

Imperata cylindrica INVASION IN JUVENILE *Pinus taeda* FORESTS:
IMPLICATIONS OF DIVERSITY AND IMPACTS ON PRODUCTIVITY AND NITROGEN
DYNAMICS

By

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A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

2007

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To Farhad and Mina Daneshgar

ACKNOWLEDGMENTS

I would like to thank my graduate committee chair, Shibu Jose, for giving me an opportunity to pursue a doctoral degree and for his support, encouragement, suggestions, and guidance with my dissertation research and writing. I would also like to thank my committee members (Dr. Eric Jokela, Dr. Michelle Mack, Dr. Tim Martin, and Dr. Rick Williams) for their contributions to my research and for allowing me to pursue my degree even after some bumps in the road. I am grateful for the work done by Dr. Craig Ramsey, who helped establish several of my projects; and to Robin, Leah, Jeremy, Jeff, Mike, Don and Eric for helping with field work.

I would like to thank all my friends and family for their never-ending support and love. I extend big thanks to my sister Shireen for her ears and her heart. Lastly, I would like to thank my mother Mina and my father Farhad for their unconditional love and support, for picking me up when I was down, and for letting me pursue my dream.

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Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

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DYNAMICS

By

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August 2007

Chair: Shibu Jose

Major: Forest Resources and Conservation

Imperata cylindrica, a C₄ rhizomatous perennial grass that invades a range of sites, is one of the most troublesome weed species in the world. Little information exists on its ecological impacts. The objective of this study was to examine the impacts of *I. cylindrica* on southeastern forests, specifically examining the role of species identity in community susceptibility to invasion and how invasion affects productivity and nutrient pools of establishing pine forests.

The role of species richness, functional diversity, and species identity of native species were tested with *I. cylindrica* in mesocosms. Results showed negative relationships between the biomass and cover of the native species and *I. cylindrica*. Grasses proved to be the most resistant functional group. *Andropogon virginicus* was the most resistant to invasion over time, suggesting that resistance is a matter of species identity. The success of *A. virginicus* can be attributed to the fact that it had significantly greater root length, root length density, and specific root length than all of the native species and *I. cylindrica*. The root morphology characteristics allow it to be a great competitor belowground where *I. cylindrica* is most aggressive.

The impacts of *I. cylindrica* and native vegetation competition on the productivity of loblolly pine (*Pinus taeda*) seedlings were evaluated in a 27-month long field study. At the end

of the study, only 26% of the seedlings growing in *I. cylindrica* survived, half of what was observed with native species. After two growing seasons, the root collar diameter, height and stem volume index of pine seedlings growing with the invasive were significantly lower than seedlings competing with native vegetation. After 27 months, the pine seedling biomass in *I. cylindrica* was 18% of the seedlings grown with native vegetation. The *I. cylindrica* pine seedlings maintained the lowest levels of light saturated photosynthesis with reduced levels of stomatal conductance. Low foliar nitrogen may explain the reduced photosynthesis. Evidence from this study suggests that *I. cylindrica* competition significantly reduces the productivity and growth of loblolly pine seedlings compared to native vegetation.

In the next study, ¹⁵N-labeled ammonium sulfate was used to compare how *P. taeda* seedlings compete for N in the presence of *I. cylindrica* and native vegetation competition. *I. cylindrica* competition led to significantly lower N content in the pine foliage and roots than the native treatment. Competition from *I. cylindrica* contributed to the pine seedlings taking up a greater percentage of the applied fertilizer than the seedlings competing with native vegetation. The belowground biomass of *I. cylindrica* was seven times higher than that of the native species despite its lower N concentration. While the native species retained more N aboveground, *I. cylindrica* held significantly more N belowground. Invasion by this grass could lead to a shift in N pools from above to belowground in infested ecosystems.

Overall, the results indicate that communities with certain species such as *A. virginicus* may better resist the invasion of *I. cylindrica*. However, once infested, *I. cylindrica* decreases productivity and alters nutrient pools. This can have serious negative implications for the health and integrity of infested southeastern forests.

CHAPTER 1 INTRODUCTION

In 1958, Charles Elton, a pioneer in population ecology, spoke of how ecological explosions were threatening the world. What he meant by ecological explosions was that living organisms were experiencing enormous increases in number. Today, we refer to species having explosive growth and spread outside their native range as invasive species. Biological invasions have caused more species extinctions than human induced climate change (D'Antonio and Vitousek 1992) and are the second leading cause of species extinctions after changes in habitat. Invasive plants, in particular, are to blame for much native species decline and ecosystem degradation (Wilcove et al. 1998). The invasion of native ecosystems by exotic plants can lead to alterations in nutrient cycling, fire regime, hydrology, energy budgets, and native species abundance and survival (Mack et al. 2000).

With few limits on range and distribution, combined with relatively easy transport of propagules, grasses in aggregate may be one of the most widespread invading plant groups in the world with serious implications for ecosystem function (D'Antonio and Vitousek 1992). Of the invasive grasses, *Imperata cylindrica*, a rhizomatous C₄ perennial, is particularly troublesome. It has been spreading throughout natural and disturbed ecosystems all over the world, infesting over 500 million hectares and is considered a pest in over 73 countries (MacDonald 2004). In the southeastern United States, *I. cylindrica* poses a serious threat to native ecosystems. Over 500,000 hectares are infested by the exotic in Florida alone (MacDonald 2004). *I. cylindrica* is also becoming a problem in establishing pine forests in the Southeast, thus becoming a dilemma for forest land managers (Jose et al. 2002; Miller, 2000).

To date, no studies have been conducted to examine the impacts of *I. cylindrica* on establishing forests, which became the primary goal of this research. Our approach to

understanding these impacts began with a review of all the current theories on invasion success, particularly examining the factors that make communities susceptible to invasion and also traits of successful invaders. To follow, we explored what characteristics of an establishing pine forest, its understory diversity in particular, influence the community's susceptibility to invasion. Next, we asked the question, what are the impacts of *I. cylindrica* competition on young pine seedlings after a successful invasion and how do these impacts compare to competition from native vegetation? Lastly, with evidence that *I. cylindrica* competition reduced pine seedling physiology and growth, we used ^{15}N enriched fertilizer to determine if competition for nitrogen explained the reduced pine seedling productivity.

Review of Literature

Biology of *Imperata cylindrica*

Imperata cylindrica is a C_4 grass that is found mainly in tropical and subtropical regions with annual rainfall between 75 and 500 cm (Bryson and Carter 1993). *I. cylindrica* is generally tolerant of variable soil conditions, but grows most favorably in acidic soil (pH 4.7) (Wilcut et al. 1988). Because of its C_4 photosynthetic pathway, *I. cylindrica* is able to thrive in environments with high temperatures and light intensity. In areas with low water supplies, C_4 plants have higher water use efficiencies. *I. cylindrica*'s C_4 photosynthetic pathway allows it to be a great competitor with C_3 plants.

Imperata cylindrica has basal leaf blades that grow up to 1.5 m tall and 2 cm wide in conditions of good soil moisture and fertility (Lippincott 1997) with a noticeably off-center whitish mid-vein. The serrated leaf margins of *I. cylindrica* accumulate silicates, which deter herbivory (Dozier et al. 1998). Estimates of leaf biomass report 10 Mg per hectare consisting of 4.5 million shoots (Soerjani 1970).

Imperata cylindrica, considered a r-strategist, is a prolific seeder producing as many as 3000 seeds per plant (Holm et al. 1977). Flowering and seed production of *I. cylindrica* in the U.S. occurs in late winter/early spring (Shilling et al. 1997; Willard 1998). *I. cylindrica* seeds are dispersed long distances ranging from 15m to 100m (Shilling et al. 1997). The viability of *I. cylindrica* seeds is highest within the first three months and the seeds do not have a dormancy period (Shilling et al. 1997). Because seeds completely lose viability after one year (Shilling et al. 1997), it is questioned as to whether or not they are the primary mechanism for spread. *I. cylindrica* can also reproduce asexually with its rhizomes, which comprise greater than 60% of its biomass (Sajise 1976) giving *I. cylindrica* a low shoot/root ratio (Brook 1989). Terry et al. (1997) report fresh rhizome biomass in monoculture to be 40 Mg per hectare.

The regenerative capacity of rhizomes increases with maturity, allowing *I. cylindrica* to regenerate from fragments as small as 0.1g (Ayeni and Duke 1985). Resistant to heat and breakage, rhizomes occur in the top 0.15 m in heavy clay soils and 0.1 m of sandy soils, but may penetrate the soil more than a meter deep (Holm et al. 1977). The rhizomes are long and tough with short internodes, which lead to the formation of dense mats just below the soil surface.

Impacts of *Imperata cylindrica*

The impacts of *I. cylindrica* in the Southeast have only recently been examined. Several have reported evidence that *I. cylindrica* penetrates through the roots of other vegetation with the sharp apical ends of its rhizomes, which potentially leads to infection and/or death (Boonitee and Ritdhit 1984; Dozier et al. 1998; Jose et al. 2002). By producing allelopathic phenolic compounds, *I. cylindrica* is capable of preventing the growth of other plants including some pines by inhibiting germination (Sajise and Lales 1975). *I. cylindrica*'s extensive rhizome network make it particularly competitive belowground and as a result, monotypic patches of the grass form in infested areas, altering native species richness and diversity. The dense rhizome

mat in the soil often is a mechanical hindrance to root growth of native species (Jose et al. 2002). In Florida sandhill savannas, it has been demonstrated that *I. cylindrica* replaced all native understory species (Lippincott 1997). Lippincott (2000) showed that *I. cylindrica* altered fire regimes by increasing flame heights and temperature, resulting in increased mortality of even fire-tolerant *Pinus palustris*.

Soil characteristics are altered with the invasion of *I. cylindrica*. In the Florida sandhills, soil moisture taken at 10 to 30 cm depth in the *I. cylindrica* plots was about 50% lower than the natural area plots (Lippincott 1997). This reduction in soil moisture coincided with the 2 to 3 fold greater rhizome/root biomass, and 2-fold greater root length density in *I. cylindrica* plots relative to native species plots suggesting that increased rhizome/root biomass and root length leads to soil water depletion and intense below ground competition with native plant species and nearby pines. Collins and Jose (in review) demonstrated that *I. cylindrica* decreased soil nitrate and potassium levels and altered soil pH in invaded pine flatwoods. Phosphorus levels may be altered in the soil after invasion as it was demonstrated that *I. cylindrica* is particularly competitive for phosphorus (Brewer and Cralle 2003).

Community Susceptibility to Invasion

The empty niche hypothesis states that exotic plants can be successful in invading a new community by accessing resources not being utilized by the local species (Elton 1958, Levine and D'Antonio 1999, Mack et al. 2000). A community then is susceptible to invasion if there are vacant niches. The success of *Centaurea solstitialis* L. invasion into California grasslands is hypothesized to be due to its extensive, deep roots which access unused water below the shallow roots of the other vegetation (Roche' et al. 1994, Hierro et al. 2005). Unused resources are often to blame for invasion success. Davis et al. (2000) suggest that as long as the quantity of available resources is matched by the amount of resource uptake, a community will resist

invasion. Thus each community has a threshold, where resource availability equals uptake, in which invasion can not occur, but this threshold is not fixed (Davis et al. 2000). Pulses in resources or declines in uptake offset this threshold allowing community invasion explaining why invasion success often occurs after disturbances, when mortality contributes to a reduction in resource uptake.

Efficient uptake of resources and occupancy of all niches in a community, both of which may prevent invasion, may be the result of high diversity. This is the concept that Charles Elton (1958) used to propose the diversity-invasibility hypothesis, which states that more diverse are less susceptible to invasion. Several authors have tested the relationship between diversity and invasion success producing conflicting results. A negative relationship, in support of Elton (Fargione and Tilman 2005; Milbau et al. 2005; Fargione et al. 2003; Ruijven et al. 2003; Dukes 2002; Kennedy et al. 2002; Naeem et al. 2000; Knops et al. 1999; Hooper 1998; Tilman 1997; Rejmanek 1989) a positive one, rejecting the hypothesis, (Smith et al. 2004; Stohlgren et al. 2003; Foster et al. 2002; Pysek et al. 2002; McKinney 2001; Lonsdale 1999; Stohlgren et al. 1999) and no relationship (Collins et al. 2006; Crawley et al. 1999) have been shown.

A number of community effects have been attributed to the negative relationship between diversity and invasion. A crowding effect in a diverse community may prevent invasion when there simply is no room for introduced species. In experimental grassland plots, crowding from up to 24 species reduced the cover of exotic species by up to 98% (Kennedy et al. 2002). In a diverse community, a complimentary effect may be observed when multiple species utilize different resources while occupying the same area. Exotic grass leaf-blade length was reduced by enhanced complementarity in an European grassland with increased neighborhood richness (Milbau et al. 2005). The possibility of having a species, which is strong competitor with

invading species increases with increasing diversity (a sampling effect). For example, the presence of *Bromus diandrus* was observed to prevent the establishment of the ruderal, *Eschscholzia californica* (Robinson et al. 1995).

A sampling effect may also be the basis for diversity to have a positive relationship with plant invasion. Stachowicz et al. (2002) contests that diverse systems are more likely to have species that facilitate invasion, making the community more susceptible. Others suggest that communities with increased species richness also have high turnover resulting in resource pulse which favor invasion (Stohlgren et al. 2003). The success of exotic colonization may be driven by the same factors that contribute to high native diversity, resource availability and high propagule pressure.

Invasive Impacts on Resources of Communities

Invasive species can alter resource cycling and availability after successful introduction and spread. Simply through shading, invasives can reduce light availability to other community species. For example, in New Zealand, increases in *Tradescantia fluminensis* biomass reduced light availability which led to an exponential decrease in native forest species richness and abundance (Standish et al. 2001). Gorchoff and Trisell (2003) reported that light reduction by *Lonicera maackii* caused reduced survival and growth of *Acer saccharum* in Ohio, USA. By altering light availability, invasive species also affect water availability. Introductions of grasses into open spaces can lead to less evaporative loss by covering the soil surface (Hughes et al. 1991; D'Antonio et al. 1998). Changing the microclimate, including soil temperature and soil water, can have important implications for mineralization rates and nutrient availability in the soil.

Plant introductions into communities can lead to changes in nutrient availability either directly or indirectly. For example, invasive species can change soil physical properties, the

microbial community, species dominance and plant functional groups, all of which can lead to changes in soil nutrient dynamics (Ehrenfeld, 2003). The effects on nutrient availability of exotic plant invasions depend on how different the new species' characteristics are from the native resident species (Chapin et al. 1996; Ehrenfeld 2003). Several studies have shown that invasive plants maintain higher amounts of nitrogen in their tissues (Vitousek et al. 1987; Vitousek and Walker 1989; Witkowski 1991; Ashton et al. 2005). Higher nitrogen concentrations in tissues could indicate higher uptake, meaning less available nitrogen in the soil. In a study comparing competition for nitrogen between ponderosa pine and associated grasses it was found that alien grasses competed heavily for soil nitrate compared to native grasses which led to poor growth of ponderosa pine seedlings in the alien grass treatment (Elliott and White 1989). Higher nitrogen uptake could also imply better leaf litter quality, which could lead to increases in cycling through accelerated rates of decomposition (Allison and Vitousek 2004; Ashton et al. 2005).

Specific Objectives

The impacts of *I. cylindrica* on forest productivity and diversity in the southeastern United States has yet to be explored. Therefore, the overall objective of the current study was to quantify the effects of *I. cylindrica* invasion on an establishing pine forest with the following specific objectives:

- Review the proposed mechanisms for successful plant invasions
- Test if the theory proposed by Charles Elton concerning the diversity-invasibility hypothesis holds true for *I. cylindrica* and native pine sandhill understory species in controlled mesocosms
- Determine how *I. cylindrica* impacts the survival, physiology and productivity of establishing loblolly pine (*Pinus taeda*) seedlings
- Quantify the competitive usage of nitrogen between *I. cylindrica*, pine seedlings and native vegetation using ¹⁵N labeled Ammonium Sulfate.

CHAPTER 2 MECHANISMS FOR PLANT INVASION: A REVIEW

With increases in transport and commerce over the last thousand years, humans have been accidentally and deliberately dispersing and introducing plants to ecosystems beyond their native range (Mack et al. 2000). Plants making the transition to a new habitat must undergo a series of filters in order to become established; a historical filter- which asks whether or not the species arrives, a physiological filter- which asks whether or not the species can germinate, grow, survive, and reproduce and lastly a biotic filter- which address whether or not the species can compete and defend itself successfully (Lambers et al. 1998).

Not every introduction results in naturalization and only a few of those that become naturalized become invasive. As a statistical generalization, Williamson and Fitter (1996) proposed the “tens rule” on the success of plants and animals as invaders when introduced to new ranges. This rule suggests that 1 in 10 of the biota brought into a region will escape and appear in the wild, 1 in 10 of those will become naturalized as a self-sustaining population and 1 in 10 of those populations will become invasive. Although the percentage of plants crossing borders becoming invasive seems low, the few that eventually do have radical effects on native species populations, communities and ecosystem processes.

Since 1958, Charles Elton and other ecologists have made attempts to understand how introduced species become invasive in order to predict where and when invasions could occur. Dispersal, establishment, and survival are necessary for successful invasion of natural communities (Hobbs 1989), but what are the underlying mechanisms for invasion? There are wide array of reasons as to why plant invaders may have rapid growth and spread in their new environments. Disturbance may reduce competition allowing for the establishment of invaders. Exotic plants may escape herbivores or parasites, which keep their populations low in their

native lands. The invaders may alter their new environment in order to promote their own growth while suppressing the growth of others. Empty niches may occur in a community that can be filled by an introduced plant. There are several plausible explanations and several mechanisms for invasion have been proposed.

In this chapter, many of the foremost theories of plant invasion of new communities will be reviewed. Several have been proposed in recent years and some of the more prominent ones with regards to plant invasion will be addressed. The discussion will begin with some of the theories of ecosystem susceptibility to invasion and the factors that may determine whether or not a community is invaded. Some of the theories on how invasion is facilitated will be then portrayed followed by some of the suspected attributes of invading plants. It should be noted that some of these theories have been heavily researched and supported or refuted, while some of the more recent ones lack experimental proof. Some of the following ideas that will be discussed are overlapping in concept and theory, while others are quite distinct.

Biotic Resistance Hypothesis

While some theories suggest that some plant species are able to easily invade new habitats because they do not encounter any herbivores that threaten their establishment and spread (*natural enemies hypothesis* discussed later), the biotic resistance hypothesis says that exotics fail to establish and spread due to negative interactions between the introduced species and the native biota (Maron and Vila 2001). Enemies of the intruders occur in their introduced habitat, which can suppress their spread and establishment. The native communities are able to resist invasion. In a common garden experiment conducted in southern Ontario, Canada, the impacts of herbivory were tested on 30 old-field plant species. It was observed that non-native species experienced equal or greater herbivory than natives (Agrawal and Kotanen 2003) suggesting some evidence of biotic resistance.

The hypothesis holds true as long as there are generalist herbivores in the community, which can attack the invaders and the amount of the invaders does not exceed the amount the herbivores can consume. Maron and Vila (2001) suggest that there is a threshold of exotic species abundance that generalist native herbivores can successfully limit. Beyond this threshold, the biotic resistance no longer exists. A species could rise above the threshold by means of propagule pressure. If a species is contributing large amounts of seed to a community, there is greater insurance of its establishment, survival and spread (Hierro et al. 2005). This concept has led to the propagule pressure hypothesis. Many acknowledge that the difference in the number of propagules arriving in a community plays a role in the level of invasion (Williamson 1996; Lonsdale 1999; Mack et al. 2000).

Fluctuating Resource Availability Theory of Invasibility

Resource availability is one of the driving factors determining what species occur within a community. When resources are limited, less species are able to establish themselves within a community and when resources increase either due to disturbance, heavy herbivory, or even fertilization the window opens up for the establishment of new species. It was this concept that led Mark Davis and his colleagues (2000) to develop the fluctuating resource availability theory of invasibility. This states that an increase in the quantity of unused resources will allow a plant community to be susceptible to invasion. Their theory relies on the assumptions that available resources such as light, nutrients and water are accessible to invading species and that as long as there is no severe competition from resident species for those resources, the species should successfully invade the community.

The theory rests on the concept that a community's susceptibility to invasion is not fixed (Davis et al. 2000). Fluctuations in resource availability will determine how prone a community is to invasion. Increases in resource availability can be driven by two means. First, resident use

of resources could decline. Damage and mortality to resident species could occur as the result of a disturbance thus reducing the uptake of resources. The other way resource availability can increase is by increasing the supply of resources at a rate faster than the uptake of the resident species. Examples of this include higher precipitation than normal that will increase water supply, eutrophication of soils increasing nutrient availability or loss of upper canopy trees allowing for greater light availability. A community can maintain its resistance to invasion with increases in resource availability as long as the species in that community increase their uptake. Decreases in resource availability will increase competition between resident species in a community and make that community even harder to invade. According to Davis et al. (2000) the invasibility of a plant community is based upon a balance between resource uptake and gross resource supply (Figure 2-1). As long as these two are equivalent, the community should be resistant to invasion. Fluctuations away from this balance either increase or decrease the community's invasibility.

The literature has demonstrated several times, scenarios in which fluctuations in resource availability have affected an ecosystem's invasibility. It was demonstrated, in Gros Morne National Park (Canada), a boreal ecosystem, that resources essential for alien plants were either not limiting to the resident species or were supplied by recent disturbances (Rose and Hermanutz 2004). The light availability and percent of bare ground partially produced by moose trampling were significantly higher than the undisturbed sites in this boreal ecosystem, which suggests that the increases in light availability allowed for invasion of aliens. Fluctuating light availability in a podocarp/broad-leaved forest in New Zealand was also shown to be a driving factor for the invasion of *Tradescantia fluminensis*, which would reach its maximum biomass at 10 to 15 percent full light (Standish et al. 2001).

Empty Niche Hypothesis

Davis et al. (2000) proposed that the fluctuation of resources is what leads to the invasion of plant communities by exotics. Disturbances often caused these fluctuations and the imbalance of resource supply and uptake. However, what if a relatively stable community just happened to have resources not being utilized by the native community that are accessible to newcomers? The empty (or vacant) niche hypothesis states that exotic plants can be successful in a new community by accessing resources not being utilized by the local species (Elton 1958, Levine and D'Antonio 1999, Mack et al. 2000).

In order to test the viability of the empty niche hypothesis, Hierro et al. (2005) suggested that parallel studies should be conducted of the invasive in its native and introduced range in order to show that the invasive species is using the unused resources in the new community while also showing that those resources were being utilized by other plants in the native community. No such studies have been documented, but several studies of invasives in their introduced communities have alluded to the uptake of unused resources by invading plants. *Centaura solstitialis* L. is believed to dominate California grasslands with its extensive, deep roots which access unused water below the shallow roots of the other vegetation (Roche' et al. 1994, Hierro et al. 2005 and the sources there in).

Studies involving cover crops preventing the spread of invasives seem to be utilizing the empty niche hypothesis. If cover crops are planted to prevent spread, they are essentially being used to occupy an unused niche and uptake unused resources that could be utilized by exotic invaders. In field experiments conducted in Nigeria, it was observed that after twelve months of planting there was up to a 71% reduction in *Imperata cylindrica* (invasive grass invading agricultural fields) biomass when cover crops such as velvetbean (*Mucuna pruriens* (L.) were planted (Chikoye and Ekeleme 2001).

Diversity-Invasibility Hypothesis

Species rich communities are considered to utilize more resources and thus there are less empty niches to occupy. With fewer resources to tap and less niches to invade, species-rich communities may be less prone to invasion. This is one of the main concepts that led to the development of Charles Elton's diversity-invasibility hypothesis, which states that more diverse communities are less vulnerable to invasion. Several studies have been conducted, as of late, to determine whether or not Elton's theory holds true. In most cases, species richness was used as a surrogate for species diversity. Stohlgren and his colleagues (1999) have been leading the argument that the hypothesis does not hold true and instead, diversity and invasibility are positively related, while Tilman (2004) disagrees and supports Elton's theory.

Using two data sets of native and non-native plant distributions from throughout the United States, Stohlgren et al. (2003) ran correlations of native and non-native plant species richness on multiple scales to determine if there was any relationship between diversity of native species and non-native invasions. The results of this study demonstrated that native species richness was, in fact, positively correlated with invasive species distributions and as spatial scales increased the correlations grew stronger between native and non-native distributions. They found that areas high in native species richness supported large numbers of non-native species and propose the primary mechanism by which diverse habitats are able to support non-native plants is through rapid turnover. Increases in richness lead to increases in turnover within the habitat resulting in pulses of available resources, which promote the growth of natives and non-natives. This concept supports the fluctuating resource hypothesis. Stohlgren et al. (1999) proposed another mechanism in which the success of exotic colonization is driven by the same factors that contribute to high native richness, including high levels of propagule supply and resource availability as well as favorable environmental conditions.

Several other studies have produced results in support of Stohlgren (Wiser et al. 1998, Higgins et al. 1999, Lonsdale 1999, Smith and Knapp 1999). Stachowicz et al. (2002) suggest that there are more likely to be facilitators or important habitat forming species that make conditions ideal for an invasive in diverse communities. In a Kansas grassland, it was observed that a reduction in the dominance of the C4 grasses resulted in the reduction of the invasive *Melilotus officinalis* (Smith et al. 2004). Removal of the dominants resulted in higher light availability of up to 35%, which negatively affected the establishment of *Melilotus* (Smith et al. 2004).

Tilman (2004) contends that as diversity increases, invasibility decreases. Recently, he justified this theory by citing stochastic theory for community assembly (Tilman, 2004). In this theory, every new species entering a community is treated as an invader. There are three requirements for the establishment of an individual in a community. First, community assembly results from the success and failures of propagules of invaders. Next, an invading propagule will survive and reproduce by only utilizing unconsumed resources. Lastly, successful establishment of an invader depends on the resource requirement of an invader relative to other species in its community. During assembly of a community, more and more invaders are utilizing unused resources and as a result when the number of invaders increases the amount of available resources decreases making it harder for new invaders to establish themselves (Tilman 2004). With these assumptions the number of invaders in a community will plateau as it becomes more diverse. This theory imitates the logistic theory and the idea of carrying capacity. As species numbers increase, the maximum number of species a system can support is approached. As species number increases, the probability of invasion by a new invader decreases (Tilman 2004).

Several mechanisms have been proposed that explain how diverse systems are resistant to invasion including the crowding effect, the complimentary effect, and the sampling effect.

The crowding effect is one mechanism by which diverse systems reduce their susceptibility to invasion. In a crowded community, there is little room for establishment of invasive seedlings. Kennedy et al. (2002) tested the relationship between species diversity and invasion in 147 experimental grassland plots of varying diversity, from one species to 24 species. The success of 13 species of exotic plants was assessed. There was a 98% reduction in invader cover in the most diverse plots compared to monocultures, which was attributed to crowding (Kennedy et al. 2002).

The complementary effect refers to the ability of multiple species to utilize different resources or different sources of resources, in such a way that they can coexist in the same area. Plants that complement each other within a community efficiently utilize the various resources allowing for the community to be resistant to invasion. Plants complement each other by occupying different niches (empty niche hypothesis). In Belgium, the effects of three invader grasses on European grasslands were assessed for varying levels of diversity and it was observed that when increasing neighborhood richness, complementarity was enhanced, which negatively affected invader leaf length (Milabau et al. 2005). By complementing each other plants in a community can discourage invasion.

Resources may be used more efficiently in diverse plots because they are more likely to have a species that is highly effective in capturing resources. This is referred to as the sampling effect and it can play a role in a community's susceptibility to invasion. A highly diverse community is more likely to include a species, which is capable of outcompeting an invader. The sampling effect stands as a possible mechanism for why more diverse communities are less

susceptible to invasion. One way to determine whether or not the sampling effect is playing a role in resistance is to test an invader in monoculture of a wide variety of species. A single species may be tolerant of an invader and this may be further demonstrated in communities of varying diversity containing that species. If the invader is consistently failing to be successful in growth or establishment each time it is paired with that particular species along different diversity gradients, then it is evident that there may be a sampling effect.

Fargione and Tilman (2005) demonstrated evidence of a sampling effect with prairie-savannah communities at varying levels of diversity (1,2,4,8,16 species). It was observed that invader biomass was inhibited in plots in the presence of strongly competitive C₄ bunchgrasses (Fargione and Tilman 2005). Soil nitrate concentrations decreased and root biomass of resident species increased with the presence of C₄ grasses across a diversity gradient, leaving the researchers to believe that communities are more resistant to invasion when they contain C₄ grasses.

Elton's theory of invasibility has brought on much debate since 1958 and currently the discrepancy is still unresolved. The diversity-invasibility hypothesis may only hold for certain types systems or only on certain spatial scales. The debate will likely continue and research will continue to test it with a variety of exotic species and invaded communities.

Facilitation by Soil Biota

Soil-borne mutualists could facilitate the invasion of exotic plants. Soil biota can alter the soil conditions enough to favor the spread of an exotic over a native species. Reinhart and Callaway (2006) proposed the enhanced mutualisms hypothesis, which acknowledges the possibility that there may be stronger facilitation of growth of invasives by soil microbes in new habitats than what the plants experienced in their native range. The mutualisms this hypothesis refers to are that formed with mycorrhizal fungi and nitrogen-fixers.

The engineers of the enhanced mutualisms hypothesis suggest that the mutualism of invasive plants with mycorrhizae may not be just a two-way association (Reinhart and Callaway 2006). Instead, nonnative plants may use the associations of mycorrhizae and multiple plants and gain advantage by tapping into the mycelial network without providing the essentials for maintaining such a symbiosis. In the presence of arbuscular mycorrhizae and the North American native grass *F. idahoensis*, the invasive *Centaurea maculosa* showed a 66% increase in growth compared to when grown in the absence of the fungi (Marler et al. 1999).

The invasion of new habitats by plants particularly legumes may be facilitated by nitrogen-fixing bacteria. Nodule production by invading legumes requires a certain threshold of nitrogen-fixing bacteria (Parker 2001). Some legumes are able to invade with the aide of native bacteria and some succeed by bringing the nitrogen-fixing bacteria with them. For example, the nitrogen-fixing actinomycetes *Frankia* maintains a symbiosis with *Myrica faya* (both from the same habitat) allowing it to invade and alter the nitrogen cycle in ecosystems in Hawaii (Vitousek et al. 1987).

The presence of certain soil biota in the exotic habitat may not facilitate greater growth and spread of plant species, but rather provide less restraint than biota in their native habitat. The activity of soil microbes may limit plant growth not only by limiting available nutrients, but also by providing negative feedback, which keeps the species under control. Thus, when the species is introduced elsewhere it may not be constrained by the same mechanisms that disallow the plant growth and spread in its native range. Callaway et al. (2004) reported that *Centaurea maculosa* experienced greater inhibitory effects by soil microbes in its native European soils than in North America. They attribute the differences in performance by the invasive in the two soils

to different feedback mechanisms. This study may be a demonstration of the plant escaping the inhibitory effects of its native soil biota, a theory, which will be discussed later in this chapter.

Invasion Meltdown Hypothesis

Facilitation of invasion by plants may not only be facilitated by soil microbes and mycorrhizal fungi, but also by a variety of flora and fauna. The phenomenon of already invading exotic biota opening the door for the invasion by other aliens by altering site conditions and by providing a positive feedback has often been observed. The invasion meltdown hypothesis states that increasing numbers of exotics species facilitate additional invasions (Colautti et al. 2004). A meltdown of an ecosystem occurs as the number of invasive species increases.

Invasion meltdowns could be facilitated by plants or animals. Plants that alter the soil characteristics may also facilitate invasion of other species. In Hawaii, several studies have demonstrated how *Myrica faya*, a nitrogen-fixing shrub has invaded volcanic nitrogen-poor soils and altered soil properties (Vitousek 1986; Vitousek and Walker 1989). Vitousek (1986) suggested that *M. faya* could further facilitate additional plant invasion. Hughes et al. (1991) experimentally showed that there was significant increase in biomass accumulation of the invader *Psidium cattleianum* in *M. faya* infested communities. Plants may also alter the soil characteristics by introducing chemicals, which may hinder the growth of native species (allelopathy, which will be discussed later), which may allow for the establishment of exotics.

The introduction of pollinating wasps to south Florida has allowed for the establishment of *Ficus* species, that depend on the pollinators for reproduction (Simberloff and Von Holle 1999). Several exotics plants invade ecosystems after herbivores from their native land have feasted on the new plants. Exotic herbivores can reduce competition of native plants for the exotic plants. In a meta-analysis of 63 manipulative field studies, Parker et al. (2006) observed that grazing by exotic herbivores allowed for 52% greater abundance of exotic plants in native communities.

They also observed that grazing by exotic herbivores led to an increase in exotic plant species richness, which they attributed to a reduction in the abundance of native species (Parker et al. 2006). An invasion meltdown of this sort requires the invasive plants to be preceded by generalist herbivores. Specialist herbivores are unlikely to impact the plants in a new habitat enough to allow for the introduction and success of new plant species.

Natural Enemies Hypothesis

With the invasion meltdown hypothesis, some plant species were successful invaders because they followed exotic generalist herbivores into new habitats. Some invasive plants may be successful because instead of following generalist herbivores, they escape from specialist herbivores that keep them from spreading in their native habitats. The natural enemies hypothesis assumes that natural enemies suppress plants in their native range and it is the escape from these enemies that allows exotic populations to explode in their new habitat (Maron and Vila 2001). These natural enemies are not limited to herbivores; fungal pathogens and destructive soil biota may also be considered enemies. The natural enemies hypothesis has also been referred to as the enemy release, enemy escape, herbivore escape, predator escape, or ecological release hypotheses. Three points drive the basis of this hypothesis, 1) plant populations are regulated by natural enemies, 2) natives are affected more by enemies than exotic species, and 3) reduction in enemy regulation should lead to increased plant population growth (Kean and Crawley 2002).

In order to demonstrate the natural enemies hypothesis, a study would have to show that native herbivores or pathogens reduce plant population sizes and growth rates and at the same time show those same plant species suffer little herbivory or diseases and have increased population size and growth rate in their introduced habitat. *Clidemia hirta*, a neotropical shrub native to Costa Rica, which is currently invading Hawaii, was used to test the natural enemies

hypothesis with the use of both insecticides and fungicides and it was observed that *Clidemia* survival in Costa Rica increased 41% when both treatments were used (figure 2-2)(DeWalt et al. 2004). Plant growth in Hawaii was unaffected by the fungicide suggesting that fungal pathogens only limit its growth in its native land (DeWalt et al. 2004). In this case, *Clidemia* escaped the suppression by fungal pathogens, which is why it was invasive in Hawaii.

Escape from natural enemies provides for the logic behind the use of biological control. If a plant is released from suppression by some sort of specialist herbivore or pathogen, then that specialist enemy could be used to regulate plant populations in habitats where that plant was introduced. A field study was conducted to test the biological control of saltcedars (*Tamarix*), an Asian tree species invading riparian areas of the United states with no real insect threat, by the Asian leaf beetle *Diorhabda elongata deserticola* in which the saltcedars were caged in with beetles (Lewis et al. 2003). A 60 to 99% defoliation of the saltcedars was observed by the beetles as well as substantial dieback, mortality of young plants, and limited regrowth in the following growing season (Lewis et al. 2003). Many insects were observed to feed on the plant species in Asia, where it grows in isolated patches, leading to the coevolution of specialized insects which feed solely on it (Lewis et al. 2003 and sources therein). The successful invasion by *Tamarix* species in the United States provides for an example of natural enemies hypothesis because it has escaped the specialist herbivores from its native range.

Evolution of Increased Competitive Ability

Plants in the presence of specialist herbivores and pathogens develop defenses and tolerances of these enemies in order to survive and proliferate in their native lands. Their relationship with their specialist enemies are often coevolved in that over time the plant species have learned to designate their resources towards surviving in the presence of enemies. When these plant species escape their native enemies and are introduced to new habitats, the resources

they have been utilizing for defense can be allocated to growth and reproduction (Blossey and Notzold 1995; Hanfling and Kollmann 2002). This may be what makes these introduced plants invasive. The evolution of increased competitive ability (EICA) hypothesis takes what was stated in the natural enemies hypothesis and takes it a step further. It states that only when plants escape from coevolved specialist enemies, they are able to gain advantage over other plants in their introduced community by using the resources that were previously used for defense for growth and reproduction (Blossey and Notzold 1995). It has been suggested that the liberation from herbivores, allows for the selection of genotypes in the new community with increased competitive abilities (Blossey and Notzold 1995).

An efficient method of testing the EICA is to grow the particular invasive species from seed from both locations in a common garden or identical conditions while excluding pests. Support for the hypothesis comes from observing the plants from the introduced habitat performing better than the native since they experience little herbivore pressure and have adapted to allocating their resources towards growth. Purple loosestrife (*Lythrum salicaria* L.) from two locations, one with herbivory, (Leselle, Switzerland, where it is native) and without herbivory (Ithaca, New York, where it was introduced) were grown in identical conditions and it was observed that plants from the region that experienced little herbivore pressure had greater vegetative growth (figure 2-3) (Blossey and Notzold 1995). The results could be explained by the fact that introduced plants had escaped pressures of herbivory and were able to allocate resources for growth.

Reproductive Traits

Some invasion success could be explained by the reallocation of resources from defenses to reproduction, while some species may simply be good invaders because they have the ability to reproduce quickly and in great numbers. Several authors have pointed out that invasive plants

tend to be r-strategists considering that they tend to invade disturbed habitats (Rejmanek 1989, Hobbs 1991). This seems to be the strategy utilized by several species of *Pinus* in invading regions outside their natural range throughout the world. Rejmanek and Richardson (1996) have identified the main reproductive characteristics, which cause certain species of pine (particularly *P. raidata*, *P. contorta*, *P. halepensis*, *P. patula*, *P. pinaster*) to be more invasive. They include short juvenile period, short intervals between large seed crops and small seed mass. Some of the other characteristics they identified include large number of seeds produced, better dispersal, shorter chilling period needed to overcome dormancy, high initial germinability, and higher relative growth rate (Rejmanek and Richardson 1996 and sources therein). It seems apparent that all these characteristics allow for quick efficient spread of the pines.

Superior Competitor

Specialized reproductive abilities allow for some species to establish earlier, faster, and in greater numbers and these abilities put invasives at a competitive advantage. Some species after establishment may be better competitors for resources than native vegetation, which may make them more successful. Bakker and Wilson (2001) proposed that differences in competitive ability may determine what species invade new areas. In their field study, they demonstrated that an introduced C₃ grass, *Agropyron cristatum* (L.) Gaertn had a stronger ability to resist competition than the native C₄ grass *Bouteloua gracilis* (HBK.) lag. from native and introduced competitors. In this case, *Agropyron* was a superior competitor than the native vegetation.

Several other studies have demonstrated an invasive's ability to outcompete native species for resources. In a study examining the invasion of a longleaf pine (*Pinus palustris*) savanna in southeastern United States by the exotic grass, *Imperata cylindrica*, it was observed that the clonal expansion of the grass was reduced when plots were fertilized with phosphorus suggesting that the invasive was a better competitor for the resource (Brewer and Cralle 2003).

When photosynthetic measurements were taken of two exotic invasive species of *Rubus* and were compared to two native species, it was observed that the exotic species had higher rates of photosynthesis than its native cousins giving implications of why the exotics were better competitors.

In addition to being a superior competitor in an introduced habitat under normal conditions, some invasives may be better competitors in stressful situations like disturbance. Ruderals, highly competitive natives and stress-tolerant species, are expected in communities immediately after a disturbance event (Grime 1979). However, it has been proposed that certain invasives are much more adapted to disturbance and thus are better competitors in the presence of disturbance than natives simply because the natives have not experienced as much disturbance over time (Gray 1879; Mack et al. 2000). This concept known as the disturbance hypothesis has received little attention since it was proposed in 1879 (Gray 1879), but would be fairly easy to test and should receive attention.

Novel Weapons Hypothesis

Over time, plants may have persisted in their native range by exuding chemicals, which help them deal with competition by inhibiting the activity of neighbors (allelopathy). Due to much exposure to these chemical exudates, the neighboring plants may have evolved resistance and thus are not impeded by them, but when these allelopathic plants are introduced to new communities, they have “weapons” that the plants in the new community have never experienced before and as a result may suffer the inhibitory affects. The inhibition of plant growth allows the introduced species to be at a competitive advantage over its new neighbors, allowing it to become invasive. The novel weapons hypothesis states that biochemicals released by a plant, which are ineffective against native neighbors who have been exposed to them over time, are inhibitory to plants or soil microbes in a new community contributing to its invasiveness

(Callaway and Ridenour 2004). The introduced species are invasive because they present their new competitors with weapons they have not been exposed to before.

Because of its high affinity for adsorbing organic compounds, activated carbon is often used to test allelopathy. Ridenour and Callaway (2001) used activated carbon to test whether or not the noxious weed *Centaurea maculosa* used novel weapons (allelopathy) to hinder the growth of the native bunchgrass, *Festuca idahoensis*. They observed that *Festuca* had reduced root and shoot growth in the presence of *Centaurea* in pure sand compared to sand mixed with activated carbon (figure 2-4), implying that the *Centaurea* uses biochemicals to gain competitive advantage. Another activated carbon study demonstrated the use of allelopathy by *Centaurea diffusa*, which had stronger negative effects on North American species than Eurasian species (Callaway and Aschehoug 2000).

As allelopathy continues to work for a species, natural selection will favor its reproduction and growth over other intruding species, which are able to compete. This has been referred to as the allelopathic advantage against resident species (AARS) (Callaway and Ridenour 2004). Just as the species that reallocated resources towards growth and reproduction (the evolution of increased competitive ability), species having success with biochemical weapons may allocate more to the production of these chemicals, thus increasing their success. Support for the AARS could then be observed by introduced species being even more allelopathic than source populations (Callaway and Ridenour 2004).

Integrated Mechanisms

Although several mechanisms for invasion have been proposed and demonstrated through examples, it is clear that many species utilize more than one mechanism to gain competitive dominance in their new habitats. Dana Blumenthal (2005) suggested that there might be an interaction between the natural enemies hypothesis and the fluctuating resource theory because

fast growing, species, which require high resources tend to be susceptible to enemies. This is due to the fact that high-resource species tend to be nutritious and lack structural material and defensive chemicals, which encourage herbivory (Blumenthal 2005). In a new range, the invader escapes its enemies and encounters a flush of resources, which may be the result from a disturbance. The mechanisms for invasion, therefore, may be integrated.

The rhizochemical dominance hypothesis integrates several mechanisms in explaining the success of invasive plants (Collins and Jose, in press). This hypothesis attributes invasive success to allelopathy (novel weapons) and alteration of soil chemical properties by the rhizosphere exudates of the invader, which in turn favors its own growth while inhibiting the growth of competing vegetation. These chemical alterations may include changes in soil pH, and nutrient levels and availability. *Imperata cylindrica* was shown to alter soil pH and decrease soil nitrate and potassium levels in invaded areas compared to noninvaded areas (Collins et al., in press). *Imperata* has also been shown to be allelopathic suppressing the growth of crops like tomato and cucumber (Eussen 1979) having greater impacts at lower pH (Eussen and Wirjihadia 1973). In this case, it seems that *Imperata* increases the potency of its weapons by altering soil chemical properties. The genus *Centaurea* has been proposed to have invasive success by suppressing the growth of native species by phytotoxicity or by altering soil microbial activity leading to restrictions of nutrient availability (LeJeune and Seastedt 2001). By root induced mechanisms, the genus may be gaining dominance.

Conclusions

The fact that several mechanisms for invasion have been proposed in recent years, (many of which were discussed in this chapter) and that basically no generalizations can be made about the nature of invasive plants indicates that research in this area is still fairly new and needs much attention. No one has yet to explain invasion patterns across a large range of systems and this

may be simply due to the fact that each invasive species is unique and that invasions are unpredictable (Williamson 1999; Dietz and Edwards 2006 and references therein). It has recently been proposed, however, that the conflicts in invasion theory result from the examination of different parts of the invasion process and it should be recognized that the processes enabling a species to invade change over the course of the invasion (Dietz and Edwards 2006). Consideration of these different phases may allow for some generalizations to be made.

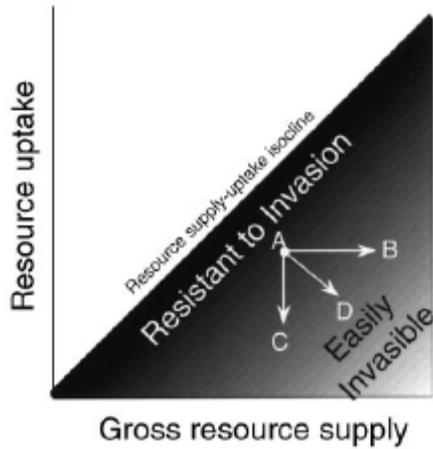


Figure 2-1. The balance between gross resource supply and resource uptake (as denoted by the isocline, where gross resource supply = resource uptake) represents a community's barrier to invasion. A quick increase in resource supply ($A \rightarrow B$), a decline in resource uptake ($A \rightarrow C$) or a combination of the both ($A \rightarrow D$) lead to an increase in a community's invasibility because the resource supply is not matched by the uptake from the community. Source: Davis et al. (2000) Reproduced after permission from Blackwell Scientific Publishers.

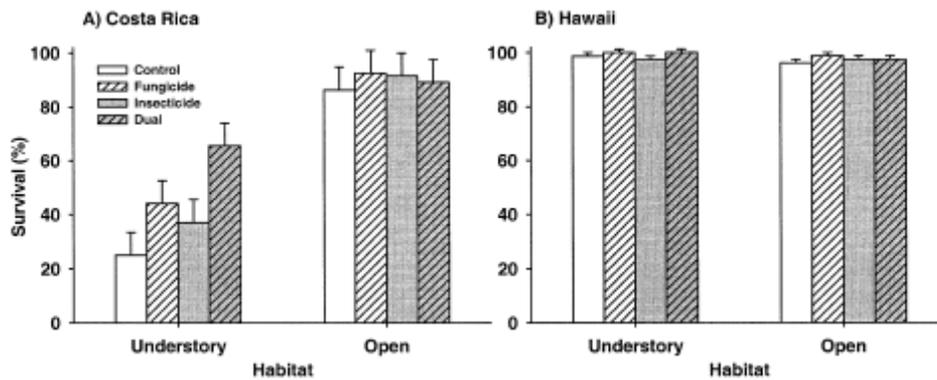


Figure 2-2. Survival of *Clidemia hirta* in A) Costa Rica (where it's native) and B) Hawaii (introduced range) in four natural enemy escape treatments in understory and open habitats. Survival was much higher in Hawaii where *Clidemia* has escape herbivores and fungal pathogens which have reduced its survival in its native land. Source: (DeWalt 2004) Reproduced after permission from the Ecological Society of America.

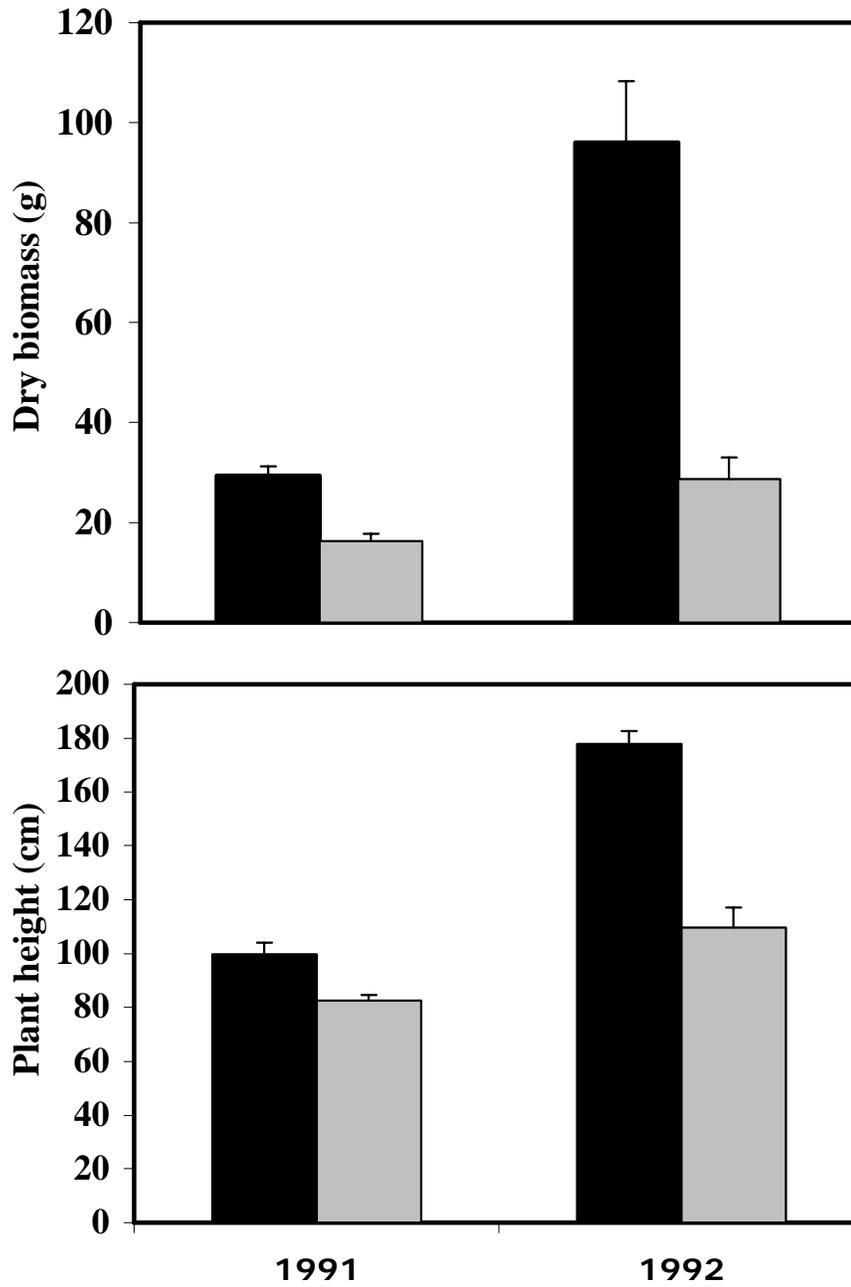


Figure 2-3. Mean (\pm SE) dry biomass and height of purple loosestrife from Ithaca, New York, USA (Black) and Lucelle, Switzerland (grey) after the growing season grown in common gardens under identical conditions. Based on data from Blossey and Notzold 1995.

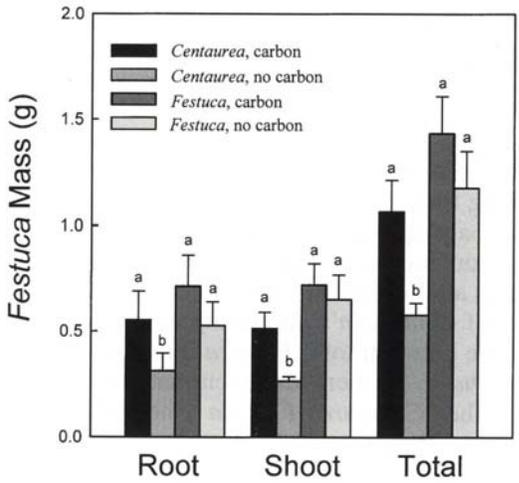


Figure 2-4. Biomass of roots, shoots, and total of *Centaurea* and *Festuca* grown together in grown in pots with and without activated carbon, which has a high affinity for organic chemicals. Shared letters designating means that are not significantly different. Source: (Ridenour and Callaway 2001) Reproduced after permission from Springer-Verlag.

CHAPTER 3
ROLE OF SPECIES IDENTITY IN PLANT INVASIONS: EXPERIMENTAL TEST USING
Imperata cylindrica

Introduction

Studies on the invasibility of communities have focused either on invader characteristics or properties of the community being invaded. A community property that has been examined and debated heavily in regards to invasion is diversity. Ever since Elton (1958) proposed the diversity-invasibility hypothesis, which states that more diverse communities are more resistant to invasion, observational and experimental studies have been conducted in a variety of communities with a plethora of invaders to determine the relationship between diversity and invasion. A negative relationship, in support of Elton (Fargione and Tilman 2005; Milbau et al. 2005; Fargione et al. 2003; Ruijven et al. 2003; Dukes 2002; Kennedy et al. 2002; Naeem et al. 2000; Knops et al. 1999; Hooper 1998; Tilman 1997; Rejmanek 1989) a positive one, rejecting the hypothesis, (Smith et al. 2004; Stohlgren et al. 2003; Foster et al. 2002; Pysek et al. 2002; McKinney 2001; Lonsdale 1999; Stohlgren et al. 1999) and no relationship (Collins et al. 2006; Crawley et al. 1999) have been shown.

The discrepancy amongst all these studies may be a matter of scale. Levine (2000) proposed that correlations between native and exotic species will be positive at large scales and negative at small scales. Other factors that vary with species richness including disturbance, biomass, propagule pressure, resident cover, and climate, which have not always been accounted for may explain the conflicting results (Von Holle 2005). Despite the variability in these factors, scientists have proposed mechanisms for the relationship between diversity and invasion they observe.

Rejection of the diversity-invasibility hypothesis and the success of exotics in diverse systems have been given several explanations. The success of exotic colonization may be driven

by the same factors that contribute to high native richness including propagule pressure and resource availability (Stohlegren et al. 1999). Increased rates of plant turnover, that might result from increased native richness, lead to pulses of resources that allow exotic species establishment (Stohlegren et al. 2003). Others contest that diverse systems are more likely to have a facilitator(s) or habitat forming species, which make the conditions ideal for invasion (Stachowicz et al. 2002). For example, when the dominant C₄ species were removed from a Kansas grassland, establishment of the invasive *Melilotus* was reduced because increased light availability altered microsite evapotranspiration and soil moisture (Smith et al. 2004).

Diverse systems may be unsaturated and propagule limited (Bruno et al. 2004), which may explain the positive relationship between native species richness and invasion. With an ample amount of unutilized resources, community assembly can occur. However, when the availability of resources decreases, invasion becomes difficult. As the community becomes more diverse and more resources are used, the number of invaders will plateau and the success of invasion will decrease, thus supporting Elton's hypothesis (Tilman 2004). In other words, invasion success will be low when the community is crowded and all resources are utilized. A crowding effect has been suggested as a mechanism of resistance. For example, Kennedy et al. (2002) reported that crowding of up to 24 species in experimental grassland plots in Cedar Creek, Minnesota reduced the cover of 13 exotics species by up to 98%.

In a diverse community, the ability of multiple species to utilize different resources while coexisting in the same area (complementary effect) may prevent invasive success. Increased neighborhood richness of an European grassland enhanced complementarity, which negatively affected exotic grass leaf-blade length (Milbau et al. 2005). Species representing different functional groups tend to complement each other because of the different roles they play in the

community. For example, Hooper (1998) found that late season forbs (*Hemizonia luzulaefolia* and *Lessingia micradenia*) combined with perennial bunchgrasses (*Sitanion jubatum* and *Stipa pulchra*) resulted in increased relative growth yield. Lavorel et al. (1999) suggested that studies examining invasion success should not focus on species richness, but on the functional groups since functional diversity might play a larger role in invasion. Experimental evidence exists to support this hypothesis. In a microcosm study using eight different Californian grassland species of varying functionality, the success of *Centaurea solstitialis* was reduced with increased functional diversity, which utilized more resources (Dukes 2001).

A single functional group may enhance or deter invasion. Legumes increased the biomass and net fecundity of *Conyza*, while members of the *Asteraceae* family improved its survival (Priour-Richard et al. 2000). With high nitrate consumption and root biomass production, C₄ bunchgrasses were shown to prevent establishment of invaders in prairie grasslands (Fargione et al. 2003; Fargione and Tilman 2005). Thus, a community with increased functional diversity may have the functional group that will determine the success of an invader (sampling effect). The sampling effect by a diverse system may not be limited to a functional group, but a particular species. Species identity may be the limiting factor to invader establishment and growth. For example, *Bromus diandrus* dominance prevented the establishment of the ruderal, *Eschscholzia californica* in a California winter annual grassland (Robinson et al. 1995).

The conflicting results of the many studies that have examined the relationship between invasion and diversity have left many questions. One criticism, however, for several of these studies is that all new species to a community, whether they were native or exotic, were treated as invaders. The dilemma arises when not all the species that are addressed as invaders in these experiments are truly aggressive or invasive, providing for poor evidence of a community's

resistance to invasion. We tested the validity of diversity-invasibility hypothesis in a mesocosm experiment with Florida sandhill forest understory species and an aggressive rhizomatous invasive C₄ grass, *Imperata cylindrica*, which is considered a pest in over 73 countries (MacDonald 2004).

A perennial grass, *I. cylindrica*, thrives in both undisturbed and disturbed areas in a wide variety of soil types (Jose et al. 2002). *I. cylindrica* spreads sexually, through prolific seed production (3000 1-millimeter long grains per plant; Holm et al. 1977), and vegetatively through rhizomes, which are resistant to heat and breakage. Rhizomes comprise over 60% of the plant's biomass resulting in a low shoot/root ratio that allows it to survive and thrive after burns or cuttings (Sajise 1976). Regeneration of new plants can occur from rhizome fragments weighing as little as 0.1 g (Ayeni and Duke 1985). The extensive growth of *I. cylindrica* results in dense mat of rhizomes in the soil weighing up to 40 Mg per hectare (Terry et al. 1997) that can produce approximately 4.5 million shoots (Soerjani 1970). Because *I. cylindrica* occupies a lot of space belowground, it prevents the root growth of germinating seeds. Lippincott (1997) showed that *I. cylindrica* replaced most understory species in a Florida sandhill savanna, greatly reducing plant diversity.

Criticisms of small scale experiments examining diversity's role in invasion suggest that the observed trends reveal little about the processes and patterns that occur in reality in larger more complex ecosystems (Stohlgren et al. 2003). However, isolated mesocosms may allow for the elimination of extrinsic factors, which may disrupt the potential for diversity to reduce invasion (Naeem et al. 2000). Collins et al. (2006) have reported no relationship between *I. cylindrica* invasion and native diversity in both disturbed and undisturbed forest ecosystems.

These authors suggested that extrinsic factors in the study might have prevented them from drawing a relationship.

The primary objective of this study was to test if the diversity-invasibility hypothesis proposed by Elton held true in controlled mesocosms. We hypothesized that as diversity increased from monocultures to more diverse communities *I. cylindrica* invasion rate would decrease. We also examined whether or not functional diversity or species identity were a factor in invasion success. Because *I. cylindrica* is primarily an underground competitor, we hypothesized that the species that competed better belowground would be more successful in reducing invasion and spread of *I. cylindrica*. For this reason, we also examined species characteristics belowground including biomass, root length, root length density and specific root length.

Methods

Experimental Design and Study Site

A completely randomized block design consisting of eight blocks and ten treatments was used to test the diversity-invasibility hypothesis with the exotic invasive *I. cylindrica* and five common Florida sandhill understory species (based on Buchanan et al. 1999). The understory species included a shrub, *Ilex glabra*, two grasses, *Aristida stricta* and *Andropogon virginicus*, and two forbs, *Chamaecrista fasciculata*, and *Pityopsis graminifolia*. The design allowed for the comparison of five levels of species richness (0, 1, 2, 3, and 5 species) and three functional groups, grasses, forbs and shrubs. The ten treatments used in this study (Table 3-1) included a control with no native species, five monocultures of the previously mentioned species, a treatment with a grass mix, a treatment with a forbs mix, a 3-species treatment with a representative species from each functional group (*I. glabra*, *A. stricta* and *C. fasciculata*) and a 5-species treatment with all of the native species. The *I. glabra* monoculture was treated as the

shrub functional group treatment. The monoculture treatment mesocosms were used to determine if particular species were effective in preventing invasion. The three grass treatments, the three forbs treatments, and the shrub treatment were compared to identify a particularly resistant functional group.

The study was conducted on a flat unshaded 3600 m² field on the West Florida Research and Education Center Farm of the University of Florida, located in northwestern Florida, USA (30°77' N, 87°14' W). In June 2004, native species were purchased from a local nursery and planted in eighty mesocosms (117 liter galvanized iron cans). Six individual plants from 1.9 liter pots were planted in each mesocosm, except in the 5-species treatment, which had only five individuals. To ensure establishment and survival of healthy mesocosm communities, the plants were planted in a soil matrix commonly used in horticultural practices for growing Florida native species. This media was 90% bark (50/50 blend of aged and semi-aged) by volume and 10% sand. To each can, 18-6-12 Osmocote® fertilizer was applied at a rate of 150 g of N, 50 g of P and 100 g of K per can. Lime was also applied to maintain the pH between 4.5 and 5. The mesocosm communities were watered daily with a programmed sprinkler system through October 2004 and weeded when undesired species appeared. Holes were drilled at the bottom of each mesocosm to ensure proper drainage. By November 2004, the annual *Chamaecrista fasciculata* had died, but was able to reestablish from seeds in the same mesocosms by January 2005. In May 2005, a square meter of *I. cylindrica* (including rhizomes) was dug up from a local infestation. A single fragment of rhizome 5 cm long each with a single shoot less than 10 cm tall was cut from the sample and planted directly in the center of each mesocosm. The mesocosms were continually weeded after the introduction of *I. cylindrica* to ensure that only the original six species were present.

Data Collection

Starting in May 2005 and throughout the summer, the number of *I. cylindrica* shoots were counted and the percent cover of each species was determined by ocular assessment by the same individual biweekly for each mesocosm. In October, all of the aboveground biomass was harvested from all 80 mesocosms, separated by species, dried at 65 °C for 48 hours and weighed. The belowground biomass from 4 blocks was harvested and separated by species to a depth of 60 cm by 20 cm increments. After all the biomass was washed, a subsample was taken from each species from each mesocosm to measure root length. Root length was measured using the line intercept method developed by Newman (1966) and as modified by Tennant (1975). Root fragments were evenly distributed over a grid of lines 2 cm apart and the number of intersections between roots and grid lines were counted. Root length was determined with the number of intersections and the size of the grid units. The samples were used to quantify the total root length of each species and root length density (RLD). The roots were then dried at 65 °C for 48 hours and weighed. The dry weights of roots were used to calculate specific root length (SRL).

Statistical Analyses

For all the measurements that were taken at the conclusion of the study (species biomass, root length, RLD, SRL, final % cover, and final *I. cylindrica* shoot number) a one-way analysis of variance (ANOVA) was used to detect treatment differences using the PROC GLM procedure (SAS Institute, Cary, NC) within the framework of a completely randomized block design. Treatment means were declared significantly different at $\alpha < 0.05$. Tukey's HSD post-hoc test was used for mean separation. For the biweekly measurements of species cover and number of *I. cylindrica* shoots, a repeated measures ANOVA was used to correlate the repeated observations within treatments as well as to determine treatment differences. The success of *I. cylindrica* as

measured by cover and biomass was regressed with the independent variables, % cover and biomass of native species and with number of species (richness) using PROC REG in SAS.

Results

There were not any significant changes in the native species cover throughout the summer of 2005 after *I. cylindrica* invasion, in all the treatments except for the *C. fasciculata* treatment, which dropped from 63% in June to 27% in August ($P = 0.0002$). Throughout the summer the *A. virginicus* treatment had significantly more cover than all of the other monoculture treatments with a summer mean of 89% ($P < 0.001$). The *A. stricta* treatment had significantly greater cover than the remaining three monoculture treatments ($P < 0.001$). Comparing the three functional group treatments, the grass mix maintained the highest level of cover (summer mean 85%), which was significantly greater than the forbs mix and shrubs treatments at 37 and 39%, respectively ($P < 0.001$). There was no significant difference between the 3 and 5-species treatment covers, but both were significantly less than the grass mix and *Andropogon virginicus* treatment. At the end of the study, there was a significant difference in the cover of *I. cylindrica* between all the treatments ($P < 0.0001$) (Table 3-2). There was not significant difference in the *I. cylindrica* cover when all the grass treatments were compared to all the forbs treatments and the shrub treatment ($P = 0.05$). By the end of August, there was a significant negative relationship between the mean % cover of native species and the cover of *I. cylindrica* ($r^2 = 0.59$, $P = 0.01$) (Figure 3-1).

At the end of the study, there was a significant difference in the native biomass amongst all the treatments ($P = 0.035$) (Table 3-2). Of all the treatments, the grass treatment had the most overall native biomass, while the *Pityopsis graminifolia* treatment had the least. The final total biomass of all of the monoculture treatments was not significantly different. Of the three functional groups, the grass mix treatment had the most biomass, being significantly greater than

forbs mix ($P = 0.034$). The shrubs treatment was not different than the grass mix or forbs mix treatments in total biomass. Nonlinear regression analysis revealed that the total biomass of *I. cylindrica* at the time of harvest had a negative logarithmic relationship with the treatment mean total native biomass ($r^2 = 0.70$, $P = 0.003$) (Figure 3-2).

The biomass of *I. cylindrica* by the time of harvest was highest in control (84.8 g) and lowest in the grass treatment (1.2 g) ($P = 0.0203$). Of the treatments with native species, the forbs mix treatment produced the most *I. cylindrica* biomass (60.3 g). Because of the variability in *I. cylindrica* biomass production there were no significant differences between the remaining treatments. There was not a relationship between the number of species and the biomass of *I. cylindrica* (Figure 3-3).

Of the three functional groups that were tested, the grass mix treatment had the least number of *I. cylindrica* shoots and smallest amount of *I. cylindrica* cover at harvest ($P < 0.0001$), while having the greatest reduction of *I. cylindrica* cover from the control (Table 3-3). These results of the grass mix treatment were not significantly different than the treatment that had all three functional groups. The shrub and forbs mix treatment were the same in terms of the number of shoots, biomass and cover of *I. cylindrica*. These two also had much less reduction in cover and biomass of *I. cylindrica* compared to the grass mix, 3-species and 5-species treatments.

Repeated measures analysis revealed that as early as June 15, a month after introduction, there were differences in *I. cylindrica* cover among the treatments ($P < 0.001$) (Figure 3-4); the grass mix treatment had significantly less cover than the control, *I. glabra*, *C. fasciculata*, forbs mix, and 3-species treatments, while the control and *I. glabra* treatments had more *I. cylindrica* cover than all of the grass containing treatments and the *P. graminifolia* treatment. By July 18,

all the grass containing treatments had significantly less *I. cylindrica* cover than all the other treatments. By the first of August, the *I. cylindrica* cover greatly increased in the *A. stricta* treatment and it no longer was grouped with the other grass treatments. By August 15th, there were three significantly different groups of treatments; the first group having the highest *I. cylindrica* cover included the control, the *I. glabra* and the *A. stricta* treatments, the second group included the *C. fasciculata* and the *Pityopsis graminifolia* treatments and the forbs mix treatment, the third group with the lowest *I. cylindrica* cover included the 3-species, 5-species, grass mix and *A. virginicus* treatments.

Belowground in monoculture, the *A. virginicus* and *A. stricta* treatments had significantly greater root length than the other species including *I. cylindrica* ($P = 0.0017$) (Table 3-4a). *A. virginicus* had the highest RLD at 1.97 cm cm^{-3} , which was significantly greater ($P = 0.0109$) than *C. fasciculata*, *Pityopsis graminifolia*, and *I. cylindrica*, but not *A. stricta* and *I. glabra*. *A. virginicus* had the highest SRL as well at 1184 cm g^{-1} , significantly greater ($P < 0.0001$) than *Ilex glabra*, *C. fasciculata*, *Pityopsis graminifolia*, and *I. cylindrica*, but not *A. stricta*.

In mixed communities, *A. virginicus* had longer root length ($P = 0.0012$) and greater RLD ($P = 0.0001$) than all of the other species and *I. cylindrica* (Table 3-4b). With interspecific competition, *A. virginicus* maintained the greatest SRL ($P < 0.0001$), while *I. cylindrica* had the lowest.

In monoculture, all the species had roots in the top 40 cm of soil (Table 3-5). *Ilex glabra*, *A. virginicus*, and *I. cylindrica* roots reached the bottom of their mesocosm (60 cm). In mixed communities, *I. glabra*, *C. fasciculata*, and *P. graminifolia* had their roots only in the top 20 cm of soil. Two and four percent of *A. stricta* and *I. cylindrica* roots respectively were found at soil depth of 20 to 40 cm. Nineteen percent of the roots of *A. virginicus* occurred at this depth and six

percent occurred in the bottom 20 cm. Only one percent of the *I. cylindrica* roots reached the bottom. The distribution of *A. virginicus* roots was relatively the same in monoculture and in mixed communities.

Discussion

Previous work, using *I. cylindrica* as a model invasive plant, showed no relationship between community properties and resistance to invasion (Collins et al. 2006). It had been suggested that properties of the exotic species, including its extensive rhizome network, tolerance of low fertility, and low light compensation point allowed its invasive success regardless of the community's composition (Collins et al. 2006). However, extrinsic factors such as disturbance and varying soil fertility may have precluded a relationship between *I. cylindrica* invasion and community properties. In this controlled mesocosm experiment, most of the identifiable extrinsic factors were eliminated and still no relationship between diversity and invasion were observed ($R^2 = 0.12$, $p = 0.32$).

Increasing the cover of native species, within each mesocosm community, resulted in a decrease in the cover of *I. cylindrica*, a negative relationship, which likely was due to a decrease in available light. Although *I. cylindrica* can survive in the shade [Ramsey et al. (2003) reported a light compensation point of 32 to 35 $\mu\text{mol m}^{-2}\text{s}^{-1}$], it is best adapted for full sun conditions (Hubbard et al. 1944). Several studies have demonstrated that as light penetration increases so does invasion success (Knops et al. 1999; Milbau et al. 2005). Thomsen and D'Antonio (2007) showed that in native Californian grass monocultures, as light penetration decreased as a result of increased cover, the number of the European perennial grass, *Holcus lanatus*, seedlings and culms decreased.

The observed negative relationship between *I. cylindrica* and native cover could simply be the result of the short duration of the study. Data collection ceased at the end of August, four months after *I. cylindrica* was introduced. Had we pursued the study for multiple growing seasons, there was a possibility that the trend would disappear. Patterson (1980) suggests that *I. cylindrica* can adapt to changes in light level through changes in specific leaf area and leaf area ratio, thus with time the invasive could adjust, survive and even maintain some cover in conditions of increased cover by native species. Field observations in mature forests, however, reveal that *I. cylindrica* generally is limited to forest edges and tree-fall light gaps, where there is ample light penetration.

It was also observed that *I. cylindrica* biomass decreased logarithmically with increasing native biomass. When the native species had accumulated a dry biomass of approximately 50 g, the biomass of *I. cylindrica* decreased dramatically. Because both native species biomass and cover were significantly related with *I. cylindrica* invasion, these results suggest that there may be a crowding effect. On small scales a crowding effect is commonly observed. Kennedy et al. (2002) demonstrated, over the course of two years in small experimental grassland plots, a greater than 90% reduction in invader cover, which they attributed to an increase in neighbors and a rise in crowding index. Community saturation happens quickly at small scales (Brown and Peet 2003), which results in plants competing more directly for space and resources (Huston 1999). Limited space and resources reduce the probability of invasion. On the shorelines of Rhode Island, invasive plants were successful regardless of the level of diversity because of bare space (Bruno et al. 2004). With greater than 60% of *I. cylindrica* biomass occurring belowground (Sajise 1976), space, especially in a containerized mesocosm, would be a factor. It is likely that a crowding effect would occur.

With increasing species richness, there is an increase the probability that a community has a particular functional group that aids the community's resistance, a sampling effect (Pimm 1991). The grass group, including *A. stricta* and *A. virginicus*, demonstrated the greatest resistance to invasion by reducing *I. cylindrica* cover by 90% and its biomass by 98% compared to the control. When combined with the other functional groups, the grasses performed nearly as well, reducing *I. cylindrica* biomass by 95%. This result suggests that as long as there are grasses within a community's composition, some resistance to *I. cylindrica* will occur. Dukes (2001) tested the impacts of functional groups on the biomass of the invader *Centaurea solstitialis* and found that in combination, four functional groups reduced community invasibility, which he attributed to reductions in resource availability.

The forbs mix and shrub treatments were less successful in resisting invasion. The shrubs treatment was not significantly different from the control in terms of *I. cylindrica* cover. Of the functional groups that were tested, the forbs mix treatment reduced *I. cylindrica* biomass the least (29%) compared to the control. The lack of resistance by these two treatments are likely due to the fact that both averaged the least amount of native cover throughout the summer compared to all nine treatments that had native species, which suggests that increased light availability may have favored *I. cylindrica*.

Light availability may not be the sole reason for *I. cylindrica* success. These functional groups may be facilitating the growth of *I. cylindrica*. The forbs mix group was composed of a legume (*C. fasciculata*) and an *Asteraceae* (*P. graminifolia*), two plant types that have been shown to facilitate invasion. In Mediterranean old fields, it was shown that two *Conyza* species' biomass and net fecundity increased with the presence of legumes, while *Asteraceae* favored its survival (Priour-Richard et al. 2002). *C. fasciculata*'s effect on nitrogen availability may play a

role in *I. cylindrica* success. Alone, forbs could facilitate invasions, but their role as facilitators are reduced in functionally mixed communities. The presence of forbs in the functionally mixed communities may be the reason why the mixed communities were not as resistant as the grass only treatments.

Based upon the biomass and cover of *I. cylindrica* at the end of the study (Table 3-3), it was clear that the grasses were the most resistant functional group. A temporal examination of the mesocosms revealed that *I. cylindrica* spread was fastest in the *I. glabra* treatment over the course of the summer, with the cover increasing by 16.4%. All the mesocosms containing forbs allowed *I. cylindrica* to spread at approximately same rate (increasing *I. cylindrica* cover by 7 to 10%). The four best performing treatments, with *I. cylindrica* spreading the slowest, all contained grasses (the 3-species, 5-species, grasses, and *Andropogon virginicus* monoculture treatments). Community resistance thus appears to be a sampling effect with all treatments that contain grass being resistant.

The results reveal, however, that not all grasses equally resist *I. cylindrica* invasion. For example, in the *A. stricta* monoculture treatment, *I. cylindrica* cover increased by 15.7% over the course of a month (from the middle of July to middle August; Figure 3-4). The sampling effect that we observed may be a matter of communities containing *A. virginicus*. The three treatments that had *A. virginicus* had the strongest resistance to *I. cylindrica* and none of these had *I. cylindrica* cover increase by more than 1%. In fact, the *A. virginicus* monoculture treatment saw a decrease in *I. cylindrica* cover by 0.25%. This was mostly due to *I. cylindrica* mortality. Because the presence of *A. virginicus* dictated a community's resistance to *I. cylindrica*, our work suggests that a community's resistance to invasion is a matter of species identity and not richness. As long as a community's composition includes *A. virginicus*, it should have some

resistance regardless of its richness or functional diversity. Species identity has also been shown to dictate a community's resistance to invasion in a perennial grassland in the United Kingdom (Crawley et al. 1999), a Californian winter annual grassland (Robinson et al. 1995), a Californian coastal prairie (Thomsen and D'Antonio 2007), a Californian serpentine grassland (Hooper 1998), and amongst mycorrhizal communities in Hawaii (Stampe and Daehler 2003).

The success of grasses and in particular *A. virginicus* against an exotic grass suggests that resistance comes from native species that are similar in function as the exotic. The invasive nature of *I. cylindrica*, in general, has been attributed to its competitive interactions belowground with its extensive rhizome network. *I. cylindrica* retains a large amount of biomass belowground [40 Mg per hectare according to Terry et al. (1997)], which occupies large amount of physical space and surface area for nutrient absorption. Whether in monoculture or in mixed communities, *A. virginicus* had the greatest root length, RLD, and SRL of all the native species that were tested. These values exceeded that of the *I. cylindrica* rhizomes. With the greatest root length, *A. virginicus* was the most competitive at accessing new areas in the soil profile for resources. With the highest RLD, *A. virginicus* occupied the greatest volume of soil as well. Given these two conditions, it can compete heavily for belowground resources. Apparently, *A. virginicus* uses the same belowground competitive strategy that *I. cylindrica* uses as its invasion strategy.

The idea that resident species resist species functionally similar to themselves has been shown in several studies (Fargione and Tilman 2005). Fargione et al. (2003) showed that species from the same functional guild as the invader had the greatest negative effect on the invader cover. In monocultural microcosms, in which the invader *Centaurea* was introduced, the most effective competitor was a similar summer-active annual forb (Dukes 2002). In an experimental

grassland, the two species that most strongly predicted the composition in a community were similar in growth form and history (Crawley et al. 1999).

Andropogon virginicus also proved to be a successful competitor with other species by displaying little root morphological plasticity between the monoculture and mixed community treatments. While the other native species showed reduction in root length, RLD and SRL, *A. virginicus* maintained statistically similar values for both monoculture and mixed community treatments. Interspecific competition did not affect the morphology and distribution of *A. virginicus* roots. We also observed that *A. virginicus* maintained the same proportion of roots throughout the soil profile of the mesocosms, while interspecific competition limited the roots of other native species to the uppermost part of the soil column. *A. virginicus* extensive roots and position in the soil profile suggest that the species was dominant in the belowground environment as well.

Comparison of *A. virginicus* to *A. stricta* in the treatments that contained both species showed that *A. virginicus* accumulated more biomass (Figure 3-5). In the grass treatment, 87% of the total biomass belonged to *A. virginicus*, dominating over *A. stricta* and in the 5-species treatment, the largest portion of the total biomass (57%) belonged to *A. virginicus*. *A. stricta* was never the dominant species. Fargione and Tilman (2003) observed a similar trend in grasslands, with C₄ bunchgrasses dominating and occupying 50% of the biomass. It was these bunchgrasses that were involved in inhibiting invaders. Having such a dominant species in a community's composition may benefit a community by increasing its resistance to invaders. In a California winter annual grassland, dominance by one species of *Bromus* reduced the invasibility of the native ruderal, *Eschscholzia californica* (Robinson et al. 1995). The same study demonstrated that in the absence of *Bromus*, more invasions occurred. These works suggest that a

community's resistance to invasion depends on having a particular dominant species that can outcompete the invader. Our study demonstrates that a dominant native species can resist invasion through the same mechanisms that make the introduced species invasive. Resistance, then, is a matter of species identity.

One criticism of this work may be related to the fact that only a single introduction of *I. cylindrica* was made to each mesocosm and that the results do not account for propagule pressure. Several studies have indicated that propagule pressure lead to increased invader richness and success despite the levels of richness of the native species (Tilman 1997; Lonsdale 1999; Levine 2000). Brown and Peet (2003) found greater success of invasion with high propagule pressure in riparian areas of high diversity. With *I. cylindrica* being such a prolific seeder, multiple introductions to a small-scale area are probable. However much of *I. cylindrica* spread is belowground and encroachment into new communities usually happens through single rhizome fragments or single seedlings, which then develops into circular patches.

The result of this work has implications for restoration of areas that have been invaded by *I. cylindrica*. Countless studies have been done examining methods of control, whether by mechanical, cultural, biological, or chemical means (Macdonald 2004). Jose et al. (2002) suggested that an integrated approach that utilizes all the available methods such as mechanical, chemical and biological may be necessary to control *I. cylindrica* infestations. The results of this study suggest that the proposed integrated management could be taken a step further. Following herbicide application, *A. virginicus* could be considered as a possible cover crop in sandhill communities. By doing this, there is insurance of the return of native species to the infested areas as well as preventing future infestations and spread of this troublesome weed.

Conclusions

This work demonstrates evidence of negative relationships between the biomass and cover of native species and *I. cylindrica*. Grasses proved to be the most resistant functional group providing resistance alone and in mixed functional communities. Repeated measures analysis demonstrated that treatments including *A. virginicus* were the most resistant to invasion over time, suggesting that resistance is a matter of species identity and the diversity-invasibility hypothesis held true by means of the sampling effect. The success of *A. virginicus* can be attributed to it having significantly greater root length, RLD and SRL than all of the native species and *I. cylindrica* in monocultures. The same trends were observed of *A. virginicus* in mixed communities. The root morphology characteristics allow it to be a strong competitor belowground where *I. cylindrica* is most aggressive. The native grass is able to compete with the invasive by utilizing the same growth and competitive strategies. Future work should explore using more functionally similar species to an invasive in testing community resistance. Bunchgrasses were used in this experiment, however, grasses that spread clonally by rhizomes should be tested with *I. cylindrica*, which may result in even greater resistance to invasion. The implications of this work are that *A. virginicus* should be planted to prevent invasion and in restoration areas following treatments of *I. cylindrica*.

Table 3-1. Summary of the ten treatments used.

Treatment	Functional group(s)	Richness
Control		0
A. stricta monoculture	Grass	1
A. virginicus monoculture	Grass	1
I. glabra monoculture	Shrub	1
C. fasciculata monoculture	Forb	1
P. graminifolia monoculture	Forb	1
Grass mix - A. stricta and A. virginicus	Grasses	2
Forbs mix - C. fasciculata and P. graminifolia	Forbs	2
3-Species A. stricta, I. glabra, and C. fasciculata	Grass, Shrub, Forb	3
5-Species A. stricta, A. virginicus, I. glabra, C. fasciculata, and P. graminifolia	Grass, Shrub, Forb	5

Table 3-2. Analysis of variance of measurements taken at the end of the study between all treatments of by functional group.

	Source of variation	df	F	P
Native biomass	All treatments	9	2.409	0.0352
I. cylindrica biomass	All treatments	9	2.703	0.0203
	By functional group	2	0.794	0.4636
I. cylindrica cover	All treatments	9	4.965	<0.0001
	By functional group	2	3.078	0.0544
I. cylindrica shoots	All treatments	9	8.253	<0.0001
	By functional group	2	8.4526	0.0007

Table 3-3. Summary of the *I. cylindrica* shoots, cover and biomass in the functional group treatments as well as the reduction of these values from the control. Significantly different means are accompanied by different letters ($\alpha = 0.05$).

	Number of <i>I.</i> <i>cylindrica</i> Shoots	% <i>I.</i> <i>cylindrica</i> cover	% <i>I.</i> <i>cylindrica</i> cover reduction	<i>I.</i> <i>cylindrica</i> biomass	<i>I.</i> <i>cylindrica</i> biomass reduction
Control	18.1(0.9) a	29.6(4.7) a	0	84.8(29.8)	0
Forbs mix	7.9(2.2) b	12.5(4.1) bc	58	60.3(45.4)	29
Grass mix	1.1(0.3) c	3.0(0.3) c	90	1.2(0.03)	98
Shrubs	9.7(2.4) b	21.2(5.9) ab	28	31.9(8.6)	62
Forbs+grasses+shrubs	2.2(0.4) c	5.0(0.8) c	83	3.9(2.2)	95
df	4	4		4	
<i>F</i>	25.82	11.56		3.17	
<i>P</i>	<0.0001	<0.0001		0.06	

Table 3-4. Summary of root length, root length density and specific root length means(SE) for the native species and *Imperata cylindrica* in a) monoculture and in b) mixed communities. Significantly different means are accompanied by different letters ($\alpha = 0.05$).

a)			
Species	Root Length (cm)	RLD (cm cm ⁻³)	SRL (cm/g)
<i>A. stricta</i>	107362(65900) ab	1.17(0.75) ab	1084(280) ab
<i>I. glabra</i>	68796(11228) b	0.55(0.05) ab	562(80) bc
<i>C. fasciculata</i>	4544(1149) b	0.08(0.01) b	264(56) c
<i>P. graminifolia</i>	7010(1820) b	0.12(0.02) b	772(153) bc
<i>A. virginicus</i>	226800(54089) a	1.97(0.54) a	1841(244) a
<i>I. cylindrica</i>	7631(4020) b	0.07(0.03) b	119(37) c
p-value	0.0017	0.0109	<0.0001
b)			
Species	Root Length (cm)	RLD (cm cm ⁻³)	SRL (cm/g)
<i>A. stricta</i>	23834(9570) b	0.23(0.104) b	1052(148) b
<i>I. glabra</i>	1383(897) b	0.03(0.02) b	110(37) bc
<i>C. fasciculata</i>	1768(529) b	0.03(0.013) b	300(173) bc
<i>P. graminifolia</i>	1694(223) b	0.03(0.005) b	1087(241) b
<i>A. virginicus</i>	212427 a	1.83(0.945) a	2691(715) a
<i>I. cylindrica</i>	606(353) b	0.005(0.003) b	31(6) a
p-value	0.0012	0.0001	<0.0001

Table 3-5. Percentage of total roots accounted for each species by depth in the soil profile.

Species	In monoculture			With competition		
	0-20 cm	20-40 cm	40-60 cm	0-20 cm	20-40 cm	40-60 cm
<i>A. stricta</i>	87.5	12.5	0	98	2	0
<i>I. glabra</i>	59.5	28.75	11.75	100	0	0
<i>C. fasciculata</i>	98.25	1.75	0	100	0	0
<i>P. graminifolia</i>	91	9	0	100	0	0
<i>A. virginicus</i>	77.5	17	5.5	75	19	6
<i>I. cylindrica</i>	75	24	1	95	4	1

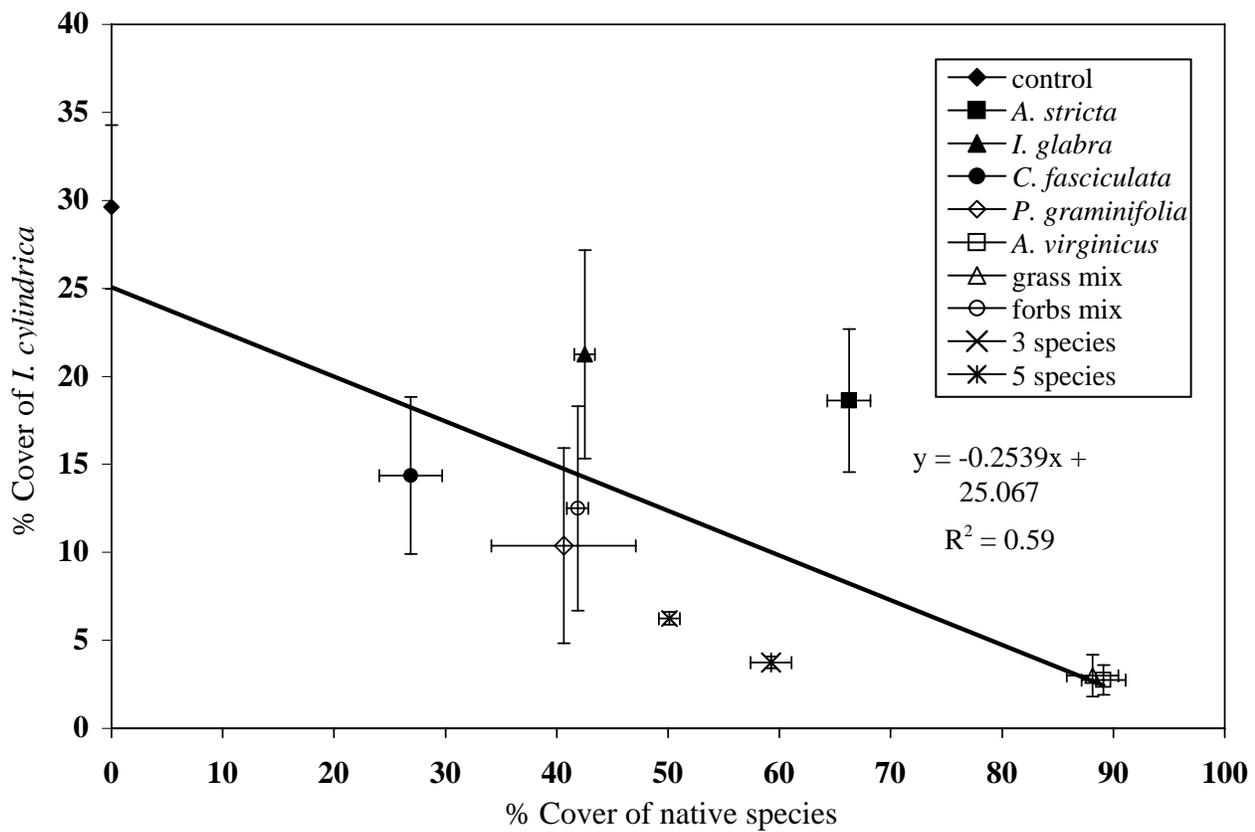


Figure 3-1. Relationship between % cover of native understory species treatment means and mean % cover of *Imperata cylindrica*.

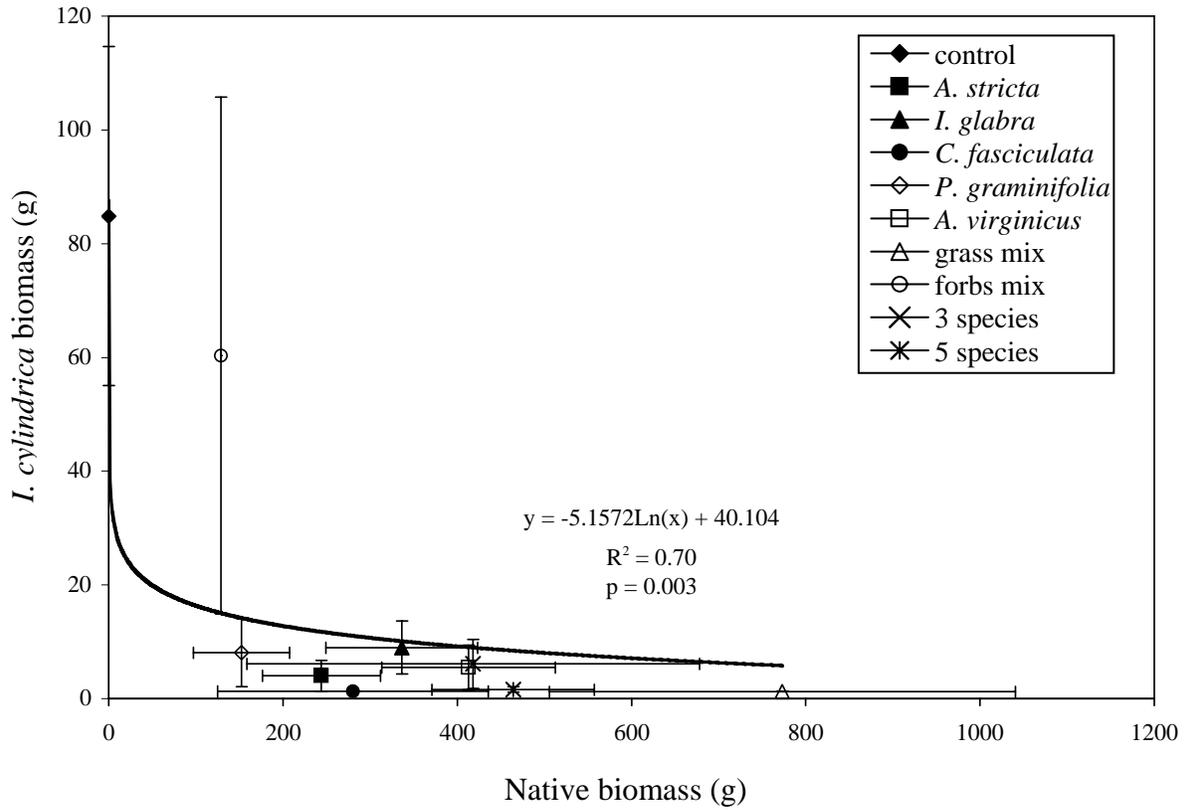


Figure 3-2. Relationship between native treatment total biomass means and biomass of *Imperata cylindrica*.

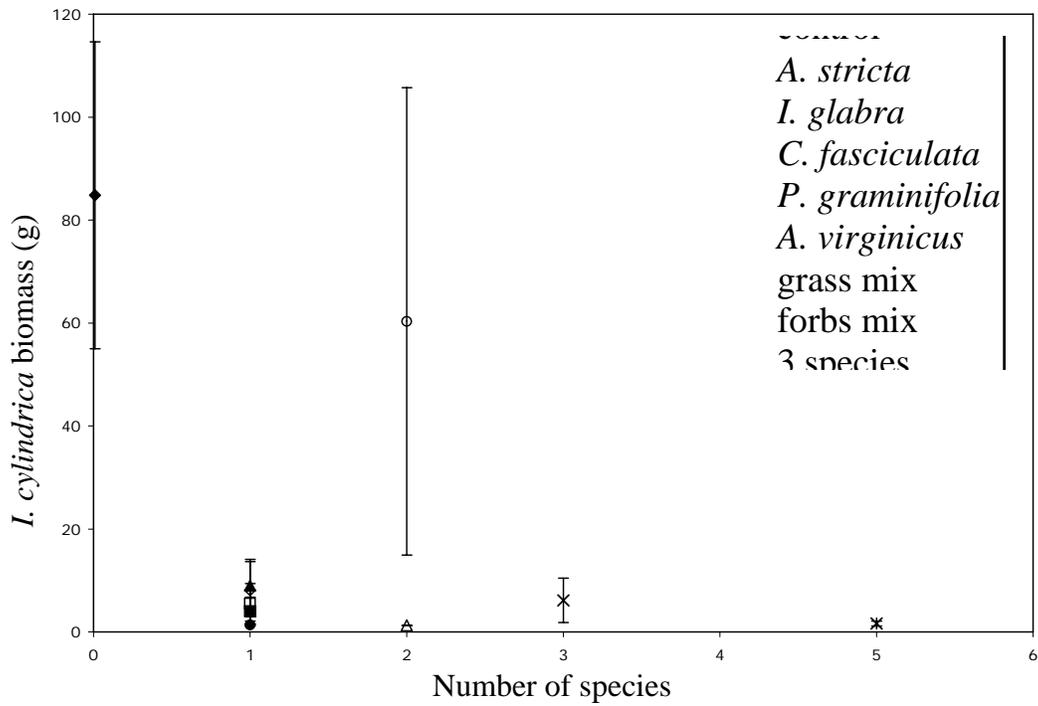


Figure 3-3. Relationship between species richness as represented by species number and *Imperata cylindrica* biomass.

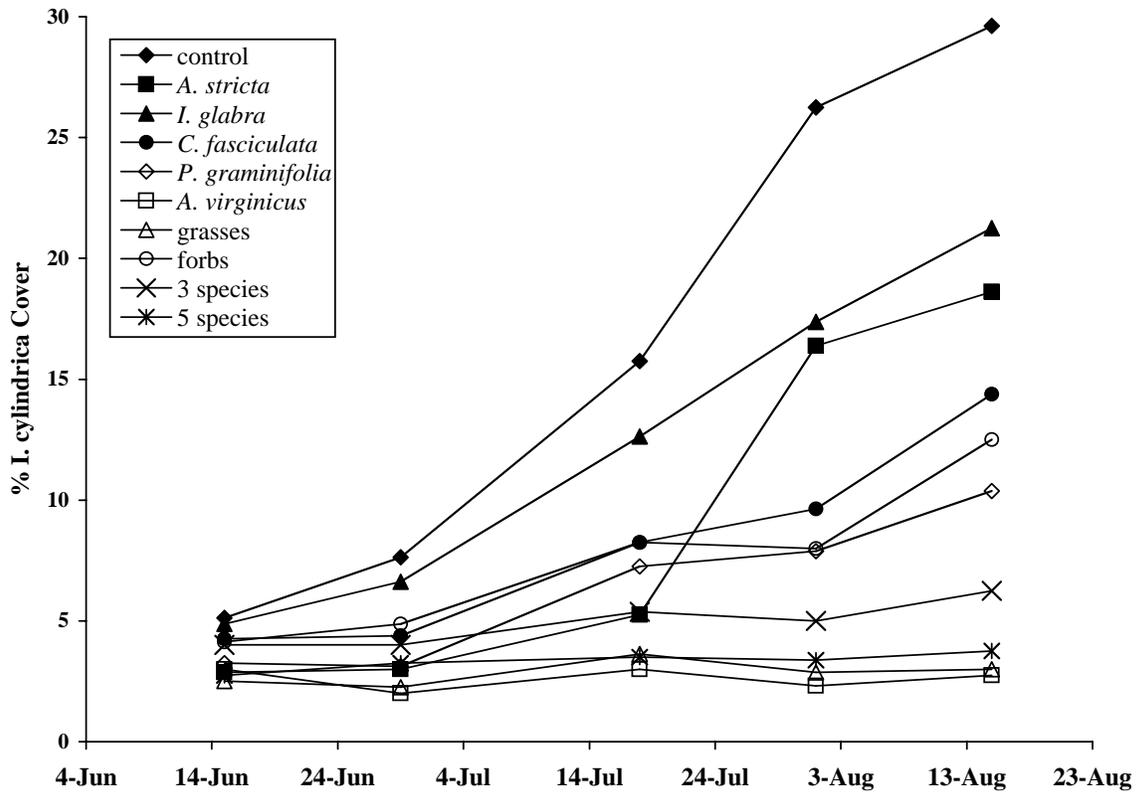


Figure 3-4. Percent cover of *Imperata cylindrica* in each mesocosm for the ten treatments in the summer of 2005.

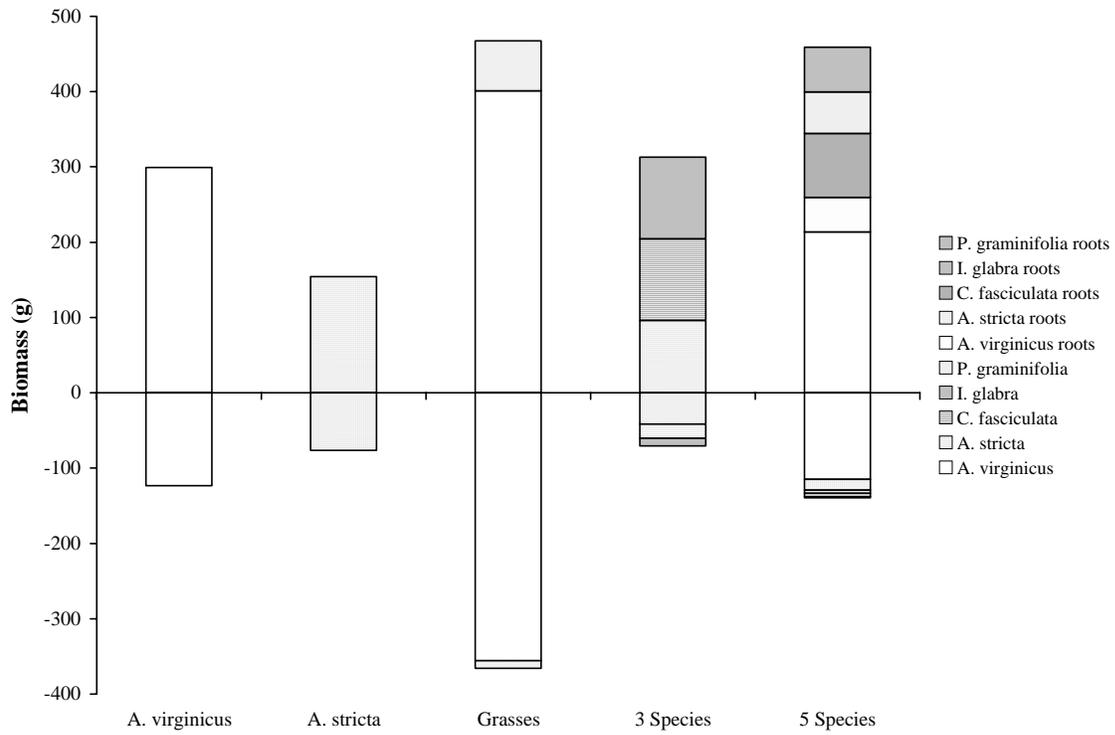


Figure 3-5. Above and belowground biomass means of native species in all the grass containing treatments.

CHAPTER 4
IMPACTS OF *Imperata cylindrica*, AN ALIEN INVASIVE GRASS, ON THE
PRODUCTIVITY OF AN ESTABLISHING PINE FOREST

Introduction

Invasion by non-indigenous species can have major impacts on native ecosystems with both ecological and economic consequences (Mack et al 2000). The structure and function of an ecosystem can be altered by the presence of an exotic invasive (Vitousek et al. 1997) due to changes in system-level rates of resource supply, trophic structure, and disturbance regime (D'Antonio and Vitousek 1992). Such changes are clear in forests, where invasive plants affect the establishment, growth and productivity of new seedlings, which represent the future canopy species.

Several studies have been conducted testing the impacts of invasive plants on forest regeneration and growth and the mechanisms by which they do so. In Hawaii, it was observed that the dominant native tree *Metrosideros polymorpha* was not able to establish a single seedling beneath the canopy of the invasive nitrogen-fixing *Myrica faya* due to physical characteristics of the leaf litter (Walker and Vitousek 1991). Increasing biomass of *Tradescantia fluminensis* led to an exponential decrease in the species richness and abundance of native forest seedlings in New Zealand by rapidly reducing the light availability (Standish et al. 2001). Competition for light was also implied to be the mechanism by which *Lonicera maackii* was reducing survival and biomass of *Acer saccharum* in Ohio, USA (Gorchov and Trisel 2003). The shrub *Rhamnus frangula* reduced the growth and survival of *Acer rubrum*, *Acer saccharum*, *Fraxinus Americana* and *Pinus strobus* in New Hampshire, USA, which the authors suggested might be due to belowground competition from *Rhamnus* with its extensive shallow root system (Fagan and Peart 2004).

A species that is making a significant impact on forests in Southeastern United States is *Imperata cylindrica*, (cogongrass), a perennial, rhizomatous grass thriving in both undisturbed and disturbed areas with soil types ranging from nutrient-poor, coarse sands to nutrient-rich, sandy loams (Jose et al. 2002). *I. cylindrica* spreads by both sexual and asexual mechanisms. *I. cylindrica* is a prolific producer of seeds, with as many as 3000 1-millimeter long grains per plant, which generally are dispersed within 15 m of the plant (Holm et al. 1977), but may be carried by wind up to 24 km over open country (Hubbard et al. 1944). Established plants spread vegetatively through rhizomes, long tough, white underground stems with short internodes. They comprise over 60% of the plant's biomass, resulting in a high root/shoot ratio that allows it survive and thrive after fire or cuttings (Sajise 1976). Regeneration of new plants can occur from rhizome fragments weighing as little as 0.1 g (Ayeni and Duke 1985). The extensive growth of *I. cylindrica* results in dense mats of rhizomes in the soils forming dense monocultural patches with fresh weights ranging up to 40 Mg per hectare (Terry et al. 1997), producing approximately 4.5 million shoots (Soerjani 1970).

Imperata cylindrica can negatively affect forests in a variety of ways. The density of the belowground rhizome network makes *I. cylindrica* a mechanical hindrance to growth of roots of native species. The rhizome tips are sharp; they may even penetrate the roots of native species leading to damage or mortality by infection (Eussen and Soerjani, 1975). *I. cylindrica* occupies a significant of space belowground, which may prevent root growth of germinating seeds. Lippincott (1997) showed that *I. cylindrica* replaced most understory species in a Florida sandhill savanna and greatly reduced the diversity. The leaf blades of *I. cylindrica* have been observed to reach heights of 1.5 m under good moisture and fertility conditions (Holm et al 1977), which suggests that *I. cylindrica* may compete for light on the forest floor especially with

understory species and young tree seedlings. The dense carpet of leaf blades may prevent sun light from reaching the upper soil layer, eliminating the opportunity for seedling germination.

Allelopathy has been suggested to be another mechanism by which *I. cylindrica* gains dominance over native species. Several studies have demonstrated the impacts of *I. cylindrica* extracts on the germination, growth and survival of crop plants (Hubbard et al. 1944; Soerjani, 1970; Eussen et al. 1976). It was shown that *I. cylindrica* suppressed tomato (*Solanum lycopersicum*) and cucumbers (*Cucumis sativus*) especially at low pH (Eussen and Wirjahardja 1973). Koger and Bryson (2004) demonstrated that extracts of *I. cylindrica* roots and foliage with concentrations as low as 0.5% inhibited germination and *Cynodon dactylon* (L.) and *Lolium multiflorum* Lam. by up to 62%.

Imperata cylindrica has been shown to alter disturbance regimes of forests. Lippincott (2000) suggests that fires from swards of *I. cylindrica* burn at high temperatures reaching 450° C and at greater heights. If fires this hot persist longer than a few seconds in any given area, not only will the understory species die, but also the juvenile trees. Mortality was even observed for longleaf pine juveniles (*Pinus palustris*), which normally are fire tolerant (Lippincott 2000). Because *I. cylindrica* allocates significant carbon belowground, it is able to recover quickly after fire, which is why Lippincott (2000) suggests that frequent intense fires can convert a pine savanna into a *I. cylindrica* dominated grassland. *I. cylindrica* is also favored by disturbances other than fire. King and Grace (2000) showed that *I. cylindrica* can germinate, survive and grow in wet pine savanna communities after several types of disturbance including mowing, tilling, and light gaps created by cutting or natural stand mortality.

All the evidence thus far has demonstrated that *I. cylindrica* does pose a threat to forests by altering trophic structure and disturbance regime and by belowground interactions. Most of the

studies, however, have focused on the impacts of this invasive on crop or understory species and little on how it impacts the overstory canopy species. Pine forests throughout the southeastern United States are being impacted by *I. cylindrica* and little work has been done to quantify the impacts of the invasive on the pine themselves. In this study, we examined how *I. cylindrica* impacts the survival, growth and productivity of young loblolly pine seedlings (*Pinus taeda*) up to three years after planting. We compared how the seedlings performed in the absence of competition, with competition from native species and with competition from *I. cylindrica* using growth parameters and physiological measurements. With pine seedlings growing in the absence of competition as a reference for their growth potential for our site, we hypothesized that *I. cylindrica* competition would have a much greater impact on seedling growth and productivity than competition from native species by reducing their photosynthetic and growth rates.

Methods

Site Description

This field study was conducted on an industrial plantation site in Santa Rosa County, Northwest Florida, U.S.A. (30°50'N. 87°10'W). The site was a 60 ha cutover area (site index = 24.4m), which quickly became infested with *I. cylindrica* after harvesting of the 17-year-old loblolly pine in early 2002. The climate in this area is temperate with moderate winters and hot, humid summers. Total annual precipitation in 2003 was 1928 mm with the wettest month being June (418 mm) and the mean annual temperature was 19.4°C and with August being the hottest (27.3 °C) (NOAA). The soils on the site were mapped a Lakeland series of a Typic Quartzipsamment (89% sand, 7.8% silt, and 3.4% clay). Native species on the site included *Smilax rotundifolia*, *Smilax aspera*, *Rubus occidentalis*, *Ilex glabra*, *Andropogon virginicus*, *Asclepius veriegota*, *Carphephorus paniculatus*, *Ilex vomitoria*, and *Erechtites hierarifolia*.

Cultural Treatments

The experimental design consisted of 15 plots (7.9 x 10.4 m) in which the following three treatments were replicated five times:

VF: vegetation free- maintained by weekly hand weeding

NC: native competition- natural establishment and growth of native vegetation was allowed. The major native species on site included *Smilax rotundifolia*, *Smilax aspera*, *Rubus occidentalis*, *Ilex glabra*, *Andropogon virginicus*, *Asclepius veriegota*, *Carphephorus paniculatus*, *Ilex vomitoria*, and *Erechtites hierarifolia*.

IC: *I. cylindrica* competition- a dense *I. cylindrica* monocultural patch from local seed or rhizome sources

In fall 2002, a uniform patch of *I. cylindrica* of about 1 ha in size was selected for the five IC treatment plots. The VF and NC treatment plots were randomly established in an area 20 m away from the advancing front of the *I. cylindrica* patch. The 20 m buffer zone was considered appropriate since *I. cylindrica* spread had been estimated to be about 2 m per year at this site (Collins et al. 2006). All the plots, except for the IC treatment, were site prepared in October 2002 with a tank mix of imazapyr and triclopyr at a rate of 936.2 ml ha⁻¹ in order to ensure that there was no *I. cylindrica* infestation. All treatment plots had a 3 meter buffer around them. Because of the close proximity of the plots (all were within an area approximately 2 ha), the soil conditions were assumed uniform before installment of the treatments. On March 6, 2003, 1-yr-old bareroot loblolly pine seedlings, purchased from a local nursery, were planted in four rows of eight seedlings in each plot (32 seedlings per plot) with spacing of 1.1m x 2.0 m. Seedlings were fertilized with Ammonium Sulfate fertilizer at the rate of 55kg N per ha in March 2003. Four randomly selected seedlings were fertilized with ¹⁵N labeled Ammonium Sulfate (5% enrichment) at the same rate for a companion project (Daneshgar et al. 2007).

Growth and Gas Exchange Measurements

The root collar diameter (RCD) and height were measured for every seedling at planting and re-measured at the end of the growing season in 2003, 2004 and 2005. These values were used to calculate stem volume index (SVI; $RCD^2 \cdot \text{height}$). Seedling survival was quantified during each measurement period. In December 2003 and June 2005, four seedlings from each plot were harvested. The needles of all the seedlings harvested in December 2003 were scanned with a LI 3100 leaf area meter (LiCor Inc., Lincoln, NE, USA) to estimate total leaf area. The roots, leaves and stems of all the harvested seedlings were separated, dried at 65°C for 72 hours and weighed. The dried foliage of the December 2003 harvest was ground using a Wiley Mill to pass through a 1 mm screen. Foliar N concentration was determined using an isotope ratio mass spectrometer (UC Davis Stable Isotope Laboratory) since we also quantified foliar ^{15}N of the same samples for the companion study (Daneshgar et al., 2007).

Light saturated net photosynthesis (A_{max}), stomatal conductance (g_s), and internal leaf CO_2 concentration (C_i) of four pine seedlings per plot, were measured using a portable open leaf gas exchange system (LI-6400, LiCor Inc., Lincoln, NE) with a photosynthesis photon flux density (PPFD) of $1600 \mu\text{mol m}^{-2} \text{s}^{-1}$ and a flow rate of $500 \mu\text{m/s}$ of CO_2 with a reference concentration of 370ppm. Measurements were taken between the 1000 and 1400 hours, monthly from July 2003 through October 2003. The uppermost fully developed needles were measured. Approximately three fascicles (9 needles) were utilized for each measurement. The gas exchange measurements were recalculated using the total surface area of the needles, which was calculated based on the assumption that each fascicle was a cylinder (Madgwick 1964).

Water Potential Measurements

At a companion study site adjacent to the study plots, tensiometers (Soil Measurement Systems, Tuscon, AZ) were used to measure water potential in three identical treatments. Four tensiometers were placed in the ground in each treatment (12 total), two at a depth of 30 cm and two at 60 cm . The tensiometers were refilled with water after each measurement.

Statistical Analysis

Seedling productivity and growth parameters (height, RCD, SVI, biomass, specific leaf area, and light saturated photosynthesis) were compared for the three treatments. One-way analysis of variance (ANOVA) was used to detect differences in the means with PROC GLM of the SAS statistical software package. (SAS Institute, Cary, NC 1999). Differences were declared significant at $\alpha < 0.05$. Using SAS, Levene's test for homogeneity among variances was used to determine which pairwise post hoc comparison method should be used. For homogenous variances, Duncan's post hoc test was used; for heterogeneous variances, Dunnett's T3 test (Dunnett 1980) was used.

Results

Survival and Growth

At the end of the study, approximately 27 months after planting, only 26% of the seedlings growing in the IC treatment survived compared to 51 and 61% survival observed in the NC and VF treatments, respectively (Table 4-1). At planting, the seedling mean root collar diameter was 4.23 mm and grew to 31.5, 13.4, and 5.9 mm for the VF, NC, and IC treatments, respectively ($p < 0.0001$) (Figure 4-1a) by the end of the study. The root collar diameter differed twenty months after planting ($p < 0.0001$). Mean seedling height at the start of the study was 27.7 cm and grew to 136.6, 75.7, and 50.8 cm by the end of the study for the VF, NC, and IC treatments, respectively ($p < 0.0001$) (Figure 4-1b). The seedling heights for the IC and NC

treatments did not differ after the first growing season, but did so by the end of the second growing season ($p < 0.0001$). Mean SVI for the seedlings in all treatments was 4.95 cm^3 at planting and rose to 1455.8, 158.6, and 21.8 cm^3 for the VF, NC, and IC treatments, respectively ($p < 0.0001$) (Figure 4-1c). The SVI did not differ between the IC and NC treatments until the second growing season ($F = 44.63$, $p < 0.0001$).

Above and Belowground Biomass

After one full growing season, pine seedlings growing in the VF treatment had a mean foliar, stem and root biomass that differed from the other two treatments ($p < 0.0001$) (Figure 4-2). Foliar and stem biomass did not differ between the NC and IC treatments. Only the root biomass differed between the two ($p < 0.0001$). By the end of the third growing season, all treatments showed significant differences in foliar ($p < 0.0001$), stem ($p < 0.0001$) and root biomass ($p < 0.0001$) (Figure 4-2). Seedlings in the VF treatment had the highest biomass ($612 \pm 79.9 \text{ g}$) followed by NC ($83.3 \pm 12.8 \text{ g}$) and IC ($14.0 \pm 3.8 \text{ g}$) treatments, with significant differences ($F = 59.4$, $p < 0.0001$) detected among them.

Gas Exchange and Leaf Characteristics

There was significant difference in A_{max} between the treatments throughout the summer of 2003 (Figure 4-3). The A_{max} summer means were 3.97, 5.07 and $5.85 \mu\text{mol m}^{-2}\text{s}^{-1}$ for the IC, NC and VF treatments, respectively ($p = 0.0006$). The seedlings growing in the IC treatment maintained the lowest levels of A_{max} each month and always differed significantly from the seedlings growing in the absence of competition (Figure 4-4).

Stomatal conductance of the pine seedlings in the VF treatment was higher than the other treatments, but was only significantly higher than the IC treatment ($p = 0.0157$) (Figure 4-3). There was no significant differences in the summer means of the three treatments for pine seedlings internal CO_2 .

After one growing season, the seedlings in the VF treatment had significantly greater total leaf area and specific leaf area (SLA) than the other two treatments ($p < 0.0001$) (Table 4-2). There was no difference in leaf area and SLA between the NC and IC treatment seedlings. The pine seedlings in the IC treatment had the lowest nitrogen concentration ($p = 0.0004$) compared to the other two treatments, which were not significantly different.

Discussion

Competition from native species and *I. cylindrica* prevented the pine seedlings from reaching the full growth potential that was observed in the VF treatment. It was evident, as early as nine months after planting, that competition limited the growth of loblolly pine seedlings. The seedlings growing in the presence of competition had reduced height, diameter and mean SVI compared to the seedlings in the VF treatment. The mean SVI of the NC treatment was 27% of the VF treatment, while in the IC treatment it was only 7%. Nine months after planting, the seedlings growing in NC and IC treatments reached only 21 and 11% the total biomass of the seedlings grown in the VF treatment, respectively. Competition reduced the root biomass the most, with the NC and IC pine seedlings growing to only 18 and 7% of VF treatment, respectively. These trends in growth continued through the end of the study. Height, RCD, and SVI for both NC and IC treatments were all less than half of what was observed in the VF treatment. The seedlings growing in the NC treatment had a total biomass that was 13% of their full potential, while in the *I. cylindrica* it was 2%. The greatest difference at this point was observed in the foliage biomass. Interspecific competition impacts on loblolly pine seedlings has been well documented in experiments using weed control to create competition free treatments (Britt et al. 1990, Cain 1991, Miller et al. 1991, Morris et al. 1993, Martin and Jokela 2004) and these results support previous findings that the growth of seedlings are heavily impacted by competing vegetation.

Because all seedlings experience a reduction in growth due to competition, the impacts of *I. cylindrica* on the pine seedlings are better seen when compared to the impacts of native vegetation. Nine months after planting, the IC treatment seedlings had a smaller mean root collar diameter (44% of NC) and smaller mean SVI (27% of NC). The total biomass of the seedlings grown in the IC treatment was 54% of what was measured in the NC treatment. For the growth parameters that were measured, the difference between the two treatments nine months after planting was not significant (with the exception of the root biomass and RCD). All the growth parameter measurements became significantly different between the two treatments by the end of the second growing season and the differences increased with time. By the end of the third growing season, the seedlings in the IC treatment had smaller diameters (44% of NC), lower SVI (15% of NC), were shorter in height (71% of NC) and had a much lower total biomass (18% of NC). Concerning the biomass, the foliage biomass of the seedlings in the IC treatment was most reduced compared to the NC treatment (12% of NC).

Competition, as demonstrated by both the NC and IC treatments, impacted the rates of photosynthesis of the young pines within the first year after planting. For the first three months of measurement, the seedlings growing free of competition maintained the highest rates of A_{max} . This conflicts with the findings of Green et al. (1991) who observed that competition control had no effect on 4-year-old loblolly pine photosynthesis and Munger et al (2003) who reported a decrease in loblolly pine light-saturated photosynthesis with competition control.

In October, pine seedlings in NC treatment exhibited their highest rate of A_{max} , a rate that was higher than the VF treatment. The IC treatment pine seedlings also showed increased level of photosynthesis compared to how they had been performing all season. This significant increase in A_{max} in the two treatments may be explained by the decrease in temperature (from

26.7 °C in the summer to 20.1 °C in October) or by dieback of competing vegetation. Because several of the competing species in the NC treatment were annuals, it is possible that their mortality at the end of the season would result in an increase in light, nutrients, and moisture, which would favor an increase in photosynthesis of the remaining species. As temperature declines, *I. cylindrica*, like most grasses, shifts its allocation of nutrients and biomass belowground, resulting in browning and death of the aboveground biomass. This may favor competing species that are still capable of photosynthesizing such as the pine seedlings.

The results of the gas exchange measurements demonstrated that *I. cylindrica* competition impacts the pine seedlings' physiological function greater than NC competition. Every month, the seedlings in the IC treatment had lower rates of light-saturated photosynthesis than other two treatments. The lower rates of photosynthesis were matched by lower stomatal conductance (g_s), suggesting that photosynthetic rate of the pine seedlings may be limited by greater stomatal limitation brought about by *I. cylindrica* competition. The stomatal limitations may have been due to water limitation caused by *I. cylindrica* invasion. At the companion study site, with the same three treatments, it was observed that *I. cylindrica* reduced water availability leading to the lowest soil water potential of the three treatments at multiple depths throughout the summer (Figure 4-5). The water stress was more severe at shallower depths, where most of the belowground biomass of *I. cylindrica* occurs (Holm et al. 1977).

Water limitation may play a role in the decreased photosynthetic capacity of pine seedlings, however, a stronger case may be made for nutrient deficiencies that result from *I. cylindrica* invasion. *I. cylindrica* was shown to decrease soil nitrate and potassium levels in invaded compared to non-invaded pine flatwoods (Collins and Jose, 2007). The invasive was shown to be more competitive for phosphorus than native pine-savanna species in the southern

U.S. (Brewer and Cralle 2003) implying that phosphorus levels in the soil may drop with the presence of this invasive species. The same study also demonstrated that the extent of *I. cylindrica* invasion was negatively correlated to the number of legumes present (Brewer and Cralle 2003), which would lead to the assumption that species that are capable of obtaining nitrogen from other sources (fixation) are able to compete with the grass. *I. cylindrica* thus, may be efficient at gathering nitrogen hindering competing species from absorbing nitrogen. Analysis of the foliar nitrogen concentration revealed that seedlings growing in IC treatment had significantly lower levels of nitrogen. Because a large proportion of nitrogen in the leaves occur in photosynthetic enzymes, reduced nitrogen concentrations in the IC pine seedlings may account for the reduced levels of photosynthesis. Several authors have demonstrated that capacity for photosynthesis correlates with leaf nitrogen concentration (Field and Mooney 1986, Reich et al. 1999, Henderson and Jose 2005), which was also observed in this study across the three treatments (Figure 4-6). The reduced levels of foliar nitrogen may also have contributed to the reduced total leaf area and specific leaf area (SLA) that were observed of the IC treatment seedlings. Reduced SLA and leaf area imply reduced light capturing ability and productivity, which explains why the biomass of the seedlings was reduced.

The decrease in photosynthesis in pines in the IC treatment, whether it was due to decreased nutrient or water stress, does indicate belowground stress caused by the invasive. It was demonstrated that *Liquidambar styraciflua* had reduced leaf photosynthetic capacity not only from aboveground competition with vines *Lonicera japonica* and *Parthenocissus quinquefolia*, but from belowground competition as well (Dillenburg et al. 1995). After a full growing season, the roots of the seedlings grown in the IC treatment were the most affected part of the seedling compared to the NC treatment. This suggests that in the presence of *I. cylindrica*

emerging juvenile trees deal with the greatest competitive stress belowground. *I. cylindrica* retains more of its biomass belowground (over 60% according to Sajise, 1976) which has been reported to be 5 to 10 times that of native understory belowground biomass in southeastern forests (Ramsey et al., 2003). This clearly indicates that the intensity of resource competition belowground between *I. cylindrica* and pine seedlings could be far greater than that between pine seedlings and native vegetation. Species that maintain high levels of density either above or belowground decrease the growth of competing trees. After one season, loblolly pine growing with *Andropogon virginicus* showed decreases in SVI with increasing density; 4 individuals/m² reduced SVI by 60% compared to a competition control and 16 individuals/m² reduced SVI by an additional 22% (Perry et al. 1993). *I. cylindrica* maintained greater than 90% cover of the ground in all the plots during the course of this study suggesting that its high density, both above and below, could be a factor in the reduced growth of pine seedlings.

Conclusions

Only recently, has attention been brought to the potential impact of *I. cylindrica* invasion on establishing forests. Though forest managers have acknowledged the negative effect of this species on new plantations (Jose et al 2002), this is the first work to demonstrate the impacts of *I. cylindrica* on establishing pines. Compared to native vegetation, competition from this alien grass leads to half the survival of pine seedlings after three years. Pine seedlings competing with *I. cylindrica* were significantly smaller in RCD, height and biomass than those competing with native species. We believe that *I. cylindrica* reduces the productivity of young pines by altering conditions (water and nutrient availability) belowground where its presence may be felt the most. We show some evidence here of *I. cylindrica* altering soil water availability and foliar nitrogen which causes reduction in photosynthetic capacity. Detailed examination of its impacts on

belowground resources is essential to fully understand the mechanisms responsible for the observed reduction in growth.

Table 4-1. Percent survival (%) of total loblolly pines seedlings planted in each treatments in March 2003.

Treatment*	Growing Seasons		
	1	2	3
VF	63	62	61
NC	62	57	51
IC	57	51	26

*Treatments: VF- vegetation free (no competition), NC- native competitor, IC- *I. cylindrica* competition

Table 4-2. Mean (SE) leaf area, specific leaf area (SLA) and % foliar nitrogen of 9-month-old loblolly pine seedlings for different treatments . Different letters represent significant differences in means ($\alpha = 0.05$)

Treatment	Total leaf area (mm ²)	SLA (mm ² /g)	%N
VF	3450.8(279.6) a	50.63(2.4) a	1.71(0.03) a
NC	631.1(223.8) b	14.58(4.6) b	1.57(0.09) a
IC	265.8(33.1) b	7.06(0.8) b	1.10(0.1) b
P-value	<0.0001	<0.0001	0.0004

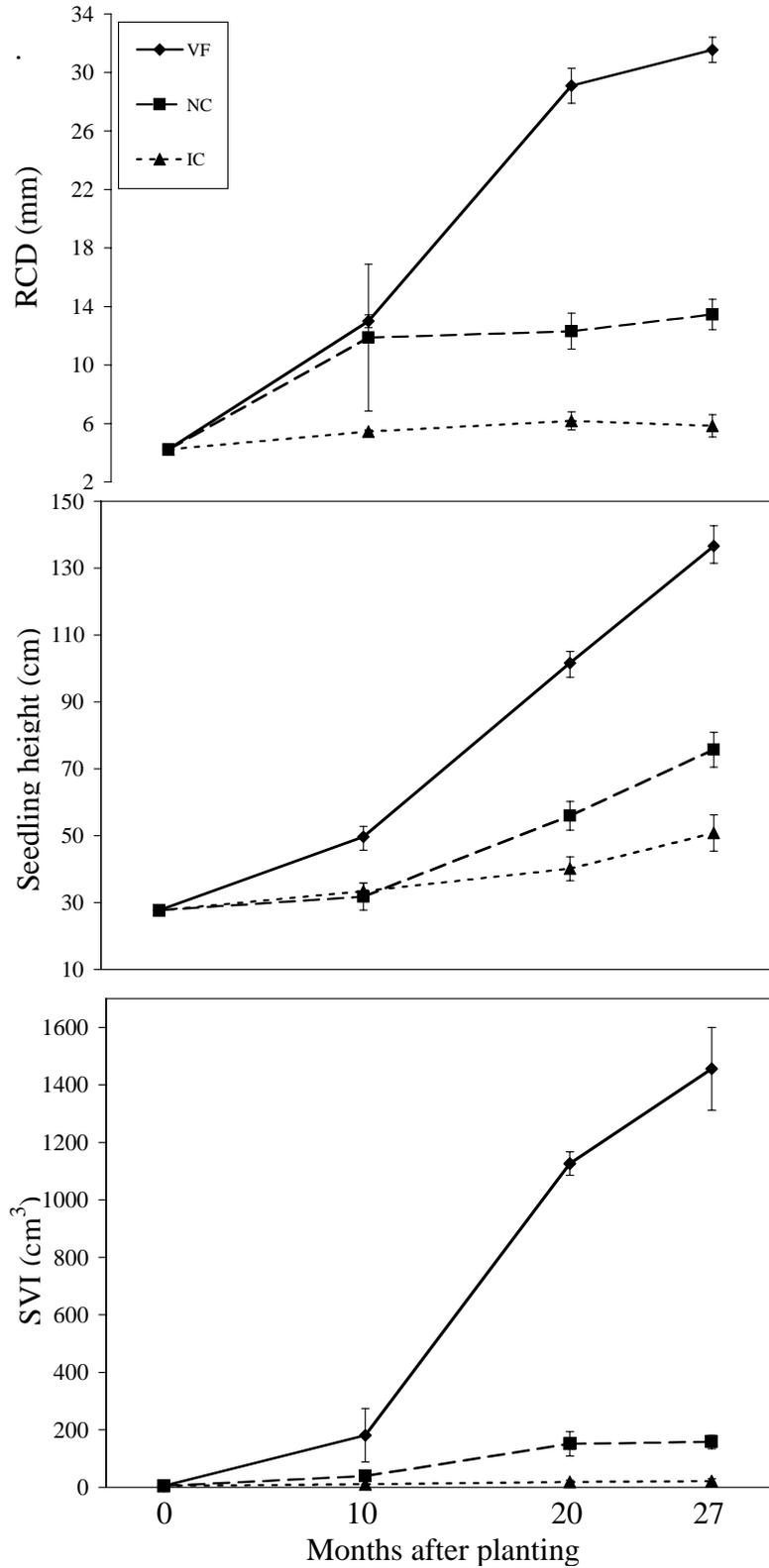


Figure 4-1. Pine seedling root collar diameter (RCD), height, and stem volume index (SVI) means(SE) for the three treatments from planting through the end of the study.

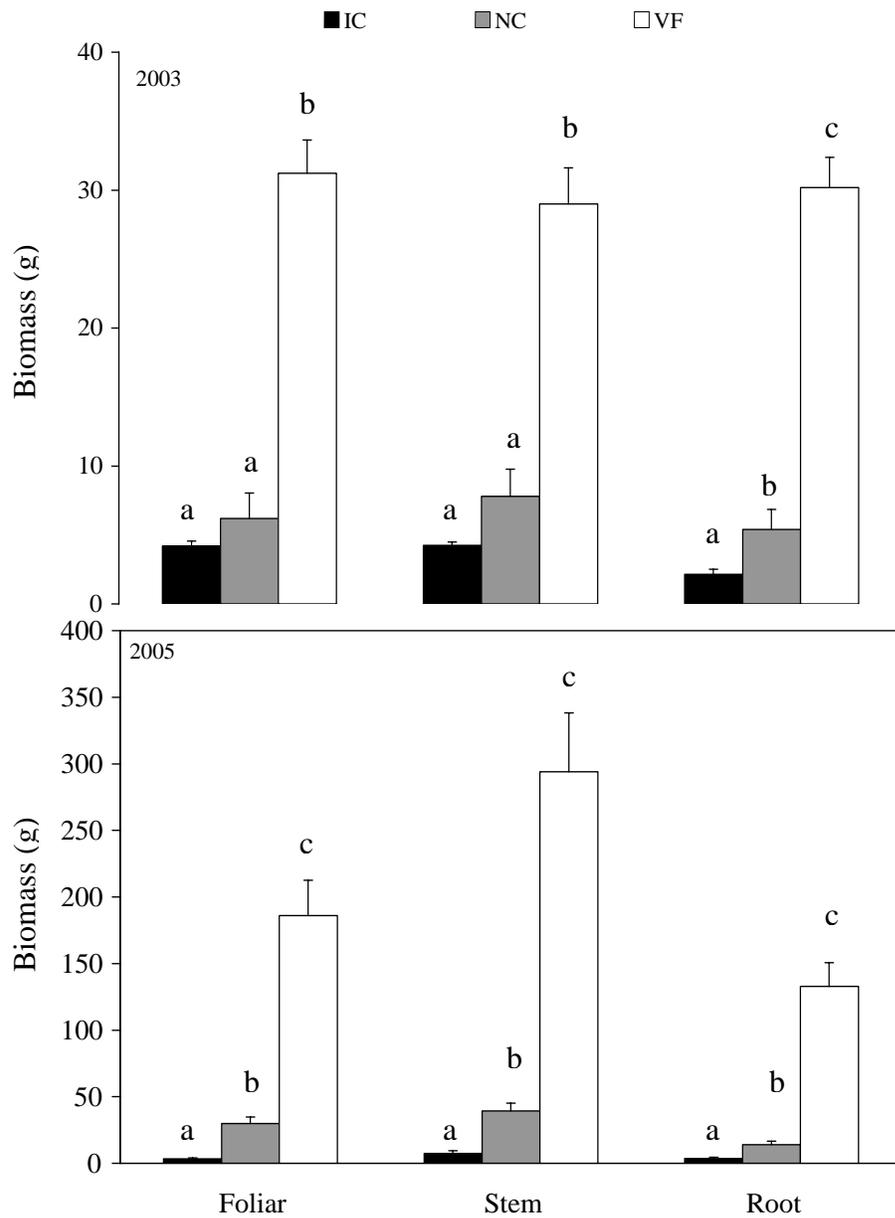


Figure 4-2. Mean biomass(SE) of the pine seedling foliage, stems, and roots for the three treatments after one growing season (2003) and three growing seasons (2005). Different letters represent significant differences in means ($\alpha = 0.05$)

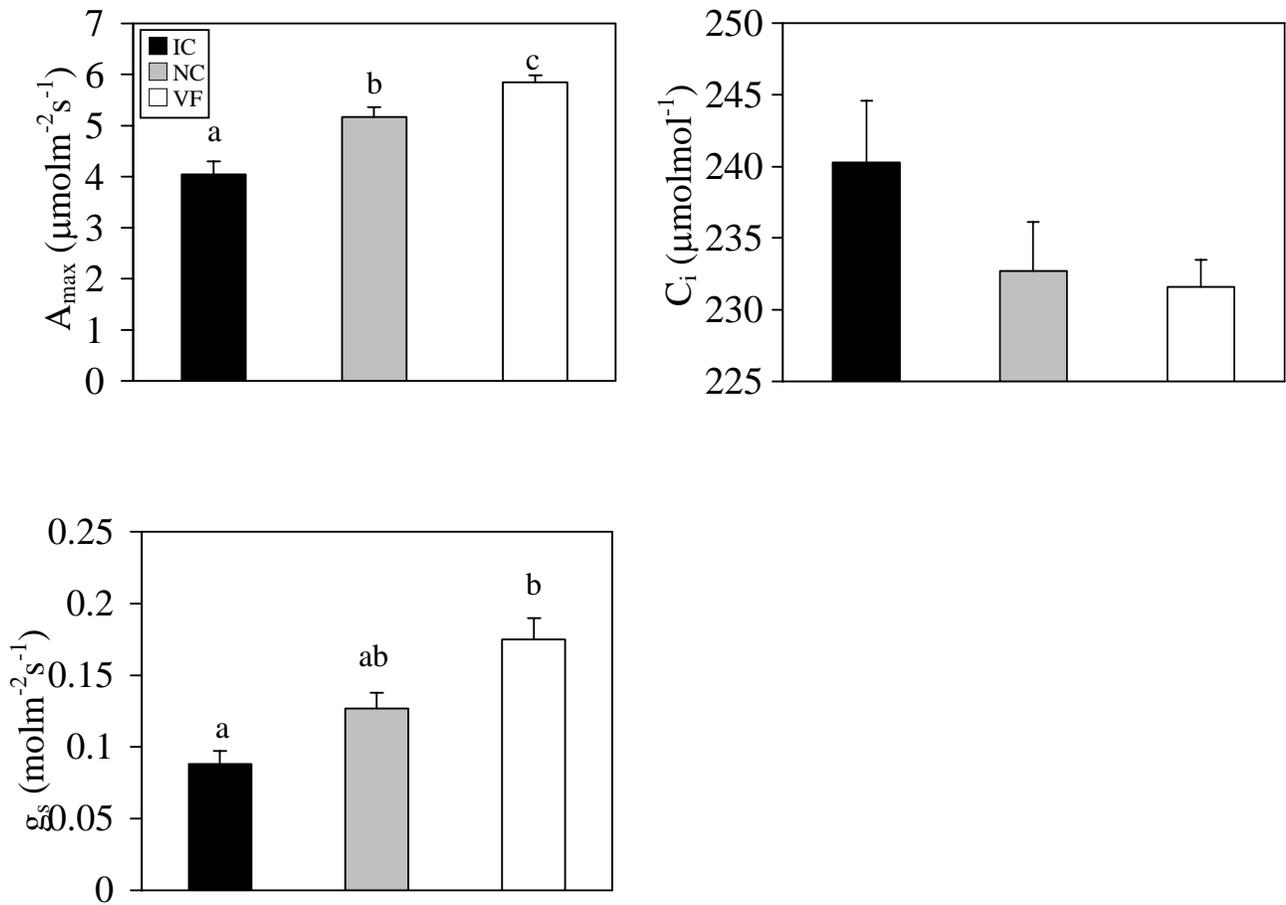


Figure 4-3. Mean light saturated photosynthesis (A_{max}), stomatal conductance (g_s), and internal leaf CO_2 concentration (C_i) summer means(SE) for pine seedlings in the three treatments. Different letters represent significant differences in means ($\alpha = 0.05$).

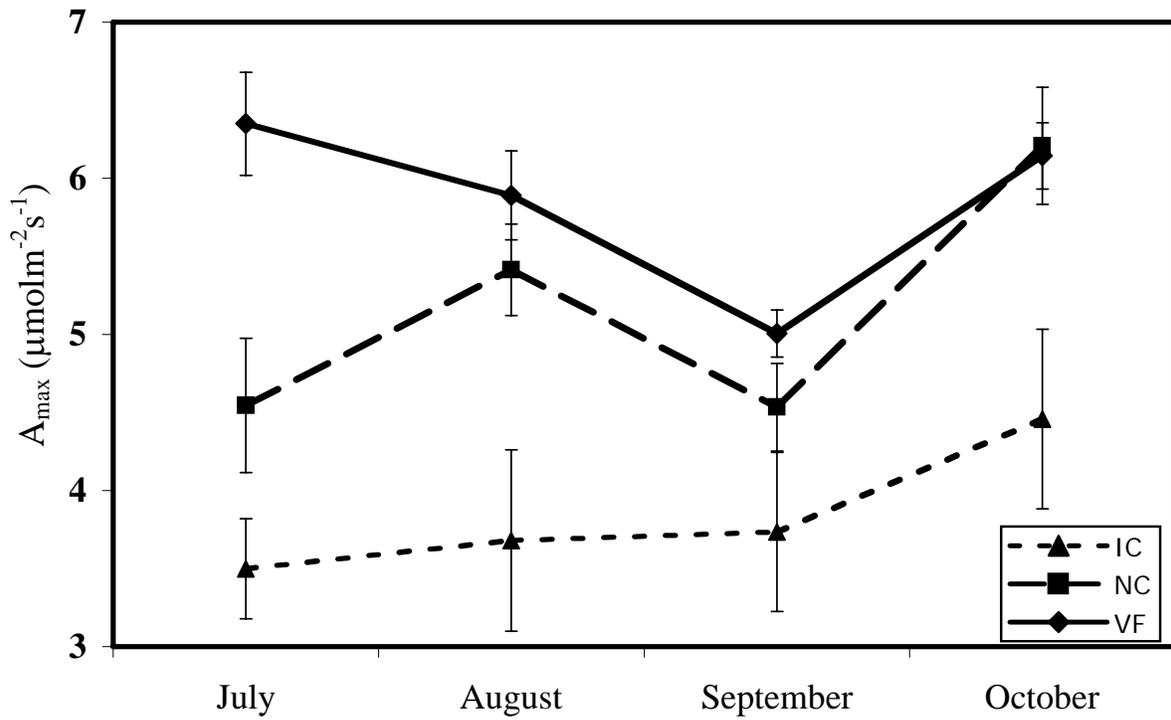


Figure 4-4. Monthly light saturated photosynthesis (A_{max}) of the pine seedlings in the VF, NC, and IC treatments.

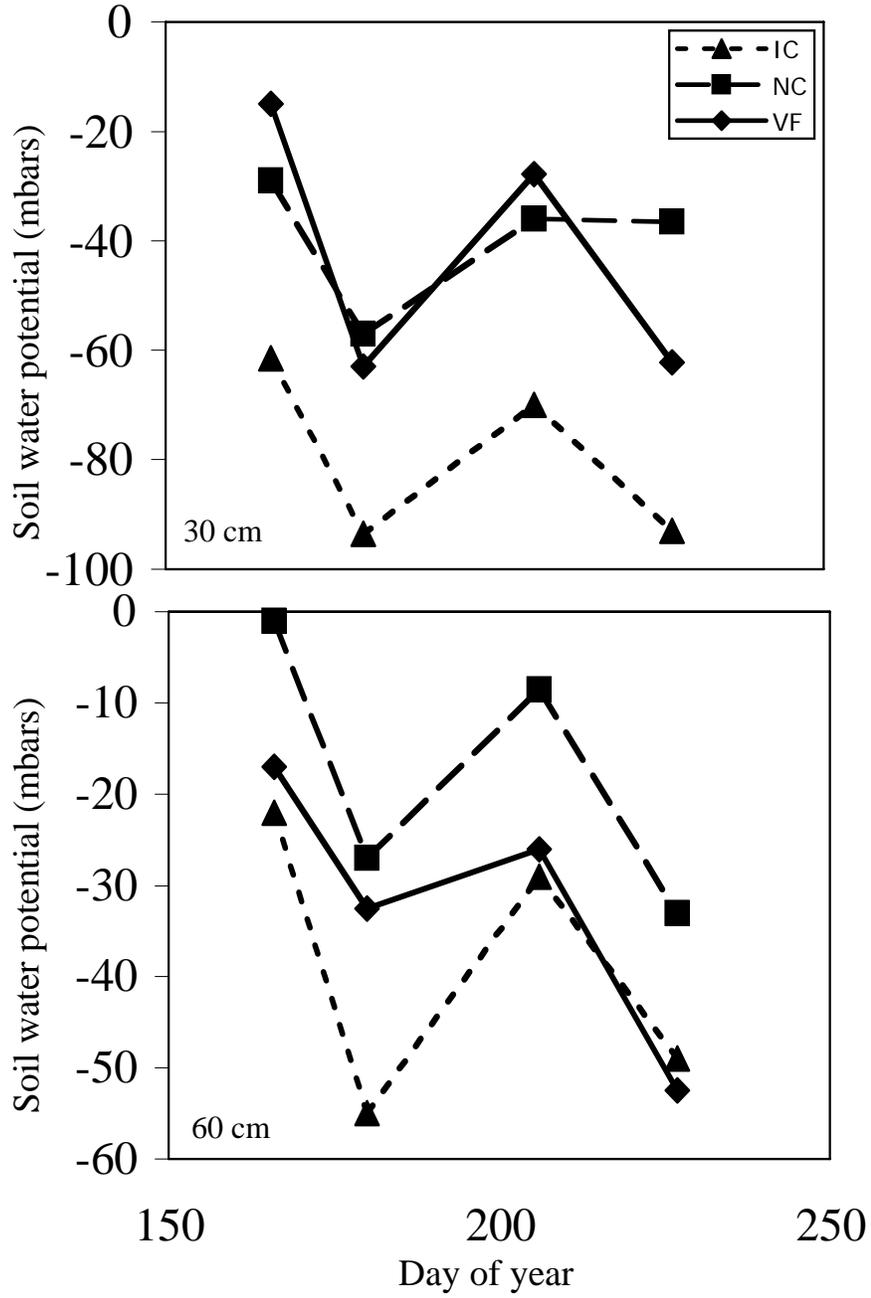


Figure 4-5. Soil water potential of the three treatments at two soil depths (30 and 60 cm).

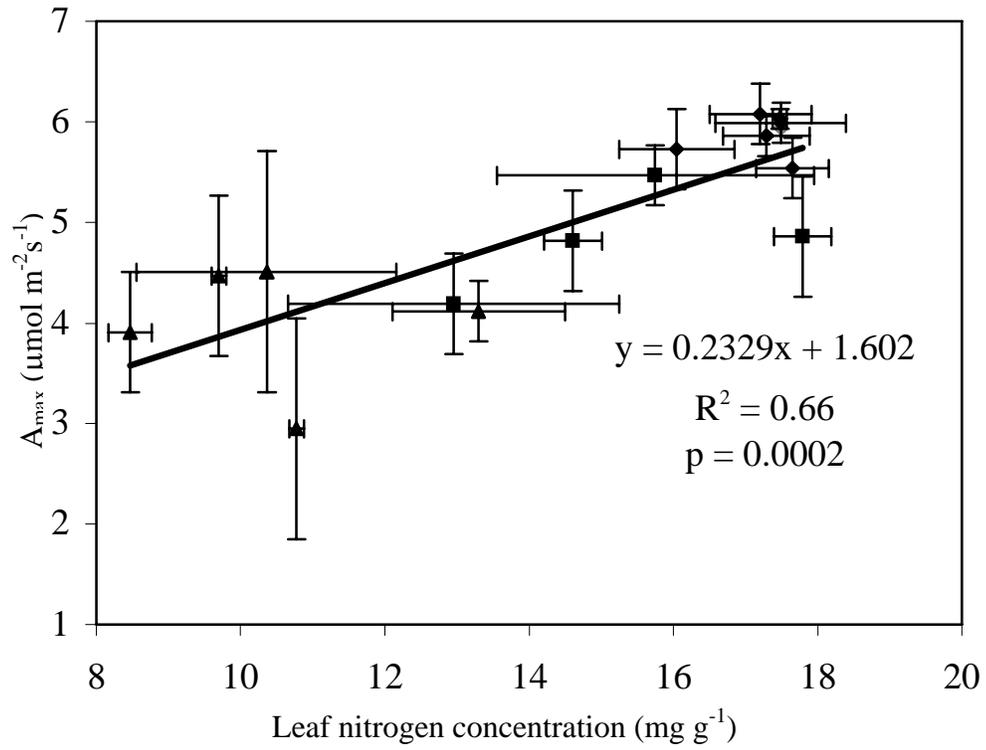


Figure 4-6. Relationship between leaf nitrogen concentration and light saturated net photosynthesis (A_{max}). Each point represents a plot mean (Diamonds- VF, squares- NC, triangles- IC).

CHAPTER 5
Imperata cylindrica, AN ALIEN INVASIVE GRASS, MAINTAINS CONTROL OVER N
AVAILABILITY IN AN ESTABLISHING PINE FOREST

Introduction

It is well known that exotic invaders threaten the biodiversity and stability of native ecosystems (Wilcove et al. 1998; Mack et al. 2000). The changes in ecosystems brought about by biological invasion include, but are not limited to, alterations in trophic structure and disturbance regime, and in system-level rates of resource supply (Vitousek 1990). The implications of plant invasion on soil resource supply, in particular soil nutrients, have received much attention in the recent past. Ehrenfeld (2003) suggested that changes in nutrient cycling associated with plant introductions might result from invasive species induced changes in soil physical and microbiological properties. This may be preceded by changes in species dominance and/or plant functional groups. New species in an ecosystem that do not cause any of these changes are not likely to cause shifts in nutrient cycling. The effects of exotic plant invasions depend on how different the new species' characteristics are from the native resident species (Chapin et al. 1996; Ehrenfeld 2003),

The traits that make a particular species invasive may also lead to impacts on nutrient cycling. Invasive species that achieve success by utilizing resources not being taken up by the local species (Elton 1958, Levine and D'Antonio 1999, Mack et al. 2000), alter nutrient cycling by capturing untapped nutrients and redistributing them through litter decomposition. According to Davis et al. (2000), the invasibility of a plant community is based upon a balance between resource uptake and gross resource supply and as long as these two are equivalent, the community should be resistant to invasion. Pulses in nutrients, from outside sources, promote invasion and so nutrient increases would be utilized and retained in the ecosystem by the invasive plants.

Some exotics are invasive due to higher photosynthetic rates and specific leaf area that lead to higher growth rates (Baruch and Goldstein 1999; McDowell 2002), which could be driven by increased uptake of nutrients. Some invasive plants maintain a higher nitrogen (N) concentration in their tissues (Vitousek et al. 1987; Vitousek and Walker 1989; Witkowski 1991; Ashton et al. 2005) indicating increased uptake. Increases in N in plant tissues imply improved litter quality leading to increased rates of decomposition followed by more uptake. Invasive plants can affect nutrient availability simply through their litter inputs and can increase cycling through accelerated rates of decomposition and uptake (Allison and Vitousek 2004; Ashton et al. 2005).

Exotic grass invasions can alter nutrient cycling directly or indirectly. Grasses can modify the microclimate of the soil by filling in all available space and thereby preventing radiation from reaching and drying the soil surface (Hughes et al. 1991; D'Antonio et al. 1998). Conversion of woodlands to grasslands or changes in species dominance of grasslands can have major implications for nutrient cycling due to changes in litter type and quality and decompositions rates. The conversion of Hawaiian woodlands to grasslands by invasion lead to 3.4 times greater N cycling rates (Mack and D'Antonio 2003). Grass invasions alter fire regimes, sometimes even enhancing them (D'Antonio and Vitousek 1992), which can reduce nutrient availability through litter loss by burning and volatilization of nutrient containing compounds. Because grasses generally have shallow roots, they may reduce the nutrient availability of the uppermost soil layers. When they form dense root systems with significant biomass belowground, they can retain increased amounts of nutrients making them unavailable to other species. In a study comparing grasses, Tilman and Wedin (1991) demonstrated that grasses that allocate more carbon to roots reduce soil N the greatest.

The changes in nutrient cycling caused by exotic grasses can endanger young tree seedlings in a regenerating forest. Weed control experiments have been conducted on many crop tree species throughout the world, showing that reduction in competing vegetation promoted the growth of the tree species (Britt et al. 1990, Cain 1991, Miller et al. 1991, Morris et al. 1993, Martin and Jokela 2004). Supplementing nutrients through fertilization can have similar effects as vegetation control, suggesting that competition with other vegetation for nutrients plays a major role in limiting tree growth. Exotic species that are better competitors for nutrients than natives are more likely then to be greater constraints on competing tree species.

An exotic grass species that threatens emerging pine forests in the southeastern United States is *Imperata cylindrica*, a C₄ rhizomatous perennial grass introduced from Asia. Although *I. cylindrica* can have leaf blades of up to 1.5m tall in conditions of good soil moisture and fertility (Holm et al. 1977), the majority of its biomass occurs belowground (Ramsey et al. 2003). It has a low shoot-to-root/rhizome ratio, with greater than 60% of the total biomass occurring as rhizomes that are resistant to heat and breakage (Sajise 1976). Their rhizomes, which generally occur in the top 15 cm in clay soils, can reach depths of one meter or more (Holm et al. 1977). With its rhizomes, *I. cylindrica* can reproduce asexually from fragments as small as 0.1g (Ayeni and Duke 1985). Sexual production also occurs by way of seed production. *I. cylindrica* is a prolific seeder producing as many as 3000 seeds per plant (Holm et al. 1977). Whether by seed or by rhizome, *I. cylindrica* can invade a variety of ecosystems from xeric uplands to shaded mesic sites (Jose et al. 2002), tolerating a variety of soil conditions, mostly favoring acidic soils (Wilcut et al. 1988). Its invasion and spread lead to changes in the functioning of an ecosystem by altering soil chemistry, nutrient availability, hydrology and disturbance regimes. Collins and Jose (2007) showed that *I. cylindrica* decreased soil nitrate and

potassium levels and altered soil pH in invaded pine flatwoods. It was demonstrated that *I. cylindrica* was more competitive for phosphorus than native pine-savanna species (Brewer and Cralle 2003). In Florida sandhills, *I. cylindrica* reduced soil moisture by 50% in the upper 30 cm of soil (Lippincott 1997). *I. cylindrica* increased fire temperatures and heights in a longleaf pine forest (Lippincott 2000).

Whether *I. cylindrica* is successful in outcompeting native vegetation and young pines by manipulating nutrient cycling and availability remains unexplored. Using ^{15}N nitrogen isotope as a tracer, we compared how *I. cylindrica* and native vegetation competed for N, while examining which exerted a greater competitive stress on emerging one-year-old *Pinus taeda* seedlings. With its greater amount of belowground biomass, we hypothesized that *I. cylindrica* was a better competitor than native vegetation for N available in the soil. We also hypothesized that *P. taeda* growth would be impacted more severely by *I. cylindrica* than native vegetation as a result of the higher degree of belowground competition.

Methods

Site Description and Experimental Design

The study was conducted in 2003 in Santa Rosa County in Northwest Florida, U.S.A. (30°50',N. 87°10',W). The region has temperate climate with moderate winters and hot, humid summers. The mean temperature for this region in 2003 was 19.4°C with August being the hottest month (27.3°C) (Figure 5-1) (NOAA). Total annual precipitation was 192.8 cm with the wettest month being June (41.8 cm). The soils on the site were mapped a lakeland series of a Typic Quartzipsamments (89% sand, 7.8% silt, and 3.4% clay) and were acidic (pH of 4.8) and had a mean observed soil temperature of 29°C during the growing season. The study area became infested with *I. cylindrica* when a 17-year-old *P. taeda* plantation was harvested the

previous year. A design was used consisting of 15 plots (7.9 x 10.4 m) of the following three treatments replicated five times:

- **Vegetation free (VF):** plots were hand weeded weekly in order to represent the full growth potential in the absence of other vegetation.
- **Native competition (NC):** Establishment and growth of native vegetation from natural sources was allowed. The major native species on site included *Smilax rotundifolia*, *Smilax aspera*, *Rubus occidentalis*, *Ilex glabra*, *Andropogon virginicus*, *Asclepius veriegota*, *Carphephorus paniculatus*, *Ilex vomitoria*, and *Erechtites hierarifolia*.
- ***Imperata cylindrica* competition (IC):** Established dense monocultural patches of *I. cylindrica* from local seed or rhizome sources.

In fall 2002, a uniform patch of *I. cylindrica* of about 1 ha in size was selected for the five IC treatment plots. The VF and NC treatment plots were randomly established in an area 20 m away from the advancing front of the *I. cylindrica* patch. The 20 m buffer zone was considered appropriate since *I. cylindrica* spread had been estimated to be about 2 m per year at this site (Collins et al. 2006). All the plots, except for the IC treatment, were site prepared in October 2002 with a tank mix of imazapyr and triclopyr at a rate of 936.2 ml ha⁻¹ in order to ensure that there was no *I. cylindrica* infestation. All treatment plots had a 3 meter buffer around them. Because of the close proximity of the plots (all were within an area approximately 2 ha), the soil conditions were assumed uniform before installment of the treatments. In each plot, 32 1-year-old bareroot *P. taeda* seedlings, purchased from a commercial nursery and graded for uniform size, were planted on March 6th in four rows with spacing of approximately 1 x 2m, corresponding to 3900 trees/ha.

Fertilizer Application

In order to trace the movement of N in the three treatments, four *P. taeda* seedlings were randomly selected from each plot (totaling 60 trees for the study) and fertilized on 27 May, 2003

with 5% ^{15}N enriched Ammonium Sulfate in a 1 meter square around each seedlings at a rate equivalent to 55kg of N per ha.

Sampling Methods

Initial data collection began in May 2003. Monthly percent cover was assessed of each plot for the duration of the study by placing a square meter quadrat randomly in four locations within each plot and estimating the mean percentage vegetative cover. The means of the quadrat measurements were scaled up for each plot.

Above and below ground biomass of the competing vegetation was collected monthly (June 2003 to October 2003) from each plot. Aboveground *I. cylindrica* and native vegetation was clipped at ground level from two quadrats (0.5 m^2). Live and dead foliage was separated and all samples were dried at $65\text{ }^{\circ}\text{C}$ for 72 hours and weighed. Below ground biomass was collected using soil augers from the same plots used for aboveground biomass harvesting. Three soil cores were taken within each quadrat up to a depth of 18 cm. Roots and rhizomes were washed, dried at $65\text{ }^{\circ}\text{C}$ for 72 hours and weighed.

In December 2003, the ^{15}N -fertilized loblolly seedlings were harvested. All competing vegetation, surrounding the seedlings within the enriched area was harvested as well. The foliage, stems and roots were separated for all harvested species and were dried at $65\text{ }^{\circ}\text{C}$ for 72 hours. All dried plant tissues were ground using a Wiley Mill to pass through a 1 mm screen. Cross-contamination of the ^{15}N plant material was prevented by thoroughly cleaning the grinder between each sample with a vacuum and ethanol.

On the same days the pine seedlings were harvested, four soil cores up to a depth of 90 cm were extracted from each ^{15}N micro-plot using a soil auger, with a 3.5 cm diameter. The cores

were divided into 30 cm increments to give 3 soil depths. Soil samples were air-dried and subsamples were fine-ground with a mortar and pestle.

Total N and ^{15}N concentration of plant materials and soil were determined on an Isotope Ratio Mass Spectrometer (UC Davis Stable Isotope Laboratory). We calculated %N derived from fertilizer, %utilization of fertilizer N, and %N recovery in soil using the data.

A measure of the relative amount of N the pine seedlings obtained from the soil and from applied fertilizer, the percentage of plant N derived from fertilizer (%NDF), was calculated using the following formula (Wienhold et al. 1995):

$$\text{NDF (\%)} = 100 * (a - b) / (c - d),$$

where a = atom % ^{15}N abundance in loblolly seedling needles, stems or roots;
b = atom % ^{15}N abundance in control loblolly seedling needles, stems, or roots;
c = atom % ^{15}N abundance of fertilizer applied; and
d = natural atom % ^{15}N abundance.

The percentage utilization of fertilizer N (%UFN), was calculated for *P. taeda* seedlings as follows (Wienhold et al. 1995, Barber et al. 1996):

$$\text{UFN (\%)} = (\% \text{NDF} * S) / R,$$

where %NDF = percentage of plant N derived from fertilizer;
S = kg N ha⁻¹ in *P. taeda* seedling needles, stems, and roots; and
R = kg N ha⁻¹ applied.

Percentage recovery of ^{15}N fertilizer in soil (RFN_{soil}), a representation of the applied ^{15}N remaining in soil, was determined using the equation as follows (De Mattos, 2000):

$$\text{RFN}_{\text{soil}} (\%) = 100 * ((a - c) / (b - c)) * (N_p / N_f),$$

where a = atom % ^{15}N abundance in fertilized soil material;
b = atom % ^{15}N abundance in labeled fertilizer;
c = atom % ^{15}N abundance in non-fertilized soil (average background level);
N_p = total N of soil sample (in g); and
N_f = total amount of ^{15}N applied to the soil as labeled fertilizer (g).

Statistical Analyses

One-way analysis of variance (ANOVA) was used to detect differences in the means with the PROC GLM procedure of the SAS statistical software package. (SAS Institute, Cary, NC

1999). Differences were declared significant at $\alpha < 0.05$. Using SAS, Levene's test for homogeneity among variances was used to determine which pairwise post hoc comparison method to use. For homogenous variances, Duncan's post hoc test was used; for heterogeneous variances, Dunnett's T3 test (Dunnett 1980) was used (SPSS ver. 9, SPSS Inc.).

Results

The aboveground biomass of the competing vegetation in the native and IC treatment plots were not significantly different throughout the summer months (Table 5-1). The summer mean of aboveground biomass for competing vegetation for both treatments were nearly identical at 239.7 g/m² for the IC treatment plots and 234.8 g/m² for the NC treatment plots. However, the IC plots maintained significantly greater percent cover than the NC treatment plots each month (Table 5-1). The IC treatment plots had greatest cover in July (97.2%), while the NC treatment plots peaked in August (88.7%). Both treatments had their highest amount of biomass in September.

The belowground biomass was significantly higher for the IC treatment compared to the NC treatment. The IC treatment plots consistently maintained significantly higher belowground biomass than the NC treatment plots each month (Table 5-1).

After one full growing season, the pine seedlings growing in the VF treatment had a mean total dry biomass of 90.4 ± 9.5 g, which was significantly greater ($p < 0.0001$) than what was observed in the other two treatments. The mean total dry biomass of the pine seedlings grown in the NC treatment (19.3 ± 3.7 g) was not significantly different from the IC treatment pine seedling biomass (10.4 ± 1.0 g).

The pine seedlings in the IC treatment pine seedlings had the lowest amount of nitrogen in their biomass, while the VF seedlings had the greatest (Figure 5-2). The N content of the foliage

in the VF and NC treatment seedlings were significantly greater than IC treatment pine seedlings ($p < 0.0001$). The amount of N in the seedling stems in the IC treatment did not differ from NC treatment, but both were significantly lower than the VF treatment ($p < 0.0001$). All three treatments differed in the amount of N in the pine seedling roots ($p < 0.0001$). The amount of N in the competing vegetation was greater in the NC treatment plots than the IC treatment plots both above and belowground ($p < 0.001$).

The pine seedlings growing in the VF treatment had the highest N content per hectare. The N content of the pine seedling foliage was 2.05 kg N/ha in the VF treatment, which was significantly greater ($p < 0.0001$) than both of the other treatments (Table 5-2). The NC treatment and IC treatment did not differ in pine seedling foliage N content. All three treatments were significantly different in the N content of pine seedling stems ($p < 0.0001$) and roots ($p < 0.0001$), with the IC treatment pine seedlings consistently being the lowest and the VF treatment being the highest. The seedling pine roots of the *I. cylindrica* treatment plots had the lowest overall N content (0.04 kg N/ha). The N content of the native competing foliage (24.3 kg N/ha) was significantly greater ($p < 0.0001$) than the N content of the *I. cylindrica* foliage (10.14 kg N/ha); however, the reversed was observed belowground; *I. cylindrica* had stored 32.9 kg N/ha, while it was only 14.7 kg N/ha in NC treatment belowground. This was significantly different ($p < 0.0001$).

The N derived from fertilizer (NDF) in the VF treatment was significantly lower than the other treatments in the pine foliage ($p < 0.0001$), pine stem ($p = 0.0143$), and pine root ($p = 0.0011$) (Table 5-3). In the pine foliage, stems and roots, the NDF was not significantly different between the NC and IC treatments. The greatest NDF was observed in the pine foliage of the IC treatment (11.3 %), while the lowest NDF was in the pine roots of the VF treatment (4.2%). The

I. cylindrica had significantly higher NDF than the native vegetation both above ($p=0.0016$) and belowground ($p<0.0001$) (Table 5-3).

The total fertilizer N use efficiency (UFN) was significantly higher in the VF treatment than the other treatments in the pine seedling foliage ($p<0.0001$), stems ($p<0.0001$), and roots ($p<0.0001$) (Table 5-4). The pine seedlings in the other treatments were never half as efficient as the ones growing in the VF treatment. The UFN was significantly higher in the pine stem and pine root of the NC treatment than the IC treatment. There was no significant difference in the UFN of the competing native and *I. cylindrica* foliage; however, the *I. cylindrica* roots/rhizomes were significantly more efficient (7.68%) than the native roots (0.99%; $p<0.0001$).

The percent recovery of ^{15}N in the soil (RFN) at the end of the growing season was significantly less in the VF treatment plots than the other treatments at depths of 0-30 cm (8.2%; $p=0.0037$) and 30-60 cm (1.4%; $p=0.0032$) (Figure 5-3). The RFN of the NC and IC treatments never differed at any depth. There was no difference in the recovery of ^{15}N in the soil between any of the treatments at a depth greater than 60 cm.

Using the treatment means of the N derived from fertilizer in pines and competing vegetation as well as the ^{15}N recovered from the soil, an estimate was made of the total percentage of applied fertilizer that was accounted for in the vegetation and soil. Approximately 81.5 % of the applied fertilizer N was accounted for in the IC treatment, while 62.2% and 24.7% was accounted for in the NC and VF treatments respectively (Figure 5-4).

Discussion

Throughout the growing season, the *I. cylindrica* had significantly greater cover than the native vegetation despite that aboveground biomass in both treatments was the same. The even-spread *I. cylindrica* shoot biomass matched the patchy woody tissues of the shrubs in the NC treatment. The conversion from mixed species to a grass, by invasion, makes the forest floor

more homogenous, filling more space and reducing radiation transmittance to the soil surface (Hughes et al. 1991; D'Antonio et al. 1998). This has implications for the microclimate conditions of the invaded forest floor. The surface soil moisture of the *I. cylindrica* invaded plots was the wettest of the three treatments in July and August (Figure 5-5). Similarly, Ashton et al. (2005) showed that mixed deciduous forest sites invaded with exotic woody species were wetter than uninvaded sites. The changes in microclimate brought on by invasion might affect the cycling of nutrients and the productivity of other species. In the conversion of Hawaiian woodland to grassland, by invading exotic grasses following fire, alterations in microclimate were observed, which had implications for N mineralization (Mack and D'Antonio 2003).

Belowground, the biomass of the *I. cylindrica* was far greater than native vegetation. Each month, the *I. cylindrica* mean belowground biomass was at least 5 times greater than the native mean belowground biomass. The greater total biomass of *I. cylindrica* suggests that the invasive is far more productive than native species. The increased productivity might be attributed to being more competitive for nutrients, which would have negative implications for the establishing *P. taeda* seedlings. Young *P. taeda* seedlings growing in the IC treatment grew only to 11% of their potential after one growing season, which was 54% of the biomass that was observed for the pine seedlings growing in the NC treatment. *I. cylindrica* reduced the growth of the young pine seedlings just as the shrub *Rhamnus frangula* reduced the growth and survival of *Acer rubrum*, *Acer saccharum*, *Fraxinus Americana* L. and *Pinus strobus* in New Hampshire, USA, which the authors suggest may be due to belowground competition from the *Rhamnus* with its extensive shallow root system (Fagan and Peart 2004).

The N content in the *P. taeda* seedling tissues was affected by treatment. The NC treatment prevented the *P. taeda* from maintaining VF treatment N concentrations in their stems

and roots. The pine seedlings in the IC plots never matched the N content of the VF treatment seedlings in their foliage, stems, and roots. The pine seedlings growing in the IC plots had reduced levels of N in tissues compared to the NC treatment in both the foliage and roots. This suggests that *I. cylindrica* is more competitive for N than native species causing reduced levels of N in the *P. taeda* seedlings. Analysis of the N content of *I. cylindrica* above and belowground revealed, however, that *I. cylindrica* had less than half the N concentration of native species in both foliage and roots.

On an ecosystem scale, native species stored 2.4 times the amount of N per hectare than *I. cylindrica* in foliage. On a site with native species, 61% of the total N occurs aboveground in the foliage, which drops to 23% after invasion of *I. cylindrica*. Belowground, *I. cylindrica* maintains much more N per hectare than native species. Even though the N concentration of the belowground tissues is less than native species, the fact that there is significantly greater amount of *I. cylindrica* biomass belowground permits for more N stored belowground. In a study, comparing five grasses growing along a N gradient, Tilman and Wedin (1991) showed that the two grasses, *Andropogon gerardi* and *Schizachyrium scoparium*, that reduced soil solution N the greatest had lower tissue N. These two species also had higher root allocation (Tilman and Wedin 1991) similar to the way *I. cylindrica* allocated biomass belowground. After invasion by *I. cylindrica*, the percentage of total belowground N on site increased from 37 to 76%. The invasion of *I. cylindrica* into an emerging pine forest leads to a shift in where majority of the N is stored, from above to belowground.

The low levels of N concentration in *I. cylindrica* compared to native species suggest that *I. cylindrica* may be productive at lower levels of soil N. This is contradictory to several studies, which have shown that invasives generally have higher concentrations of N in their tissues,

which leads to higher litter quality and decomposition rates (Vitousek and Walker 1989; Ehrenfeld 2001; Allison and Vitousek 2004; Ashton et al. 2005). Increased decomposition rates act as a feedback mechanism for promoting the growth of an invasive and it is the rapid cycling of nutrients that favors an invasive's success. Funk (2005) suggests that in invaded plots of Hawaiian montane forest, the herbaceous *Hedychium gardnerianum*, factors in a tight N cycle with high N resorption from senescing *Hedychium* leaves combined with lower net nitrification rates. At our study site, a majority of the N belowground that occurred prior to fertilization, must have been tightly retained in the underground network of the exotic rhizome in a rapid cycle of root/rhizome turnover and uptake. Controlling movement of N belowground may be a primary mechanism by which *I. cylindrica* maintains dominance after establishment.

The NDF of *I. cylindrica* roots was more than three times the NDF of native species roots and the NDF of the *I. cylindrica* foliage was more than twice that of the native foliage implying that *I. cylindrica* is aggressive at attaining all sources of N. Not only was the *I. cylindrica* taking up more fertilizer N, it was also using the ammonium sulfate more efficiently than the native species (total UFN of 10.4% for *I. cylindrica* compared to 3.7% for the native species). The native species and *I. cylindrica* were utilizing the fertilizer N in their foliage equally, but *I. cylindrica* was much more efficient in the roots (7.68% compared to 0.99% by the native species). This demonstrates that *I. cylindrica* is both better in taking up and utilizing N. This suggests that *I. cylindrica* maintains tight control of N cycling in infested communities.

With *I. cylindrica* capable of taking up most of available N, competing species are forced to acquire N from other sources. This explains why the foliage and roots of the pine seedlings growing in the IC plots had the highest percentages of NDF of the three treatments. These seedlings took up more of the ammonium sulfate because they were more N limited. The pine

seedlings in all three treatments were poor at utilizing the ammonium sulfate efficiently. Total UFN for foliage, stem and roots for all three treatments never exceeded 1%. However, there was a significant difference among treatments with the seedlings in the VF treatment being the most efficient. The foliage, stems, and roots UFN of the pine seedlings in the IC treatment, were significantly less than what was observed in the NC treatment indicating that *I. cylindrica* applied more competitive stress. With increases in competitive stress came reduction in pine seedling growth and fertilizer use efficiency, which has been observed in crops such as cotton (Allen et al. 2004) and maize (Jose et al. 2000b; Wienhold et al. 1995).

When quantifying the amount of applied ammonium sulfate remaining in the soil at the end of the growing season, approximately the same quantity was recovered from both the NC and IC treatments regardless of depth. Up to a soil depth of 60 cm, less than half of what was recovered in these two treatments was recovered in the VF treatment. Loss of the ammonium sulfate in the VF treatment likely is due to leaching. Loss of fertilizer in this treatment might explain why approximately 25% of the ^{15}N applied was accounted for in the VF treatment. The greatest amount of ^{15}N was accounted for in the IC treatment, nearly 20% more than in the NC treatment. A large percentage of the applied ^{15}N (81.5%) was traced in the IC treatment. In *I. cylindrica* invaded plots little N was lost suggesting tight retention of N.

Overall, our results suggest that *I. cylindrica* is more competitive than native vegetation in an emerging pine forest when it comes to acquiring and using N. Species competing with this invasive will experience greater levels of stress than from native species resulting in decreased growth and nutrient use efficiency. Although *I. cylindrica* maintains lower concentrations of N in its tissues, it is able to retain greater amounts of N than native vegetation on an ecosystem scale because of much greater amount of biomass. N is tightly retained in invaded areas, with

most of the N being stored belowground. Invasion of a native ecosystem by *I. cylindrica* results a shift in where bulk of the N occurs, from above to belowground (Figure 5-6).

The shift in N pools resulting from invasion has implications for the role fire plays on N availability. On a non-invaded site, the large percentage of N occurring aboveground could be lost in a burn. *I. cylindrica* invasion represents significant change in location of biomass and N, thus a burn of the aboveground foliage would have little effect on the amount of N. Mack et al. (2001) found that burning had little effect on the total ecosystem N of Hawaiian woodlands because >95% of the ecosystem N occurred in the soil and only high-intensity burns would result in significant loss of N from the soil pool. There have been suggestions that *I. cylindrica* will burn at greater intensity with higher maximum temperatures and heights than native species (Lippincott 2000), but there is no evidence to suggest that an intense burn would lead to losses of N belowground.

Despite the fact that N is retained belowground on a site by *I. cylindrica*, potentially even in the face of disturbance, it does not seem to be available to other species. Tightly controlling the availability of N may be a mechanism by which *I. cylindrica* is able to suppress the growth of *P. taeda* seedlings. It has been demonstrated that the pine seedlings have reduced rates of photosynthesis in invaded areas (Chapter 4), which may be due to reduced N availability. Other than controlling N availability, *I. cylindrica* may have other mechanisms by which it is able to achieve dominance and reduce the productivity of competing species. The way it is able to manipulate other nutrient cycles should be further explored. Brewer and Cralle (2003) showed that *I. cylindrica* is a better competitor for phosphorus than native species in a longleaf pine savanna based upon percent ground cover of the competing species. Collins and Jose (2007) demonstrated that *I. cylindrica* reduces potassium and nitrate in invaded forestlands in the

Florida panhandle. Work should also be done examining *I. cylindrica*'s role in water relations. In chapter 4, we showed evidence that *I. cylindrica* decreases soil water potential, but this effect on other species has not been examined. Allelopathy has been suggested as a potential mechanism for *I. cylindrica* to gain dominance over other species (Eussen 1979; Casini et al. 1998; Koger and Bryson 2003), but work has only been done exploring its effects on crop species. Further research is needed to explore these competitive interactions in detail.

Table 5-1. Summary of competing vegetation means (SE) for the native and *I. cylindrica* treatments. P values for the T-test are provided. Means were considered significantly different at $\alpha = 0.05$ level (marked with asterisk).

	June	July	August	Sept.	Overall mean
<i>I. cylindrica</i> aboveground biomass (g/m ²)	208.0(16.8)	194.9(17.8)	185.8(24.1)	369.9(46.7)	239.7(21.5)
Native aboveground biomass (g/m ²)	152.3(18.0)	226.2(23.2)	253.2(19.7)	307.7(78.4)	234.8(21.9)
P value	0.0533	0.3167	0.0623	0.5145	0.8790
<i>I. cylindrica</i> belowground biomass (g/m ²)	902.0(99.9)	595.4(128.6)	927.9(149.4)	2043.7(78.4)	1117.3(94.3)
Native belowground biomass (g/m ²)	127.8(30.3)	42.6(13.4)	177.0(24.1)	223.6(37.0)	143.7(17.2)
P value	<0.0001*	0.0027*	0.0011*	<0.0001*	<0.0001*
<i>I. cylindrica</i> % cover	91.3(4.6)	97.2(1.0)	96.5(0.9)	96.4(1.1)	95.4(1.2)
Native % cover	70.1(3.2)	80.9(4.3)	88.7(3.6)	87.7(3.3)	81.9(1.8)
P value	0.0006*	0.0007*	0.0457*	0.0176*	<0.0001*

Table 5-2. Mean nitrogen content (kg/ha) in pine foliage, stem, and roots as well as foliage and roots of competing vegetation. Different letters represent significantly different means.

Treatment*	Pine foliage	Pine stem	Pine root	Competing foliage	Competing roots/rhizomes
VF	2.05(0.22)a	1.10(0.13)a	1.06(0.13)a		
NC	0.40(0.09)b	0.19(0.01)b	0.19(0.03)b	24.35(3.39)a	14.74(1.45)b
IC	0.17(0.02)b	0.09(0.01)c	0.04(0.01)c	10.14(0.28)b	32.95(2.23)a
p-value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

*Treatments: VF- vegetation free (no competition), NC- native competitor, IC- *I. cylindrica* competition

Table 5-3. Mean percentage of N derived from fertilizer (%NDF) for pine foliage, stem, and roots as well as foliage and roots of competing vegetation. Different letters represent significantly different means.

Treatment	Pine foliage	Pine stem	Pine root	Competing foliage	Competing roots/rhizomes
VF	4.57(0.33)b	5.1(0.51)b	4.2(0.29)b		
NC	8.4(1.26)a	8.5(1.28)a	6.6(0.82)a	6.8(1.89)b	3.9(0.69)b
IC	11.3(1.12)a	7.7(0.83)ab	7.6(0.76)a	14.7(1.18)a	13.2(1.17)a
p-value	<0.0001	0.0143	0.0011	0.0016	<0.0001

Table 5-4. Mean percentage utilization of fertilizer N (% UFN) for pine foliage, stem, and roots as well as foliage and roots of competing vegetation. Different letters represent significantly different means.

Treatment	Pine foliage	Pine stem	Pine root	Competing foliage	Competing roots/rhizomes
VF	0.16(0.02)a	0.093(0.010)a	0.074(0.007)a		
NC	0.054(0.01)b	0.028(0.004)b	0.020(0.03)b	2.7(0.9)	0.99(0.11)b
IC	0.03(0.004)b	0.012(0.002)c	0.007(0.002)c	2.7(0.23)	7.68(0.68)a
p-value	<0.0001	<0.0001	<0.0001	0.986	<0.0001

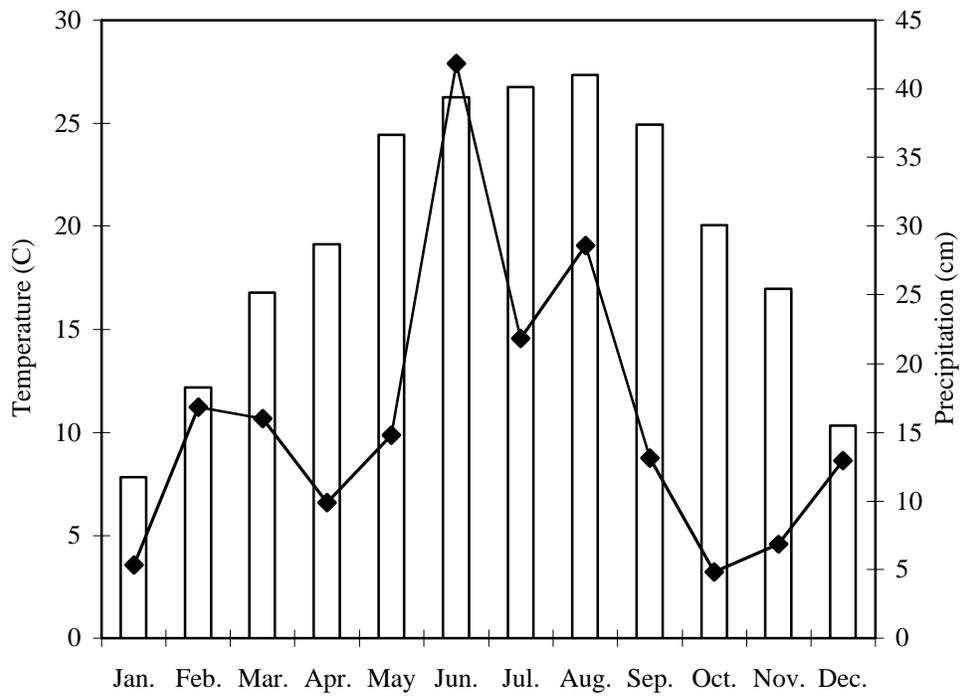


Figure 5-1. Summary of mean monthly temperature (bars) and total monthly precipitation (line) for the study site in 2003.

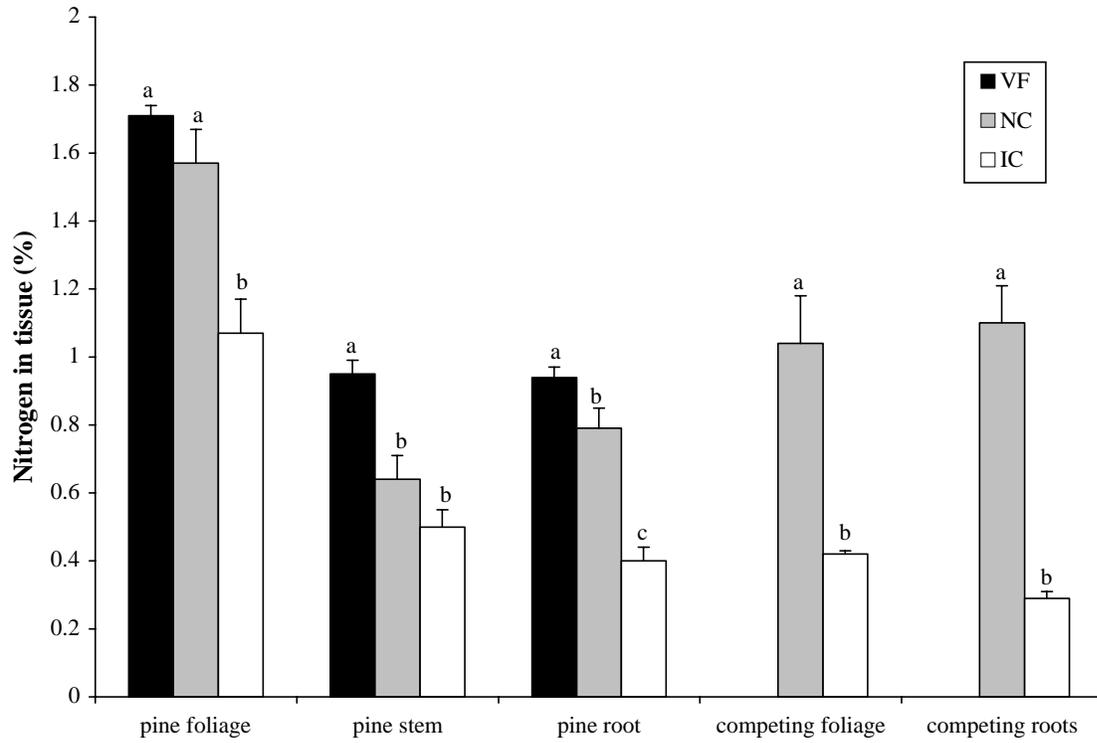


Figure 5-2. Amount of nitrogen in tissues (% of total biomass)(SE) of *P. taeda* seedlings and competing vegetation for the three treatments. Different letters represent a significant difference in % nitrogen. For all five comparisons $p < 0.0001$.

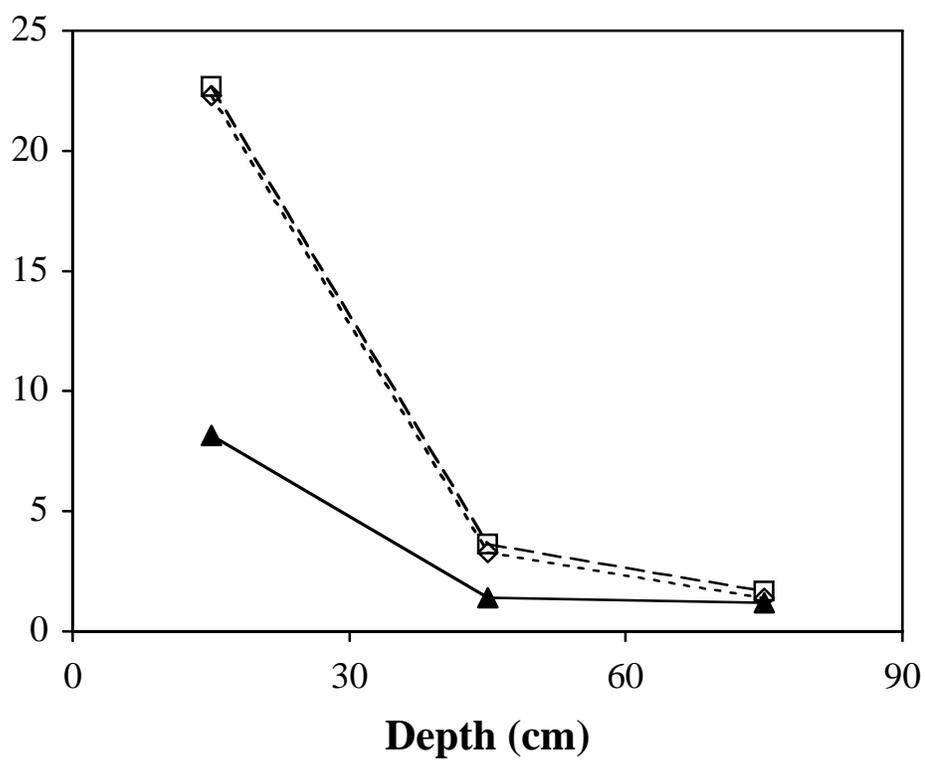


Figure 5-3. Percentage of ^{15}N recovery in soil at end of growing season in the VF (triangles), NC (squares), and IC (diamonds) treatments.

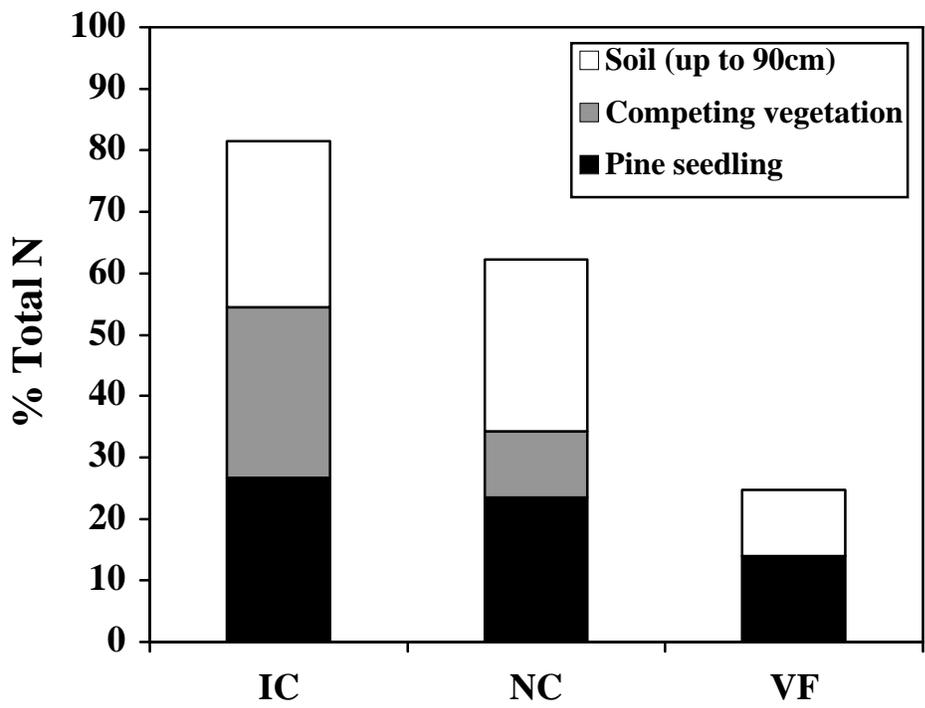


Figure 5-4. Percent total of N recovered at the end of study for the three treatments.

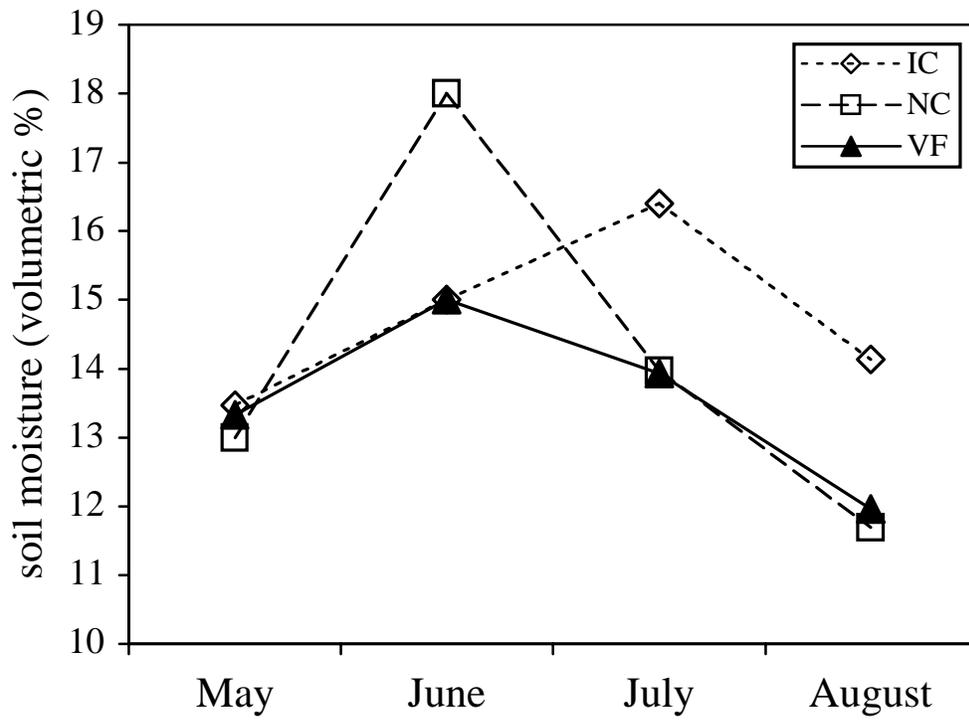


Figure 5-5. Monthly mean soil moisture of the three treatments for the summer of 2003.

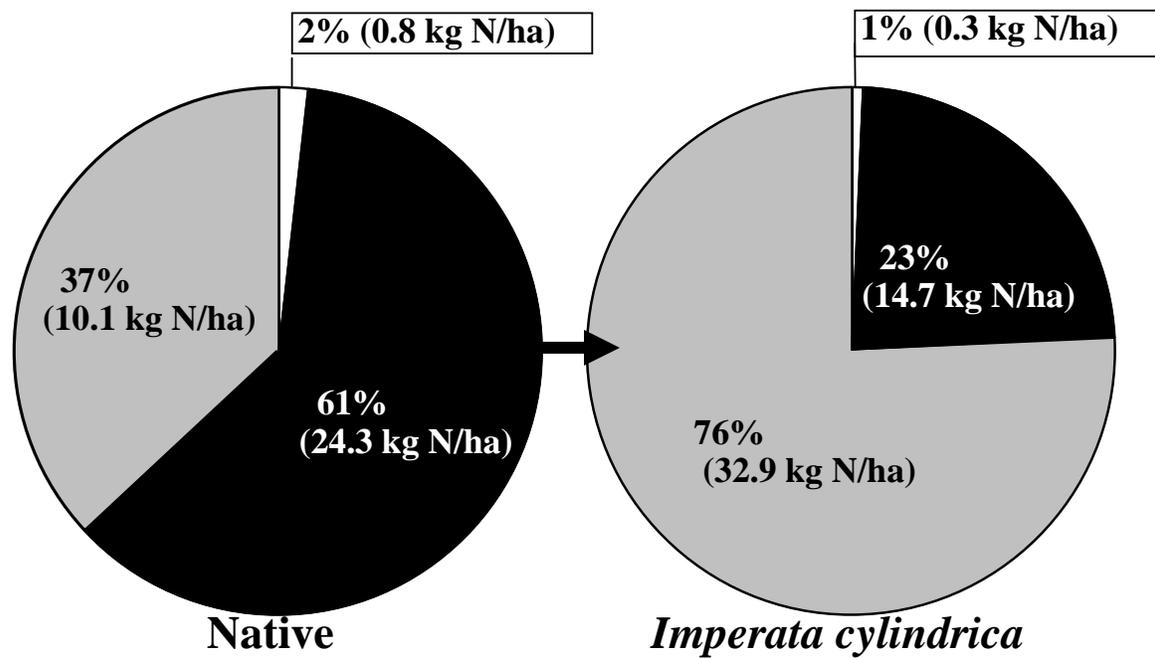


Figure 5-6. Demonstration of the percent of total nitrogen occurring in a young emerging pine forest before and after invasion by *I. cylindrica*; Nitrogen in *P. taeda* seedlings in white, competing vegetation foliage in black and competing vegetation roots/rhizomes in grey.

CHAPTER 6 SUMMARY AND CONCLUSIONS

The overall objective of this study was to examine the impacts of *Imperata cylindrica* on southeastern forests, specifically examining the role of its invasion on productivity, nutrient cycling and understory diversity of pine forests. The first objective was to review the literature for all the proposed mechanisms for invasion success as well as some of the theories that have been proposed on what makes communities susceptible to invasion (Chapter 2). With an understanding of community susceptibility, the next objective was to test the diversity-invasibility hypothesis, proposed by Elton (1958), in a mesocosm experiment with *I. cylindrica* and native pine forest understory species focusing on the importance of species richness, functional diversity and species identity (Chapter 3). Next, using measurements of size, biomass, and gas exchange, the impacts of *I. cylindrica* on the productivity of establishing pine seedlings in comparison with native species were determined (Chapter 4). The last objective was to quantify the competitive usage of nitrogen (N) between *I. cylindrica*, pine seedlings and native vegetation using stable isotopes (Chapter 5). The following are the major findings.

A review of the literature revealed that in general, there are two avenues for discussions of invasion mechanisms. The first focuses on the community characteristics that lead to invasion, while the other specifically addresses invader traits. Factors that play a role in community susceptibility to invasion include sufficient resource use, empty niches, diversity, invasion facilitators, biotic resistance, and novel enemies. Traits that make a plant species invasive include increased allocation to reproduction, better reproductive mechanisms, superior competition for resources, and allelopathy. Invasion may also occur as the result of a combination of the community and invader properties mentioned previously. The array of

hypotheses suggests that a single theory explaining invasion does not exist and that much work needs to be done to understand invasion mechanisms.

Elton's diversity-invasibility hypothesis, specifically the role of species richness, functional diversity and species identity of native species were tested with *I. cylindrica* in mesocosms. A randomized block design consisting of eight blocks and ten treatments with five common Florida sandhill understory species including a shrub, *Ilex glabra*, two grasses, *Aristida beyrichiana* and *Andropogon virginicus*, and two forbs, *Chamaecrista fasciculata*, and *Pityopsis graminifolia* was used. The treatments included a control, five monocultures, a grass mix treatment, a forb mix treatment, and a 3-species treatment with of all three functional groups (consisting of *I. glabra*, *A. beyrichiana* and *C. fasciculata*), and a 5-species treatment with all of the native species. There were five levels of diversity, (0, 1, 2, 3 and 5 species). After the native communities were allowed a year to establish, *I. cylindrica* was introduced at the start of the summer of 2005. Number of shoots and cover of *I. cylindrica* and cover of the native species were recorded biweekly through August. At the end of the study, the plants were harvested, dried and weighed. Prior to drying of the belowground biomass, root length, root length density (RLD) and specific root length (SRL) were determined. In August, there was a significant negative linear relationship between the cover of native species and *I. cylindrica* ($r^2 = 0.5925$, $p = 0.0092$). There was a negative logarithmic relationship between the biomass of the native species and *I. cylindrica* ($r^2 = 0.6986$, $p = 0.0026$). There was no relationship between the number of native species and *I. cylindrica* biomass suggesting that the diversity-invasibility hypothesis does not explain invasion success of *I. cylindrica*. Grasses proved to be the most resistant functional group providing resistance alone and in mixed functional communities. Repeated measures analysis demonstrated that treatments including *Andropogon virginicus* were

the most resistant to invasion over time ($p < 0.001$) suggesting that resistance is a matter of species identity. The success of *Andropogon virginicus* can be attributed to the fact that it had significantly greater root length ($p = 0.0017$), RLD ($p = 0.0109$) and SRL ($p < 0.001$) than all of the native species and *I. cylindrica* in monocultures. The same trends were observed of *A. virginicus* in mixed communities. The root morphology characteristics allowed it to be a great competitor belowground where *I. cylindrica* was most aggressive. The results suggest that *A. virginicus* could be used in restoration of infested ecosystems following chemical and mechanical control of *I. cylindrica*.

In Santa Rosa County, Florida, a 27-month study was conducted to compare the impacts of *I. cylindrica* and native vegetation competition on the productivity of loblolly pine (*Pinus taeda*) seedlings. In March 2003, one-year-old pine seedlings were planted in five plot replications of three treatments: 1) vegetation free (VF) 2) native (NC) competition and 3) *I. cylindrica* (IC) competition. At the end of the study, only 26% of the IC seedlings survived, half of what was observed in NC. Nine months after planting, the IC seedlings had significantly smaller root collar diameters than the NC seedlings ($p < 0.0001$) and by November 2004, the heights and stem volume index were significantly less as well ($p < 0.0001$). After one full growing season, the NC and IC pine seedlings had 21 and 11.5% of the total biomass of the VF seedlings, respectively. The NC and IC seedlings differed significantly in root biomass ($p < 0.0001$). After 27 months, the IC pine seedling total biomass was 2.4% of the VF seedlings and 18% of the NC seedlings ($p < 0.0001$). The greatest difference was in the pine needle biomass with the IC being only 11% of the NC pine needle biomass. In the summer of 2003, the IC pine seedlings maintained the lowest levels of light saturated net photosynthesis, which was matched by the lowest levels of stomatal conductances. These results may be explained by

reduced amounts of foliar nitrogen and some water stress that result from *I. cylindrica* competition. The pines in the IC treatment had the lowest total foliar surface area and the lowest specific leaf area, which may explain the reduced productivity. Evidence from this study suggests that *I. cylindrica* competition significantly reduces the productivity and growth of loblolly pine seedlings compared to native vegetation.

In the next study, ¹⁵N-labeled Ammonium Sulfate was used to compare how loblolly pine (*Pinus taeda*) seedlings compete for N in the presence of *I. cylindrica* and native vegetation competition in Santa Rosa County, Florida. *I. cylindrica* competition led to smaller pine seedlings with significantly less N content in the pine foliage and roots than those in the native treatment. Competition from *I. cylindrica* for N contributed to the pine seedlings taking up a greater percentage of the applied fertilizer than the seedlings competing with native vegetation. However, because of their reduced growth they were less efficient in utilizing the fertilizer. The belowground biomass of the invasive on average was seven times higher than the native species. Despite its lower N concentration in foliage and roots, *I. cylindrica* retained significantly more N per hectare. While the native species retained more N aboveground, *I. cylindrica* held significantly more belowground, thus invasion by this grass would lead to a shift of N pools from above to belowground. *I. cylindrica* was more competitive than the native species at attaining N because in both its foliage and roots, significantly more of the applied fertilizer N was found. The roots of *I. cylindrica* were seven times more efficient in utilizing the fertilizer. The fact that we were able to account for 81.5% of the applied fertilizer in the *I. cylindrica* plots compared to 62.2% in the native treatment suggests that *I. cylindrica* tightly retains most of the available N on site making it a particularly good invader.

The results of all these studies indicate the *I. cylindrica* poses a serious threat to the establishment and productivity of young pine forests. This work shows evidence that *I. cylindrica* is competitive for N and alters N pools by retaining large amounts of N belowground. *I. cylindrica*'s role in N cycling and cycling of nutrients still needs to be explored. Preliminary evidence, in this work, suggests that *I. cylindrica* may cause water stress. Work should be done exploring how the invasive competes for water and how water its presence affects sap flow of other species. It was demonstrated that community resistance to this invasive plant lies in the hand of specific native species, which use similar mechanisms to gain dominance. Native species more similar to *I. cylindrica* need to be tested to see if they will be more successful at resisting invasion. Bunchgrasses proved to be strong competitors, but it is possible that rhizomatous species may be more successful. Use of these native species should be considered in the integrated pest management strategies against *I. cylindrica*.

APPENDIX
MESOCOSM STUDY EXTRAS

Table A-1. Final mean % cover for each species in the ten treatments.

Treatment	% cover
Control	0
<i>A. stricta</i> monoculture	66.25
<i>A. virginicus</i> monoculture	89.12
<i>I. glabra</i> monoculture	42.5
<i>C. fasciculata</i> monoculture	26.87
<i>P. graminifolia</i> monoculture	40.62
Grass mix:	
1. <i>A. stricta</i>	11.25
2. <i>A. virginicus</i>	76.87
Total	88.12
Forbs mix:	
1. <i>C. fasciculata</i>	33.75
2. <i>P. graminifolia</i>	8.12
Total	41.87
3-Species	
1. <i>A. stricta</i>	16.25
2. <i>I. glabra</i>	0.12
3. <i>C. fasciculata</i>	33.75
Total	50.12
5-Species	
1. <i>A. stricta</i>	10.62
2. <i>A. virginicus</i>	0.5
3. <i>I. glabra</i>	17.86
4. <i>C. fasciculata</i>	15.75
5. <i>P. graminifolia</i>	23.75
Total	68.48

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BIOGRAPHICAL SKETCH

Pedram Patrick Daneshgar was born in Akron, Ohio on May 17th, 1979. He was raised in Wilmington, Delaware where he spent a majority of his time outside. His curiosity about all living things led him to study biology at the University of Delaware, (Newark) where he received his Bachelor of Arts in May 2001. At Saint Joseph's University in Philadelphia, Pennsylvania, he received a Master of Science in biology in May 2003. It was there with his mentorship from Dr. Greg Ettl that his interest in ecology grew. Under the advisorship of Dr. Shibu Jose, Pedram earned his PhD from the School of Forest Resources and Conservation at the University of Florida in Gainesville, Florida, studying the impacts of invasive species. After earning his doctoral degree he attained a post-doctoral position studying the ecology of invasive species.