Sand
	30-45	Sandy Loam

	45-60	Sandy Loam
Patch 3	0-15	Sandy Loam
	15-30	Sandy Loam
	30-45	Sandy Loam
	45-60	Sandy Loam
Patch 4	0-15	Sandy Loam
	15-30	Sandy Loam
	30-45	Sandy Loam
	45-60	Sandy Clay Loam

APPENDIX B
FUNCTIONAL RICHNESS DATA FOR LOGGED AND UNLOGGED SITE

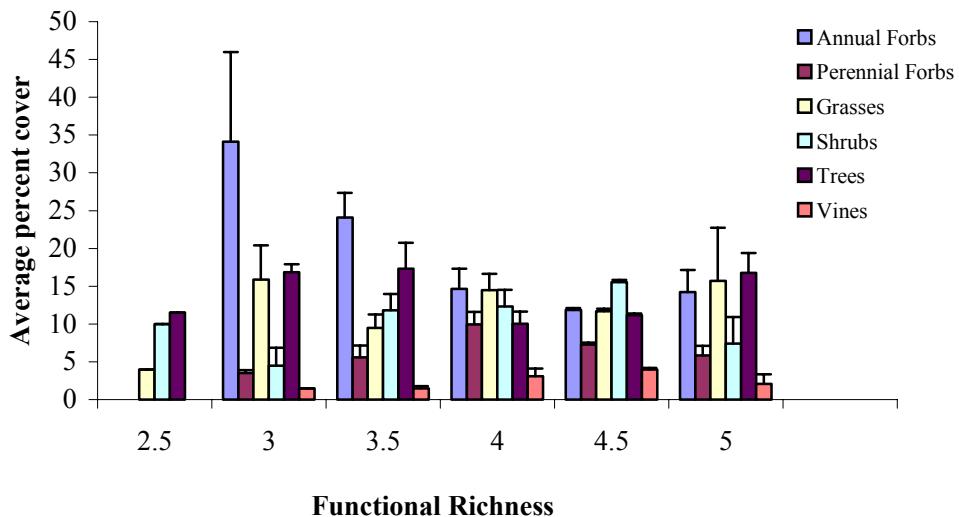


Figure B-1 Average percent cover for each functional group for each functional richness level at the logged site. Data was compiled from all plots sampled (n=118).

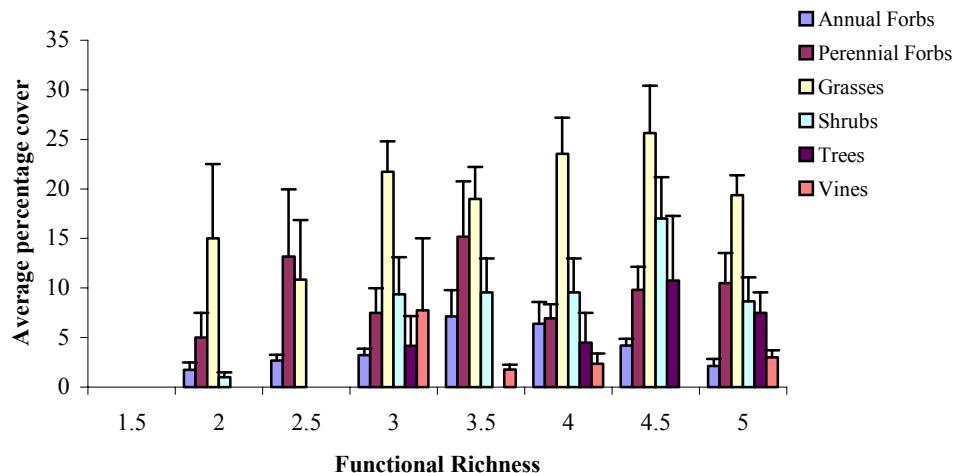


Figure B-2 Average percent cover for each functional group for each functional richness level at the unlogged site. Data was compiled from all plots sampled (n=118).

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BIOGRAPHICAL SKETCH

Alexandra Robin Collins was born in Vancouver, British Columbia, Canada, in 1981. She graduated from Burnaby Central High School in June 1999, and entered Simon Fraser University in Burnaby, British Columbia, the following September. She received her Bachelor of Science degree in biology with a specialization in ecology in April 2003.

In February of 2003, Alexandra contacted Dr. Shibu Jose and spoke with him about her experience and desire to attend graduate school at the University of Florida. In May of 2003 she made the big move from Vancouver to Milton, Florida, to conduct research at the West Florida Research and Education Center for the summer. In the fall of 2003 Alexandra moved to Gainesville to begin course work.

While living in Gainesville Alexandra was an active member of the Forestry Graduate Student Organization and Graduate Assistants United. Alexandra was a senator on student government and presented various pieces of legislation in regards to graduate student issues. Although Alexandra has many interests on campus, she was a dedicated member of the gator synchronized swimming team and competed at the national level for two years while completing her master's.

Alexandra plans to pursue a Ph.D. program focusing on ecological and economic implications of invasive non-indigenous plants.