

ESTABLISHMENT AND MANAGEMENT OF NATIVE WILDFLOWERS ON FLORIDA
ROADSIDES AND FORMER PASTURES

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

2008

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To my yaya,
Emily Osmou Velelli.

ACKNOWLEDGMENTS

I would like to express my gratitude to my chair, Dr. Jeff Norcini, and my cochair, Dr. Carrie Reinhardt Adams, for their guidance and for the many hours they contributed to this project. I would like to acknowledge Dr. Jeff Norcini for his commitment to conserving Florida native wildflowers and for conceiving of the grant project that funded this research. I am grateful to Dr. Carrie Reinhardt Adams for helping me “keep my eyes on the prize” and for devoting as much energy to being a cochair as she would a chair. I would like to thank my committee members, Dr. Doria Gordon, Dr. Debbie Miller, and Dr. Sandy Wilson, who have graciously lent their expertise and provided guidance throughout the project. I am also indebted to Dr. Bijan Dehgan for serving as my cochair during the first two years of my program and for his continued mentorship. I am fortunate to have had such a supportive and involved committee.

This project was made possible through the financial support of The Florida Department of Transportation. I am also indebted to Meghan Brennan, Mary Christman, and Ramon Littell for their statistical expertise that contributed to the project design and analysis. However, any errors contained herein are my own.

My deepest gratitude goes to the “wildflower crew,” who contributed to this project above and beyond the call of duty. Ethan Stonerook assisted with the seed bank study and with the setup of field plots in Citra. Kate Turner helped with virtually every aspect with this project and demonstrated her willingness to learn techniques in a subject far from her field of journalism. I am grateful to Claudia Peñuela for helping to coordinate and implement cutting treatments, necessary weeding, and data entry, also in a field that was not her own. I would like to thank Emily Austen for approaching this research with as much attention to detail and dedication as if it were her own. I am indebted to the “wildflower crew” as a whole for their commitment to getting the job done well, which often included spending many hours in the heat, cold, or rain,

with a seemingly endless number of pots, plots, and plants. In addition to their invaluable contribution to this project, I am also grateful for their friendship and good company.

Experiments conducted in Citra would not have been possible without the help of many capable people at the University of Florida's Plant Science Research and Education Unit. I am most indebted to Jim Boyer, who improved the project design with his knowledge of field experiments and willingly coordinated all of the experimental treatments. I am grateful to everyone who helped maintain the research plots and graciously shared their lunch room, including: Pete "Fast Eddie" Brown, Walt Davis, Ronald "Tom" Cutler, Tony Skinner, Roger Vath, Mike Durham, Carl Vining, Dan Beach, and anyone else I may have inadvertently forgotten. Their dedication made my work much easier and more enjoyable. I would also like to thank inmates from the Marion County Jail for their contribution to field work. I am especially grateful to the inmates who helped with the biomass harvest for their attention to detail and for teaching me the "Soulja Boy" dance.

The experiment conducted in Fort Pierce benefited from the help of many people at the University of Florida's Indian River Research and Education Center. I am particularly grateful to Keona Muller, who coordinated and supervised all the experimental treatments, regularly monitored and photographed the research plots, and organized and participated in data collection. Pat Frey, Sandy Wilson, Carl Frost, and several others provided valuable assistance in the field. I give special thanks to Randy Burton for carrying out the experimental treatments and for designing the "hedge trimmer on wheels" to mow the research plots. I am also grateful to Pat Frey and Judy Gersony for their gracious hospitality.

I am much obliged to Jim Aldrich, Amanda Brock, Barron Riddle, Tom Batey, Jeff Norcini, Tom Bolton, and the farm crew for assisting with field work at the North Florida

Research and Education Center in Quincy, Florida. I am grateful not only for the many hours of work they contributed, but also for their efforts to make me feel welcome. I give special thanks to the Quincy dorm, for providing a wealth of interesting stories and a greater appreciation for my own bed.

Experiments conducted in Gainesville, Florida benefited from the expertise of Jason Haugh, Joe Vasquez, Robert Smith, Brian Owens, and Doug Prevatt, who provided invaluable help in the greenhouse complex including building benches, installing irrigation, and applying pesticide. Marie Nelson, Cindy Olejownik, Richard Phelan and the rest of the Gainesville Environmental Horticulture Department helped with project logistics including reserving the state vehicle, coordinating payroll for all the field assistants, and helping with computer and network issues. Additionally, the students, faculty, and staff in the Plant Restoration and Conservation Horticulture Research Consortium provided support and a helping hand as needed throughout the project. They include Dr. Hector Perez, Dr. Mike Kane, Scott Stewart, Danielle Watts, Phil Kauth, and Daniela Dutra. I would especially like to thank Fé Almira and Nancy Steigerwalt for including me in their labs and helping me with project logistics.

Harvesting the biomass from the “competition study” (Chapter 2) required the help of many people. I am grateful to everyone who helped for working their hardest and for making it a fun experience. They include: Terry Byatt, Lisa Hager, Cassie Elowe, Kei Egan, Yaro Neils, Alison Heather, Kara Monroe, Dan Holden, Alison Lugin, Sheena Olimpo, Aron Guerrero, Stefanie Calvet, Joelle Szerdi, Jason Hyde, and Mandy Thomas. I am especially grateful to those who contributed a little extra by working in fall as well as summer, recruiting others, or otherwise giving the project their all, including: Brittany Borck, Charlene Volpe, Dallas Scott, Beau Frail, Lynette Salas, Lauren Pell, Mark Turner, Juan Carlos Calderon, Mohamed Kouider,

Felipe Osorio, Nancy Steigerwalt, and Julie Sorenson. I would also like to acknowledge the individuals who volunteered their time to the project, including: Kristen Bartlett Grace, Dr. Carrie Reinhardt Adams, Dr. Pete Adams, Regina Frances, and Simon Frances.

Although the results of the Miami roadside plots are not included in this dissertation, the study served as the basis for some of the experiments presented here. Therefore, I would like to thank Lauren Linares, formerly with the Florida Turnpike, for identifying the study areas and coordinating efforts with the Turnpike. Bruce Mantel, Bryan Nipe, and Andres Aquino, all with the Florida Turnpike, helped make the project possible. Kristie Wendelberger, Hannah Thornton, Steve Woodmansee, and Regina Frances provided invaluable field assistance. Hannah Thornton helped with the initial design and patiently taught me how to delineate plots accurately with a compass and measuring tape. Steve Woodmansee also helped identify plant specimens from the seed bank study.

I am indebted to The North Carolina Botanical Garden for introducing me to the importance of native plant conservation. I would also like to acknowledge Claudia Alta "Lady Bird" Taylor Johnson (1912-2007) for spearheading the Highway Beautification Act and for her commitment to natural resource conservation.

I would like to express my gratitude to Lisa Hager, Natalie Boodram, and Jensen Montambault for their friendship and support over the years. I am especially grateful to Lisa Hager, who not only helped to format the references in this dissertation, but also served as a mentor throughout this process.

I would like to thank Brian Frankel for his unconditional support over the past three years and for helping me to keep things in perspective. I am most grateful for his ability to take my ideas seriously while encouraging me to not take myself too seriously.

I cannot express enough gratitude to my parents, who have supported me emotionally and financially, and provided volunteer field assistance, home-cooked meals, and enough worrying to ensure that nothing could go wrong. Finally, I would like to acknowledge the sacrifices made by my grandparents and parents that made it possible for me to pursue this path.

TABLE OF CONTENTS

	<u>page</u>
ACKNOWLEDGMENTS	4
LIST OF TABLES	11
LIST OF FIGURES	12
ABSTRACT.....	14
 CHAPTER	
1 INTRODUCTION	16
Overview and Rationale	16
Use of Local Ecotypes	18
Seed and Microsite Limitations to Establishment	20
Role of Competition	22
Effects of Disturbance	24
Chemical Disturbance (Herbicide).....	25
Mechanical Disturbance (Topsoil Removal and Mowing)	26
Native Wildflower Species	28
Research Design and Objectives	29
2 EFFECTS OF PLANTING SEASON, INITIAL ADVANTAGE, AND CUTTING FREQUENCY ON THE COMPETITIVE INTERACTIONS BETWEEN A NON- NATIVE PASTURE GRASS AND TWO NATIVE WILDFLOWERS	32
Introduction.....	32
Methods	35
Study Species and Site.....	35
Experimental Design	36
Data Collection and Analysis	38
Results.....	39
Season and Species.....	39
Initial Advantage and Competition	39
Cutting Frequency	40
<i>Coreopsis</i> Fitness.....	40
Discussion.....	41
Inter- Versus Intraspecific Competition	41
Seasonal Differences	42
Species-Specific Responses.....	43
Disturbance.....	44
Initial Advantage	45
Conclusions.....	47

3	EVALUATING SEED AND MICROSITE LIMITATION TO THE ESTABLISHMENT OF A NATIVE WILDFLOWER IN A NON-NATIVE PASTURE GRASS	55
	Introduction.....	55
	Methods	59
	Study Site and Species.....	59
	Experimental Design	60
	Data Collection and Analyses	62
	Results.....	63
	<i>Coreopsis lanceolata</i> Changes Over Time.....	63
	<i>Coreopsis lanceolata</i> Establishment	64
	<i>Coreopsis lanceolata</i> Fitness.....	65
	Community Vegetation	66
	Soil Characteristics.....	68
	Discussion.....	68
	Interactive Effects of Seed and Microsite Availability	68
	Disturbance Effects on Microsite Quality	69
	Requirements for Emergence Versus Establishment	72
	Effects on Community Vegetation	73
	Conclusions.....	74
4	MOWING FREQUENCY AND HERBICIDE EFFECTS ON ESTABLISHING NATIVE WILDFLOWER POPULATIONS ON SIMULATED ROADSIDES	82
	Introduction.....	82
	Methods	84
	Study Sites and Species	84
	Experimental Design	86
	Seed Bank Study.....	87
	Statistical Analysis	88
	Results.....	89
	<i>Gaillardia pulchella</i>	89
	<i>Coreopsis lanceolata</i>	90
	<i>Coreopsis leavenworthii</i>	91
	Discussion.....	93
	Species-Specific Responses.....	93
	Effects of Imazapic.....	95
	Mowing Treatments.....	96
	<i>Paspalum notatum</i> Dominance.....	96
	Conclusions.....	97
	CONCLUSIONS.....	109
	LIST OF REFERENCES	118
	BIOGRAPHICAL SKETCH	128

LIST OF TABLES

<u>Table</u>	<u>page</u>
2-1	Effects of species (<i>Coreopsis leavenworthii</i> , <i>C. lanceolata</i>), cutting frequency (none, once/month, twice/month), planting treatment, and their interactions on above- and belowground biomass of the target (central) <i>Coreopsis</i> in fall-established plants48
2-2	Effects of species (<i>Coreopsis leavenworthii</i> , <i>C. lanceolata</i>), cutting treatment (none, once/month, twice/month), planting treatment, and their interactions on flower number of the target (central) <i>Coreopsis</i> in fall-established plants.48
3-1	Disturbance treatment effects (control, sethoxydim, glyphosate, scraped) on soil chemistry before seeding <i>Coreopsis lanceolata</i> in a former pasture in Citra, FL.75
3-2	Effects of irrigation (none, pre, full), seeding rate (low, medium, high), disturbance (control, sethoxydim, glyphosate, scraped), and time (weeks after seeding) on density and percent cover of <i>Coreopsis lanceolata</i> in a former pasture in Citra, FL76
3-3	Effects of irrigation (none, pre, full), seeding rate (low, medium, high), and disturbance (control, sethoxydim, glyphosate, scraped) on percent cover of <i>Paspalum notatum</i> , forbs, and graminoids 10 and 46 weeks after seeding <i>Coreopsis lanceolata</i> in a former pasture in Citra, FL.77
4-1	Soil characteristics and types before seeding native wildflowers (<i>Gaillardia pulchella</i> , <i>Coreopsis lanceolata</i> , <i>C. leavenworthii</i>) at the study sites located in Quincy, Citra, and Fort Pierce, FL.....98
4-2	Dates of mowing treatments used at each site (Quincy, Citra, Fort Pierce, FL) for each species (<i>Gaillardia pulchella</i> , <i>Coreopsis lanceolata</i> , <i>C. leavenworthii</i>).....99
4-3	Effects of establishment treatment (pre-seeding herbicide: control, glyphosate, and imazapic), mowing frequency (two or six times/year), and their interactions on wildflower percent cover of <i>Gaillardia pulchella</i> in Quincy and Citra, FL.....100
4-4	Effects of establishment treatment (pre-seeding herbicide: control, glyphosate, and imazapic), mowing frequency (two or six times/year), and their interactions on wildflower percent cover of <i>Coreopsis lanceolata</i> in Quincy and Citra, FL.....101
4-5	Effects of establishment treatment (pre-seeding herbicide: control, glyphosate, and imazapic), mowing frequency (two or six times/year), and their interactions on wildflower percent cover of <i>Coreopsis leavenworthii</i> in Quincy, Citra, and Fort Pierce, FL.....102
4-6	Effects of establishment treatment (pre-seeding herbicide: control, glyphosate, and imazapic), mowing frequency (two or six times/year), and their interactions on emerged wildflower seedlings from the soil seed bank in fall 2006 in Quincy, Citra, and Fort Pierce, FL.103

LIST OF FIGURES

<u>Figure</u>	<u>page</u>
2-1	Total monthly rainfall and minimum and maximum temperatures at the study site in Gainesville, FL during the experiment..49
2-2	The two monocultures and four mixtures included in the planting treatments.....50
2-3	Effects of planting season (fall or spring) and species (<i>Coreopsis lanceolata</i> or <i>C. leavenworthii</i>) on <i>Coreopsis</i> survival (target plant) eight months after planting.51
2-4	Effects of neighbor plant species on above- and belowground biomass of the target (center) <i>Coreopsis</i> in fall-established plants.....52
2-5	Effects of cutting frequency on above- and belowground biomass of the target (center) <i>Coreopsis</i> , neighboring <i>Coreopsis</i> , and neighboring <i>Paspalum</i> in fall-established plants...53
2-6	Effects of cutting frequency and planting treatment on the mean number of <i>C. leavenworthii</i> and <i>C. lanceolata</i> flowers in fall-established plants54
3-1	Minimum and maximum temperatures at 60 cm, solar radiation, and precipitation at the study site in north-central Florida78
3-2	Effects of irrigation, seeding rate, and disturbance treatments on <i>Coreopsis lanceolata</i> density and percent cover79
3-3	Effects of seeding rate and disturbance treatment on shoot biomass of <i>Coreopsis lanceolata</i> , <i>Paspalum notatum</i> , forbs, and graminoids 46 weeks after seeding80
3-4	Effects of seeding rate and disturbance treatment on percent cover of <i>Coreopsis lanceolata</i> flowers 20 weeks after seeding81
3-5	Effects of seeding rate and disturbance treatment on number of <i>Coreopsis lanceolata</i> seedlings 46 weeks after seeding81
4-1	Solar radiation, temperature, and rainfall in Fort Pierce, Citra, and Quincy, FL during the study period..104
4-2	Effects of establishment treatment (pre-seeding herbicide: control, glyphosate, and imazapic) on wildflower percent cover by site, season, and year.....105
4-3	Composition of <i>Gaillardia pulchella</i> , forbs, and graminoids in the seed bank in fall 2006 and as aboveground vegetation in spring 2007 in Quincy and Citra, FL106

4-4 Composition of *Coreopsis lanceolata*, forbs, and graminoids in the seed bank in fall 2006 and as aboveground vegetation in spring 2007 in Quincy and Citra, FL.107

4-5 Composition of *Coreopsis leavenworthii*, forbs, and graminoids in the seed bank in fall 2006 and as aboveground vegetation in spring 2007 in Quincy, Citra, and Fort Pierce, FL.....108

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

ESTABLISHMENT AND MANAGEMENT OF NATIVE WILDFLOWERS ON FLORIDA
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By

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August 2008

Chair: Jeffrey G. Norcini
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Major: Horticultural Science

Establishing native wildflowers into areas dominated by *Paspalum notatum* var. *saurae* (bahiagrass) is a common goal of roadside management and ecological restoration. Yet, there is limited information on establishment and management practices for local ecotype seeds. This research sought to determine the effects of competition and disturbance on native wildflower establishment in areas dominated by *P. notatum*.

Effects of planting season and post-planting disturbance (cutting) were assessed on competitive interactions between *P. notatum* and two Florida native congeners, *Coreopsis lanceolata* (lanceleaf tickseed) and *C. leavenworthii* (Leavenworth's tickseed) in two-species competition experiments. *Coreopsis* survival was greater in fall- than spring-established plants. In fall-established plants, *C. lanceolata* had higher survivorship than *C. leavenworthii*, although *C. leavenworthii* biomass and flower number were greater than that of *C. lanceolata*. *Paspalum notatum* reduced *C. lanceolata* biomass 58% and *C. leavenworthii* biomass 41%; however, conspecific neighbors reduced biomass of both *Coreopsis* species by at least 81%. Cutting decreased above- and belowground *Coreopsis* biomass by 55% and 30%, respectively.

Seed and microsite limitations to establishment were assessed by seeding *C. lanceolata* at 100, 600, and 1100 live seeds/m² and altering microsites with disturbance (none, sethoxydim herbicide, glyphosate herbicide, topsoil removal) and irrigation (none, pre-seeding, pre- and post-seeding) treatments. By the end of the study, microsite limitation was greater than that of seed limitation with greater *C. lanceolata* establishment in the glyphosate treatment than other disturbance treatments. *Coreopsis lanceolata* establishment was limited when seeded at 100 seeds/m² but not at 600 seeds/m². Seeding at 1100 seeds/m² provided little increase in establishment compared to 600 seeds/m².

Effects of pre-planting herbicide treatments (none, glyphosate, imazapic) and post-planting mowing frequencies (two and six times/year) were assessed for three wildflower species (*C. lanceolata*, *C. leavenworthii*, and *Gaillardia pulchella* (firewheel)) on simulated roadsides at three sites in Florida. The glyphosate treatment resulted in greater wildflower establishment than the imazapic and control treatments. The imazapic treatment improved establishment of *C. lanceolata* only, which also had moderate cover in the control treatment. Mowing frequency did not affect wildflower percent cover or seed bank density, perhaps because mowing was reduced during wildflower blooming and seed dispersal.

CHAPTER 1 INTRODUCTION

Overview and Rationale

As more land is developed for human use, biodiversity and habitat for native species continue to decline. Given increased human population growth and increased per capita consumption of resources, continued development seems inevitable (Tilman et al. 2001). Conversion of land to agriculture and development negatively affects biodiversity conservation through habitat destruction and fragmentation, climate change, pollution, and the spread of invasive species, among others. While traditional conservation efforts have focused on areas less disturbed by human development (i.e., natural areas), the presence of altered landscapes has become ubiquitous in many parts of the world. Altered landscapes may be managed or restored to lessen negative impacts on conservation areas or undeveloped habitat, and, in some cases, conserve biodiversity. Conservation efforts in altered landscapes have therefore become a necessity in achieving the overall objectives of conservation (Grimm et al. 2008).

A consequence of development and population growth is an increase in the number of roads. Within the past century, roads have become a widespread component of our landscape, ubiquitous in almost every part of the United States (Forman and Alexander 1998). The area that roads impact is much greater than the space they occupy (Forman and Alexander 1998, Watts et al. 2007). Roads not only alter the land they encompass, but also impact the terrestrial and aquatic ecosystems in which they occur and influence adjacent land use (Trombulak and Frissell 2000). Roads may also provide corridors for invasive, non-native species to expand their range (Gelbard and Belnap 2003).

Conservation efforts on roadsides are focused on minimizing negative impacts on wildlife and surrounding natural areas. Mortality of animals through vehicle collisions has been

reduced by incorporating wildlife crossings into roadside plans (Bissonettea and Adairb 2008). Modifying management activities may also help to protect rare plant species that occur on roadsides. Planting and conserving native species on roadsides may decrease the occurrence of non-native species and serve to buffer surrounding natural areas from the negative effects of roads. Native wildflowers on roadsides may also help to meet Departments' of Transportation other objectives including roadside beautification and reduced costs through decreased mowing (Florida Department of Transportation 1998, Harper-Lore and Wilson 2000). For these reasons, there has been an increased interest in planting native species on roadsides (Gordon et al. 2000).

As undeveloped land becomes increasingly scarce, restoring former agricultural land has become a goal of many restoration projects (Zimmerman et al. 2000, Stevenson and Smale 2005, Sampaio et al. 2007, Orrock et al. *in press*). Some of the area available for restoration in the southeastern United States is abandoned pastureland. In Florida alone, pasture and rangeland occupy over 2.1 million ha and often overlap sensitive wetland areas (Swain et al. 2007). However, several barriers exist to restoring native communities on former pasture. Abandoned agricultural areas often have altered hydrology and levels of soil nutrients, which can affect plant productivity. The dominant species (usually a grass) may prevent the establishment of new species and may be difficult to eradicate. Moreover, native plant propagules to recolonize the site may be lacking.

Ecological restoration and roadside beautification projects often require the introduction of desirable plant species. Plants provide the basic structure and primary production upon which many other species and processes depend and are therefore an integral part of terrestrial revegetation and restoration projects. In Florida, *Paspalum notatum* Flügge var. *saurae* Parodi (bahigrass) occurs on roadsides as well as on land slated for restoration (Violi 2000).

Therefore, establishing native wildflowers (forbs) into *P. notatum* is a common goal of roadside management and ecological restoration projects. Yet, little is known about effective establishment and management methods. Evidence suggests that wildflower establishment is limited by competition from *P. notatum*, although this has not been experimentally tested. Establishment methods may be different on roadsides and pastures than natural areas due to altered hydrology and soil nutrients. Disturbance treatments that eradicate or reduce *P. notatum* may increase the establishment and sustainability of native wildflower populations, yet this has not been confirmed. Moreover, local ecotype seeds have recently become available, which may require different establishment and management methods than seeds from nonlocal sources.

Use of Local Ecotypes

There is an increasing concern about the risks of introducing nonlocal native plants in restoration projects and roadside plantings, including genetic swamping and outbreeding depression of local populations (Booth and Jones 2001). For this reason, restoration protocol often suggests using plant sources of local provenance or local ecotypes (Booth and Jones 2001). Similarly, the Florida Department of Transportation would like to expand their current wildflower program to increase the number of local ecotype, native wildflower populations on roadsides (Florida Department of Transportation 1998). The ecotype concept was introduced by Turesson in the 1920s to describe genetic varieties within a single species (Lubchenco and Real 1991). An ecotype is a population of a species that has adapted to a particular set of environmental conditions via natural selection.

Adaptation to the introduction site is not only essential for the survival of the introduced individuals but also for the persistence of the population over time. Local ecotypes may be better adapted to the climate at the introduction site than nonlocal ecotypes. For example, in a study examining effects of population size and distance of introduced species, Vergeer et al.

(2004) found evidence of local adaptation. In plants, ecotypic differentiation can influence a number of processes including freezing tolerance and germination. For example, in response to low temperatures, northern ecotypes of two woody tree species acclimated more rapidly and developed greater tolerance to freezing than southern ecotypes (Li et al. 2004, Li et al. 2005). In several species, populations originating from sites with severe winters required long periods of chilling to break dormancy while populations from warmer sites germinated very quickly under the same conditions (Allen and Meyer 1998). Moreover, Norcini et al. (2001) found that local ecotypes of *Coreopsis lanceolata* in Florida bloomed earlier and had higher survivorship than nonlocal ecotypes.

The need to develop safe “transfer zones” for native plant material has been expressed by state and federal agencies (United States Department of Agriculture and United States Department of the Interior 2002). Transfer zones provide physical boundaries within which ecotypes of species can safely be transferred, without negatively impacting the genetics of plant metapopulations. Several state programs are already in place. For example, the Iowa Ecotype Project was developed to increase the availability of Iowa-origin seed for roadside plantings and prairie reconstructions (Houseal and Smith 2000). Similarly, Missouri started a local ecotype program with 33 species from two prairie ecozones, which were based on climate and soil conditions (Erickson and Navarrete-Tindall 2004). In addition, the Oregon Department of Forestry (2007) developed seed transfer zones for many tree species. Although some programs are already in place, a consortium of federal agencies recommended that funding and research be devoted to developing transfer zones (United States Department of Agriculture and United States Department of the Interior 2002).

In Florida, the demand for native wildflower seed for roadside plantings exceeds the availability of local ecotype seed (Florida Department of Transportation 1998). Within the last five years, local ecotype seeds of several species of native wildflowers have become available through Florida's Wildflower Seed and Plant Growers Association, Inc. (2008). Currently, limited information exists on effective methods to establish local ecotype native wildflowers on Florida roadsides (but see Norcini and Aldrich 2004, Florida Department of Transportation 2005). Because Florida ecotypes are adapted to Florida's climate, establishment and management practices may be different than those for nonlocal seed sources and on altered landscapes such as roadsides.

Seed and Microsite Limitations to Establishment

Direct seeding of propagules into restoration sites is often the most economical approach for revegetation (Pfaff and Gonter 1999). However, in order for a plant to become established at a new site, the seed (or propagule) must not only arrive at the site, but also germinate and survive the seedling stage of development. For this reason, plant establishment is said to be limited by the availability of seeds, of areas suitable for emergence and growth, or of both (Stampfli and Zeiter 1999, Turnbull et al. 2000, Zobel et al. 2000, Holzel 2005). If a species does not exist at a site due to dispersal limitation, the site is said to be seed limited.

In restoration projects and roadside plantings, the number of seeds introduced to the site is determined by the seeding rate. Yet, there is limited information on the effects of seeding rate on establishment. Seeding rates are rarely based on parameters that ensure establishment of the restored population (e.g., Cole 2007) and are more often chosen based on seed availability or limited empirical data. For example, the Florida Department of Transportation uses the same bulk seeding rate for several wildflower species because species-specific requirements are not yet known (Florida Department of Transportation 1998). Seeding at deliberately high rates is

practiced to increase the seeded species' competitive ability over existing vegetation. In a study on native grass restoration in California, doubling the seed density resulted in twice as many established grass plants (Orrock et al. *in press*). While increasing the seeding rate may increase overall emergence, Harkess and Lyons (1998) found that doubling the seeding rate did not affect the number of plants maturing to flower. Moreover, increasing the seeding rate of native legumes negatively affected individual plant establishment (Fischbach et al. 2006).

Plant establishment of introduced populations not only depends upon the appropriate seeding rate but also upon creating areas suitable for seedling emergence and survival, i.e., microsites, which are also known as safe sites or regeneration niches. Microsites suitable for germination and seedling establishment are species-specific, but usually provide water and contact with the soil (Isselstein et al. 2002). In natural systems, water is present in the soil through rainfall, groundwater, or a nearby wetland. However, water availability on degraded sites may be different than adjacent natural systems due to altered hydrology. Therefore, germination of introduced seeds on degraded sites may be particularly limited in these systems by the lack of water at the soil surface. Moreover, seeding may occur in a different season than natural seed dispersal or when rainfall is limited. In these cases, supplemental irrigation can increase the seeded species survival and establishment (Harper-Lore and Wilson 2000, Cox et al. 2004).

Microsites for new species may be limited by the existing vegetation (Pfaff and Gonter 1999), which can prevent seed-to-soil contact and limit resources like water, light, and nutrients through competition (Tilman 1994). For example, increased productivity in grasslands prevented seedling establishment of forbs by decreasing light levels (Foster and Gross 1998). Seeds of some species require exposure to high ratios of red to far-red light to germinate (Rees

1997, Baskin and Baskin 2001). Existing canopies decrease the red to far-red ratio, which inhibits germination of some species (Rees 1997). Disturbance treatments that reduce or remove the existing vegetation have led to increased establishment of desirable species in other habitats (Holzel 2005, Martin and Wilsey 2006).

Although there is little published information on the establishment of native wildflowers in *P. notatum* in Florida, evidence suggests that native forbs introduced into communities dominated by *P. notatum* often fail to establish (Uridel 1994, Violi 2000). Selected for its drought tolerance and lack of pest problems, *P. notatum* was originally introduced as a pasture grass but is also commonly planted on roadsides due to its effectiveness in controlling erosion through the formation of dense mats (Violi 2000). *Paspalum notatum* was introduced to the United States from Brazil in 1913 (Scott 1920) and was estimated to occupy over 2 million ha in the southeastern U.S. by 1978 (Beatty and Powell 1978). Studies on former pastures in Florida indicate that disturbing or removing *P. notatum* can lead to increased establishment of native wildflowers (Uridel 1994, Gordon et al. 2000). Based on these field observations, competition is hypothesized to be the driving interaction between *P. notatum* and native wildflowers, although this has not been experimentally tested.

Role of Competition

Competition is hypothesized to play an important role in structuring biological communities and has been extensively studied in both agricultural (Radosevich and Rousch 1990, Booth et al. 2003) and natural (Grace and Tilman 1990, Tilman 1990) systems. Processes governing plant-plant interactions have focused on competition because species that coexist often compete for limited resources like light, water, and nutrients (Goldberg 1990). In plants, competition occurs aboveground through shoots and belowground through roots. Aboveground competition is usually expressed as competition for light. Since light is unidirectional, taller

species usually are better competitors for light as they shade out shorter species (Hely and Roxburgh 2005, Lepik et al. 2005). Belowground competition is usually mediated through limiting resources like nutrients and water (Tilman 1994). Aboveground competition is usually stronger when light is limiting and belowground competition is usually stronger when water and nutrients are limiting. Two-species competition experiments have been used to determine the stronger competitor under a particular set of conditions (Connolly and Wayne 2005).

In field experiments involving *P. notatum* and native wildflowers, competition is assumed to be limiting establishment. However, competitive interactions may be influenced by initial advantage, seasonal differences, and disturbance treatments. Since *P. notatum* has been planted on roadsides and pastures in the southeastern United States for many years, vegetation on these sites often consists of well-established monotypic stands of *P. notatum*. Competition between species can be influenced by their order of arrival at a site (Ejrnaes et al. 2006). Regarding competition for light, the first individuals to arrive at a site (or larger individuals) often have a competitive advantage over other individuals (Hely and Roxburgh 2005). Competitive ability between two species can therefore depend on the order of arrival, species identity, or both (Hely and Roxburgh 2005). When native wildflowers are introduced into well-established monotypic stands of *P. notatum*, assessing the competitive ability between *P. notatum* and native wildflowers may be confounded with *P. notatum*'s initial advantage over the wildflower species. The importance of arrival order in determining species composition has been called historical contingency (Ejrnaes et al. 2006), while the effects of arrival order on competitive interactions are referred to as initial advantage or the founder effect (Perry et al. 2003, Hely and Roxburgh 2005).

Seasonality can influence competitive interactions between *P. notatum* and wildflower species. *P. notatum* is a long-day plant that is dormant during the short days of winter (Marousky and Blondon 1995). Flowering is initiated when day length exceeds 13.5 hours (Marousky and Blondon 1995). In Florida, *P. notatum* flowering usually begins in May and seed maturation occurs throughout the summer (Watson and Burton 1985). *Paspalum notatum* height can exceed 100 cm when in flower, compared with approximately 20 cm when dormant (personal observation). The increase in height during the summer months likely intensifies aboveground competition between *P. notatum* and wildflower species. Planting wildflowers in the fall, when *P. notatum* is dormant, may lead to increased establishment.

Disturbance can also influence competition between wildflowers and *P. notatum*. By reducing asymmetric competition for light (Lepš 1999), disturbance can temporarily disrupt competitive exclusion. For example, the competitive effects of grasses on herbaceous species can be temporarily alleviated by removing the grass via herbicide (del-Val and Crawley 2005). If competition from *P. notatum* is limiting wildflower establishment, disturbing *P. notatum* may increase wildflower establishment.

Effects of Disturbance

Disturbance is an integral component of ecological systems and can be broadly defined as any event that causes changes to community structure and function. Plant disturbance is often defined as a discrete event that reduces biomass in a community. Disturbance regime refers to both the type and frequency of disturbance. The frequency of disturbance can greatly affect the species composition and diversity of an ecosystem. Ecological theory predicts that an intermediate frequency of disturbance can increase diversity in some habitats (Connell 1978). Increased species richness and diversity in response to moderate disturbance are well-documented (Dayton 1971, Lepš 1999).

While disturbance occurs in all habitats, some habitats are maintained by frequent disturbance. For example, longleaf pine ecosystems in the southeastern United States are maintained by frequent fire (Taylor 1998). Many of Florida's native wildflowers naturally occur in habitats with frequent disturbance (Taylor 1998). However, the type and frequency of disturbance in natural systems are usually different than on roadsides and pastures. While roadsides and pastures are subject to both natural and artificial disturbance regimes, natural disturbance regimes like fire and flooding tend to be prevented or controlled on roadsides for safety reasons. Moreover, management activities on roadsides include disturbances such as herbicide application and mowing (Forman et al. 2003).

Chemical Disturbance (Herbicide)

Disturbance treatments include practices that reduce or remove the existing vegetation. Disturbance can be chemical or mechanical and can occur before or after wildflower emergence. Chemical disturbance includes the use of herbicides to eradicate or reduce undesirable vegetation without disturbing the soil. Non-selective, or broad-spectrum herbicides, are designed to injure or kill any plant they contact, while selective herbicides affect sensitive species but do not affect tolerant species (Monaco et al. 2002).

Glyphosate (e.g., Roundup®) is an example of a non-selective herbicide (Monaco et al. 2002). Applying glyphosate to *P. notatum* increased the establishment of native species subsequently planted in *P. notatum* pastures (Gordon et al. 2000; Uridel 1994). Because glyphosate is non-selective, it should be applied before wildflower seeding or planting. Sethoxydim (e.g., Poast®, Vantage®) is a graminicide, i.e., grasses are sensitive to the herbicide but dicots and non-grass monocots are either not sensitive or have very low sensitivity (Monaco et al. 2002). Since dicots and non-grass monocots are tolerant of graminicides, sethoxydim can

be used for the postemergence control of grasses with little damage to other species. Thus, sethoxydim can be applied at any time during wildflower establishment.

Imazapic (Plateau®, Impose™, Panoramic 2SL) is a selective herbicide that has improved the restoration of native species in certain habitats (Masters et al. 1996). The tolerance of wildflowers to imazapic varies considerably according to species, ecotype, and rate of application (Norcini et al. 2003). Wildflowers are generally more tolerant to imazapic when applied preemergence compared to postemergence (BASF Corporation 2003, Norcini et al. 2003). When imazapic is applied at the time of wildflower seeding, it can decrease the density and growth rate of some existing vegetation while minimally impacting the emergence or establishment of certain wildflower species (Beran et al. 1999, Norcini et al. 2003).

On roadsides, the complete eradication of *P. notatum* may not be desirable because of the possibility of increased erosion. However, while *P. notatum* effectively stabilizes roadsides, it continuously produces tall seedheads throughout the summer, which may require frequent mowing to maintain acceptable driver visibility (Baker et al. 1999). Herbicides at sublethal rates can be used as plant growth retardants to limit seedhead production of *P. notatum* and therefore reduce the frequency of mowing (Baker et al. 1999, Florida Department of Transportation 2005). The reduced *P. notatum* growth may have the added benefit of increasing wildflower establishment, without completely eradicating *P. notatum*. Glyphosate, sethoxydim, and imazapic have suppressed seedhead production of *P. notatum* when applied at low rates (Baker et al. 1999).

Mechanical Disturbance (Topsoil Removal and Mowing)

Mechanical disturbance includes treatments that physically remove the existing vegetation and typically include tilling, disking, and mowing. Topsoil removal, or scarification, is also an example of mechanical disturbance. Topsoil removal has led to increased native

species establishment in former agricultural areas by removing the dominant vegetation as well as decreasing artificially enhanced soil nutrient levels (Holzel 2005, Buisson et al. 2006, Clark and Tilman 2008). Topsoil removal may also remove the majority of weed seeds in the soil seed bank (Roberts 1981, Dalrymple et al. 2003). A combination of repeated herbicide application and sod removal through disking or plowing has been shown to effectively control *P. notatum* (Violi 2000); however, it is not clear if combining herbicide treatments with mechanical sod removal results in greater *P. notatum* control than either treatment alone.

Mowing is another type of mechanical disturbance. Unlike topsoil removal or tilling, mowing disturbs the existing vegetation but does not disturb the soil. Mowing of roadside vegetation is the most common and widespread form of roadside management, and is primarily utilized for driver safety. The purpose of mowing is to reduce the height of vegetation, which can interfere with driver visibility, and to prevent the growth of woody species, which could harm drivers who pull off of the road.

The frequency, timing, and height of mowing can influence plant species composition on roadsides. Grasses tend to thrive in areas that are frequently mowed, due to their ability to rapidly grow new shoots from a ground-level apical meristem (Forman et al. 2003). Mowing has been shown to increase species diversity (Parr and Way 1988, Collins et al. 1998, Hoffmann et al. 2004) in some habitats. In a long-term study comparing mowing frequencies, the diversity of roadside vegetation was greater in areas mowed two times per year than once per year or not at all, and the lowest diversity was found in areas that were not mowed (Parr and Way 1988). Although the frequency of roadside mowing varies, it is generally much more frequent in Florida (two-twelve times per year) than naturally occurring disturbance.

Mowing of roadsides can affect the recruitment of wildflower populations positively by providing regeneration niches and negatively by limiting reproduction. Mowing and removing litter can increase germination and establishment of seedlings (Jensen and Meyer 2001, Jutila and Grace 2002). However, the time of year an area is mowed can significantly impact the growth and recruitment of a species, especially if mowing precedes seed set (Brys et al. 2004). In both annual and perennial species, mowing that precedes seed maturation will likely limit recruitment and decrease the sustainability of the population. If the species is an annual, the population would only persist at that site if viable seeds were stored in the soil. Conversely, mowing that occurs after seed maturation could facilitate seed dispersal and subsequent emergence of dispersed seeds. Flower and seed phenology vary according to wildflower species, weather, and site conditions, making specific mowing recommendations difficult to predict.

Native Wildflower Species

Many wildflowers native to Florida are annuals to short-lived perennials that invest in reproductive growth early in life (Taylor 1998, Wunderlin and Hansen 2003). In fact, wildflowers are planted or maintained on roadsides for their attractive display of flowers. However, different wildflower species may respond differently to abiotic conditions, disturbance, and competition from *P. notatum*. Different plant traits or life-history strategies within a plant community may promote species coexistence (Coomes and Grubb 2000, Booth et al. 2003). However, plant survival strategies normally involve trade-offs. For example, plants that are good colonizers are usually not good competitors over time (Coomes and Grubb 2000). Therefore, some wildflower species may be stronger competitors while other wildflowers may recruit more successfully. Additionally, establishment of each wildflower species may be greater in certain habitats than others.

Since species-specific traits can influence the establishment of native wildflowers, three native wildflower species were included in this study. All three species are in the Asteraceae and include: *Gaillardia pulchella* Foug. (firewheel), *Coreopsis lanceolata* L. (lanceleaf tickseed), and *Coreopsis leavenworthii* Torr. & A. Gray (Leavenworth's tickseed) (United States Department of Agriculture 2008). *Gaillardia pulchella* is an annual to short-lived perennial commonly occurring throughout Florida in disturbed uplands (Wunderlin and Hansen 2003). *Coreopsis lanceolata* is an evergreen, short-lived perennial that occurs throughout much of the United States (Flora of North America Editorial Committee 2006, United States Department of Agriculture 2008). In Florida, *C. lanceolata* occurs in northern and north-central regions in sandhill and disturbed habitats (Wunderlin and Hansen 2003). *Coreopsis leavenworthii* is an annual to short-lived perennial and a facultative wetland species (Wunderlin and Hansen 2008). *Coreopsis leavenworthii* is common throughout Florida and occurs in depression marshes, disturbed wetland, marl prairie, pine rockland, wet flatwood, and wet prairie habitats (Gann et al. 2008).

Research Design and Objectives

Effective methods are needed to establish and manage native wildflowers on Florida roadsides and former pastures. Local ecotype seeds have recently become available, which may require different establishment and management methods than seeds from nonlocal sources. Moreover, conditions on roadsides and pastures often do not mimic the biotic and abiotic characteristics of native habitats. Anecdotal evidence suggests that wildflower establishment is limited by competition from *P. notatum*, although this has not been experimentally tested. Moreover, the effects of pre- and post-planting disturbance on planted native wildflower populations are unknown. This research seeks to determine the effects of competition and disturbance on native wildflower establishment and recruitment on roadsides and pastures

dominated by *P. notatum*. Results from this research will provide practical information to the Florida Department of Transportation to guide the establishment and management of local ecotype native wildflower species on roadsides.

To fulfill these objectives, three experiments were conducted, which are organized into separate chapters for this dissertation:

In Chapter 2, I examine the competitive effects of *P. notatum* on two Florida native congeners, *C. lanceolata* and *C. leavenworthii*. This experiment took place under controlled conditions, with initial establishment and density held constant in order to focus on competition. The competitive ability of each species was assessed at different frequencies of disturbance (post-planting) in a series of two-species competition experiments. The disturbance treatment involved cutting aboveground growth to simulate mowing. The effects of initial advantage and season of planting on competition were also assessed.

In Chapter 3, I examine the relative importance of seed and microsite limitation to wildflower establishment in a *P. notatum* pasture. By focusing on the establishment of one native wildflower species, *C. lanceolata*, I was able to test several levels of both seed and microsite limitation simultaneously. To test for seed limitations to establishment, *C. lanceolata* was seeded at low, medium, and high rates. To test for microsite availability, two factors were examined: supplemental irrigation and disturbance of existing vegetation. The irrigation treatment had three levels: no irrigation, a pre-seeding soak, and pre- and post-seeding irrigation. The disturbance treatment had four levels, listed in increasing level of disturbance: no disturbance, sethoxydim herbicide, glyphosate herbicide, and topsoil removal. The objectives of the experiment were to determine the relative and interactive effects of seeding rate, supplemental irrigation, and disturbance on *C. lanceolata* establishment in a *P. notatum* pasture.

In Chapter 4, I examine both establishment and management methods required for creating self-sustaining populations of native wildflowers on roadsides or former pastures. Specifically, I studied the effects of pre-planting herbicide treatments (establishment) and post-planting mowing frequencies (management) on three wildflower species: *C. lanceolata*, *C. leavenworthii*, and *G. pulchella*. To examine treatment effects across a range of climate and soil types, the experiment was conducted on simulated roadsides in three different regions of Florida. Sites were located in north (Quincy), north-central (Citra), and south-central (Fort Pierce), Florida. To facilitate evaluation of effects on wildflower establishment as well as subsequent recruitment, the experiment was conducted for two years.

CHAPTER 2
EFFECTS OF PLANTING SEASON, INITIAL ADVANTAGE, AND CUTTING
FREQUENCY ON THE COMPETITIVE INTERACTIONS BETWEEN A NON-NATIVE
PASTURE GRASS AND TWO NATIVE WILDFLOWERS

Introduction

Non-native species comprise the dominant vegetation of many areas targeted for revegetation and restoration projects. While replacing non-native species with natives is often a goal of these projects, the establishment of native species may be limited by competition from non-native species. Competition between natives and non-natives may be influenced by disturbance, species-specific traits, initial advantage, season, and site characteristics, among others. Confirming the role of competition between non-native and native species in context-specific situations can direct management activities to improve the establishment of desirable native species.

In Florida, *Paspalum notatum* Flüggé var. *saurae* Parodi (bahiagrass, hereafter *Paspalum*) occurs on roadsides and on some of the land slated for restoration (Violi 2000). *Paspalum* is a rhizomatous, mat-forming grass that can persist for decades and prevent native species establishment (Uridel 1994, Violi 2000). In restoration settings or roadside wildflower plantings in Florida, native forbs introduced into communities dominated by *Paspalum* often fail to establish. Disturbing or removing *Paspalum* can lead to increased establishment (Uridel 1994, Violi 2000). Based on these field observations, competition is hypothesized to be the driving interaction between *Paspalum* and native forbs, although this has not been experimentally tested.

In many restoration projects and roadside plantings, seeds of native forbs are introduced into *Paspalum* communities that are generally well-established monotypic stands. Assessing the competitive ability of *Paspalum* in these settings is confounded with the fact that *Paspalum* has the initial advantage. The importance of arrival order in determining species composition has

been called historical contingency (Ejrnaes et al. 2006), while the effects of arrival order on competitive interactions are referred to as initial advantage or the founder effect (Perry et al. 2003, Hely and Roxburgh 2005). Competition between species can be influenced by their order of arrival at a site (Ejrnaes et al. 2006). For example, in competition for light, the first individuals to arrive at a site (or larger individuals) often have a competitive advantage over other individuals (Hely and Roxburgh 2005). Competitive ability between two species can therefore depend on the order of arrival, species identity, or both (Hely and Roxburgh 2005). Initial size seems to affect competitive ability most when the competition is aboveground rather than belowground (Gerry and Wilson 1995, Perry et al. 2003).

Plant competition has been extensively studied in both agricultural (Radosevich and Rousch 1990, Booth et al. 2003) and natural (Grace and Tilman 1990, Tilman 1990) systems. Processes governing plant-plant interactions have focused on competition because species that coexist often compete for limited resources like light, water, and nutrients (Goldberg 1990). Generally, competition between two species is described as symmetric or asymmetric. If competition between two species is symmetric, resources are shared equally between the species. If competition is asymmetric, one species will have a competitive advantage over a coexisting species. Over time, the species with the competitive advantage will likely exclude the coexisting species from the area (Lepik et al. 2005). Asymmetry is far more common than symmetry in competitive interactions because one species is usually better able to allocate limiting resources than the other species in a particular environment (Ricklefs 1990). Aboveground, asymmetric competition occurs when larger or taller plants with more access to light competitively exclude shorter species through shading (Lepik et al. 2005, Hely and Roxburgh 2005). Belowground competition is usually mediated through limiting resources like nutrients and water (Tilman

1994). Two-species competition experiments have been used to determine whether asymmetric competition occurs between two species, and if so which species will competitively exclude the other (Connolly and Wayne 2005).

Competitive interactions may shift under different disturbance frequencies and environmental conditions. Disturbance can disrupt competitive exclusion by reducing asymmetric competition for light (Lepš 1999). Ecological theory predicts that an intermediate frequency of disturbance can increase diversity in some habitats (Connell 1978). Increased species richness and diversity in response to moderate disturbance are well-documented (Dayton 1971, Lepš 1999). Disturbance treatments reduce or remove the existing vegetation and can lead to increased establishment of desirable species in a restoration setting (Holzel and Otte 2003, Martin and Wilsey 2006). Many of Florida's native wildflowers naturally occur in habitats with frequent disturbance (Taylor 1998). However, the type and frequency of disturbance in natural systems are usually different than on managed systems like roadsides and pastures. While roadsides and pastures are subject to both natural and artificial disturbance regimes, natural disturbance regimes like fire and flooding tend to be prevented or controlled on roadsides for safety reasons. Moreover, management activities on roadsides include disturbances such as herbicide application and mowing (Forman et al. 2003).

Identifying the conditions that facilitate native forb establishment in areas dominated by *Paspalum* would provide insight into improving restoration projects and native roadside plantings. The objectives of this study were to 1) assess the competitive effects of *Paspalum notatum* on the growth and reproduction of two native forbs, *Coreopsis lanceolata* and *C. leavenworthii*, and 2) determine the effects of initial advantage, disturbance, and season of planting on competitive interactions between the species. I hypothesized that *Paspalum* would

decrease growth of both *Coreopsis* species but that the competitive ability of the *Coreopsis* species would increase with the initial advantage and a moderate amount of disturbance.

Methods

Study Species and Site

I examined effects of *Paspalum* competition on two congeners, *Coreopsis leavenworthii* and *C. lanceolata*. *Paspalum* was introduced to the United States from Brazil in 1913 (Scott 1920) and was estimated to occupy over 2 million ha in the southeastern U.S. by 1978 (Beatty and Powell 1978). Selected for its drought tolerance and lack of pest problems, *Paspalum* was originally introduced as a pasture grass but is also commonly planted on roadsides due to its effectiveness in controlling erosion through the formation of dense mats (Violi 2000). While several cultivars have been developed since its introduction, ‘Pensacola’ is the most common cultivar in Florida (Violi 2000) and was the cultivar used in this study. For this study, scarified seeds of *Paspalum* were purchased from a local agricultural supply store.

Coreopsis lanceolata L. (lanceleaf tickseed) is an evergreen, short-lived perennial that is native to much of eastern North America. Ranging from Florida west to New Mexico and north to Ontario, *C. lanceolata* typically occurs on sandy soils, ditches, roadsides, and disturbed sites and flowers from May through July (Flora of North America Editorial Committee 2006). In north-central Florida, *C. lanceolata* occurs in sandhills and disturbed sites and blooms in spring (Wunderlin and Hansen 2003). *Coreopsis leavenworthii* Torr. & A. Gray (Leavenworth’s tickseed) is an annual to short-lived perennial that is common throughout Florida (Wunderlin and Hansen 2003). A facultative wetland species, *C. leavenworthii* occurs in depression marshes, disturbed wetland, marl prairie, pine rockland, wet flatwood, and wet prairie habitats (Gann et al. 2008). Flowers may be produced year-round in south Florida, but most flowers are produced in

spring and early to mid-summer (Osorio 2001). Florida ecotype seeds of both *Coreopsis* species were purchased from Florida's Wildflower Seed and Plant Growers Association, Inc. (2008).

The study site was located at the University of Florida in Gainesville, FL, USA (lat 29 38'25" N, long 82 21' 34" W; elevation 21 m). Pots were located on benches outdoors, exposed to natural rainfall and in full sun. Rainfall averages 123 cm annually and average minimum and maximum temperatures are 6 and 32 °C, respectively (Figure 2-1).

Experimental Design

The experiment was a factorial (72 treatment combinations) arranged in a completely randomized design and replicated 10 times. The four treatments were season (fall, spring), species (*C. leavenworthii*, *C. lanceolata*), cutting frequency (none, moderate, high), and planting treatments (two monocultures and four mixtures, Figure 2-2). To examine differences in competition based on seasonality, the experiment was planted in fall 2006 and repeated in spring 2007. Fall and spring planting dates were November 9 and March 22 for *C. leavenworthii* and November 21 and March 28 for *C. lanceolata*, respectively. Planting was staggered to allow for timely treatment application and data collection.

Because I was primarily interested in testing the effects of *Paspalum* competition on *Coreopsis* growth, I used a partial additive design with a target-neighbor approach (Barbour et al. 1987, Gibson et al. 1999, Freckleton and Watkinson 2000). With this approach, the focus of the response variable is the target individual located in the center of the pot, in this case *C. leavenworthii* or *C. lanceolata* (Figure 2-2). Plugs of each *Coreopsis* species were grown alone (monoculture) or in combination with *Paspalum* (mixture). The low density monoculture treatment consisted of one *Coreopsis* plug planted in the center of the pot. To test effects of *Coreopsis* intraspecific competition, a second monoculture was planted with seven *Coreopsis* propagules (high density). Mixtures also contained seven propagules but consisted of one

Coreopsis planted in the center of the pot surrounded by six *Paspalum* propagules (Figure 2-2). The initial advantage treatment was implemented by planting mixtures with plugs of different ages. Plugs that had germinated 40 ± 7 days before planting were considered older; those germinated 10 ± 2 days before seeding were considered younger (Figure 2-2). The species planted with an older plug was considered to have the initial advantage in a mixture if the species' neighbors were younger plug(s) (Figure 2-2).

Plugs were produced in plastic germination plug trays (27.9 X 54.6 X 5.1 cm, 128 square cells) filled with soilless medium (Fafard #2 Mix, Conrad Fafard, Inc.). One seed (of each species) was placed in the center of a cell. Trays were kept in a greenhouse in Gainesville, FL (minimum/maximum temperatures—10/39 °C fall, 9/33 °C spring) and sub-irrigated as needed until saturated. *Paspalum* plugs for the spring planting were germinated on thermostatically controlled propagation mats (25 °C). Seedlings were marked with different colored toothpicks within 2 days of emergence to accurately track seedling age.

To simulate disturbance, shoot biomass taller than 10 cm was removed throughout the study twice per month (frequent), once per month (moderate), or not at all (none). Cutting treatments were initiated when the majority of plants reached a height of greater than 10 cm. This corresponded to 17 and 10 weeks after planting (WAP) for the fall and spring treatments, respectively. Cutting treatments continued until 27-28 WAP and were terminated 6-8 weeks before plants were harvested for biomass.

Plugs were planted in 26.6 L pots (34 cm diameter by 29 cm deep) filled with a soilless medium (Fafard #2 Mix, Conrad Fafard, Inc.). Propagules in mixtures and high density monocultures were planted 10.5 cm on center. To focus on effects of disturbance, fertilizer and supplemental irrigation were applied so that nutrients and water would not be limiting factors to

growth. Pots were fertilized 8-10 WAP with one-half the low label rate of Osmocote® 18-6-12 (Scotts Miracle-Gro Company) for 26.6 L pots. Supplemental irrigation was provided as needed through pressure-compensated dribble rings so that the amount and distribution of water among and within pots was uniform. Pots were watered until saturated. Pesticides were used to control disease and insect problems as they arose.

Data Collection and Analysis

All plants were harvested 33-35 WAP. Target plants were separated from neighbor plants. Above- and belowground growth were separated at the soil line, washed, and dried at 60 to 70 °C for one week. Belowground growth that could not be separated to species comprised less than 4% of total belowground biomass and was therefore not included in the analysis.

Coreopsis fitness was assessed by the number of flowers. In the high monoculture treatment, the number of flowers for the target *Coreopsis* was estimated by counting all flowers in the pot and dividing by the total number of plants present. Flowers of fall plants were counted 29 WAP for both *Coreopsis* species.

I analyzed data using mixed models with restricted maximum likelihood methodology (PROC MIXED, version 9.1; SAS Institute, Cary North Carolina, USA). The fixed effects were season, species, planting treatment, cutting frequency, and their interactions. Since this was a completely randomized design, there were no random effects in the model. Biomass results of the target *Coreopsis* (above- and belowground) were square root transformed and *Coreopsis* flower counts were $\log(x + 1)$ transformed to meet assumptions of normality and homogeneity of variance. Means were separated using least squares means (with PDIFF option) as part of the mixed models analyses; *P* values were adjusted using the Bonferroni method.

Results

Season and Species

Season of planting had a pronounced effect on survival of the target *Coreopsis*, which was much greater in fall-established plants than spring-established plants for both *Coreopsis* species (Figure 2-3). Moreover, survival of *C. lanceolata* was greater than that of *C. leavenworthii* for both seasons, even though *C. leavenworthii* biomass was greater than that of *C. lanceolata* in fall-established plants (Table 2-1, Figure 2-3). Both above- and belowground biomass of spring-established *C. lanceolata* plants were at least three times less than those of fall plants (data not presented). However, because the high mortality in spring-established plants resulted in small sample sizes, statistical analysis of biomass was performed only on fall-established plants.

Initial Advantage and Competition

Initial advantage treatments did not influence mean biomass of the target *Coreopsis* species ($P < 0.05$ for all treatment combinations within mixtures), so mixtures were combined for presentation. Target *Coreopsis* biomass was reduced by both neighboring *Coreopsis* and neighboring *Paspalum* compared to *Coreopsis* grown alone (without neighbors) (Table 2-1, Figure 2-4). Neighboring *Coreopsis* reduced aboveground *C. leavenworthii* 87% and *C. lanceolata* 88%, compared to each (target *Coreopsis*) species planted alone (Figure 2-4). *Paspalum* reduced aboveground *C. leavenworthii* 41% and *C. lanceolata* 58%, less than the reductions caused by intraspecific competition. *Coreopsis lanceolata* belowground biomass was also reduced, by 81% and 64 % when planted with *Coreopsis* and *Paspalum* neighbors, respectively (Figure 2-4). Neighboring *Coreopsis* and *Paspalum* reduced belowground *C. leavenworthii* 87% and 52%, respectively, although the difference between the treatments was not significant ($P = 0.0754$, Figure 2-4).

Cutting Frequency

Cutting decreased aboveground biomass of the target *Coreopsis* by 55% and belowground biomass by 30% (Table 2-1, averaged across *Coreopsis* species). In both *Coreopsis* species, aboveground biomass of the target species was greatest with no cutting, while there was no difference between cutting once or twice per month (Figure 2-5). The same trend was observed in belowground biomass of *C. lanceolata*, but *C. leavenworthii* belowground biomass did not differ among cutting treatments (Figure 2-5). Cutting frequency did not affect above- or belowground biomass of neighboring *C. lanceolata* or *C. leavenworthii* (high density monoculture treatment, Figure 2-5). Above- and belowground biomass of neighboring *Paspalum* was not affected by cutting when grown with *C. leavenworthii*. However, cutting once per month resulted in increased aboveground biomass of *Paspalum* when grown with *C. lanceolata*, compared to no cutting and cutting twice per month (Figure 2-5).

***Coreopsis* Fitness**

The number of target *Coreopsis* flowers varied by *Coreopsis* species, cutting frequency, and planting treatment in fall-established plants (Table 2-2). The number of *C. leavenworthii* flowers was greater than that of *C. lanceolata* ($P < 0.0001$, Table 2-2, Figure 2-6). Generally, the presence of neighbors as well as cutting treatments decreased the number of *Coreopsis* flowers. However, the effect of competition from neighbors was influenced by cutting treatment and *Coreopsis* species, which led to significant species by planting and species by cutting interactions (Table 2-2). Therefore, analyses were conducted separately for each species. In the overall model, there were no effects of initial advantage on flower number so mixture treatments (with *Paspalum* as the neighboring plant) were combined for presentation.

The presence of *Paspalum* neighbors reduced *C. leavenworthii* flowers (of the target plant) in fall-established plants ($P = 0.0167$, Table 2-2, Figure 2-6); however *Coreopsis*

neighbors did not reduce target *C. leavenworthii* flowers compared to plants grown alone (Figure 2-6). From a population perspective, the total number of *C. leavenworthii* flowers in the high density monoculture was greater than in *Paspalum* mixtures in fall ($P = 0.0011$, data not presented). Cutting once or twice per month reduced the number of *C. leavenworthii* flowers compared to no cutting ($P < 0.0001$, Table 2-2, Figure 2-6).

For *C. lanceolata*, the presence of both *Coreopsis* and *Paspalum* neighbors reduced the number of flowers compared to plants grown alone in fall-established plants ($P < 0.0001$, Table 2-2, Figure 2-6). However, *Coreopsis* neighbors reduced target *C. lanceolata* flowers more than *Paspalum* neighbors (Figure 2-6). From a population perspective, the total number of flowers in the high density monoculture was equal to the number of flowers produced by *C. lanceolata* plants grown alone ($P = 1.0000$, data not presented). Cutting twice per month decreased the number of *C. lanceolata* flowers compared to no cutting or cutting once per month ($P < 0.0001$, Table 2-2, Figure 2-6).

Discussion

Inter- Versus Intraspecific Competition

Interspecific competition from *Paspalum* reduced biomass of both *Coreopsis* species established in the fall and contributed to high levels of mortality in spring-established plants. However, intraspecific competition decreased biomass of the target *Coreopsis* more than interspecific competition in most cases. Greater biomass in mixture pots could be a result of resource partitioning among roots of the different species. However, root growth and structure were greatly affected by the container by the end of the study, complicating efforts to assess spatial partitioning of roots between species. Although intraspecific competition was more damaging to the target *Coreopsis* than interspecific competition, overall *Coreopsis* fitness (measured by flower number) in the high density monocultures was equal to or greater than

Coreopsis plants grown alone. In many instances, the total number of flowers per pot was similar, regardless of the number of propagules present.

Although competition from *Paspalum* reduced *Coreopsis* biomass, *Coreopsis* biomass was substantial in fall-established plants. On a plant-for-plant basis, *C. leavenworthii* was equal to or greater than *Paspalum* biomass. With no disturbance, *C. leavenworthii* biomass was double that of *Paspalum* (Figure 2-5). *Coreopsis lanceolata* biomass was only comparable to *Paspalum* biomass when plants were not cut (Figure 2-5). Although the presence of *Paspalum* neighbors generally decreased the number of flowers of both *Coreopsis* species, *C. leavenworthii* produced more flowers than *C. lanceolata* in both seasons (Figure 2-6). While these results suggest that *C. leavenworthii* is a stronger competitor than *C. lanceolata*, *C. leavenworthii* survivorship was much lower than that of *C. lanceolata*, especially in spring-established plants. Comparing the competitive strength of two species in a short-term, two-species competition study may be more complex than evaluating relative biomass (or growth rate) of the two species, as is traditionally done. In this case, the competitive strength of the *Coreopsis* species depended upon the season of planting and the manner in which competitive strength is evaluated.

Seasonal Differences

Increased mortality in spring-established plants may be explained by the response of *Paspalum* to seasonal changes in environmental conditions. The majority of the spring experiment occurred during the rainy season, with increased temperatures and day length (Figure 2-1). *Paspalum (notatum)* is a long-day plant that is dormant during the short days of winter (Marousky and Blondon 1995). Flowering is initiated when day length exceeds 13.5 hours (Marousky and Blondon 1995), which occurs in May at the study site. In Florida, *Paspalum* seed maturation begins in June and continues throughout the summer (Watson and Burton 1985). Fall-established *Coreopsis* were planted in November and grew for approximately 26 weeks

before *Paspalum* began to flower. In contrast, spring-established plants grew for approximately 7 weeks before *Paspalum* began to flower. *Paspalum* height can exceed 100 cm when in flower, compared with approximately 20 cm when dormant (personal observation). The increase in height during the summer months likely intensified aboveground competition between *Paspalum* and *Coreopsis*. This increased growth likely had a greater effect on spring-established plants because they were younger (and smaller) and exposed to more intense competition for a longer period of time than fall-established plants.

While competition with *Paspalum* decreased survivorship of *Coreopsis* in mixtures, there was also decreased survivorship of *Coreopsis* grown in monocultures in spring-established plants. *Coreopsis leavenworthii* mortality in response to competition was confounded with mortality due to completion of the *C. leavenworthii* life cycle. Mortality of *C. lanceolata* in monocultures occurred only in spring-established plants and may have been a result of overwatering. The increased *Paspalum* growth in mixture pots over the summer required substantial amounts of supplemental irrigation, so that water would not be limiting. However, since *Coreopsis* plants were generally smaller than *Paspalum* plants, *Coreopsis* monocultures did not require as much water as mixture pots. The growing medium in the monoculture pots was consistently wet between watering, while the growing medium in mixture pots was dry. Because *C. lanceolata* is an upland species, the increased moisture in monocultures likely affected *C. lanceolata* more than *C. leavenworthii*, which is a facultative wetland species.

Species-Specific Responses

Differences in growth form and life history strategies may account for differences in competitive strength and survivorship among the two *Coreopsis* species. At a community level, different plant traits or life-history strategies may promote species coexistence (Coomes and Grubb 2000, Booth et al. 2003). However, plant survival strategies normally involve trade-offs.

For example, plants that are good colonizers are usually not good competitors over time (Coomes and Grubb 2000). *Coreopsis leavenworthii* is an annual to short-lived perennial while *C. lanceolata* is an evergreen short-lived perennial. In this study, *C. leavenworthii* seemed to be more of an annual than short-lived perennial—flowering, seeding prolifically, and then dying. In contrast, *C. lanceolata* produced fewer flowers and biomass than *C. leavenworthii* but had higher overall survivorship. *Coreopsis lanceolata* appeared to be able to tolerate the stress of reduced light for longer periods of time than *C. leavenworthii* by surviving as a small plant underneath the canopy of *Paspalum*. The trade-off between competitive ability and recruitment opportunities is often related to trade-offs between seed size and number (Jakobsson and Eriksson 2000). Plants that produce many, small seeds increase recruitment opportunities whereas plants that produce few, large seeds are good competitors (Jakobsson and Eriksson 2000). Although the seeds of *C. lanceolata* seeds are relatively small, their mass is approximately seven times that of *C. leavenworthii* (based on a sample of seeds weighed before the study). The results from this study suggest that *C. leavenworthii* is a better colonizer than *C. lanceolata*, while *C. lanceolata* is a better long-term competitor than *C. leavenworthii*.

Disturbance

Cutting generally resulted in decreased aboveground biomass and flower production of the target *Coreopsis* for both species (Figures 2-5 and 2-6). However, cutting had little effect on the biomass of neighboring *Paspalum* or *Coreopsis* (Figure 2-5). Neighboring plants may have been able to compensate for loss of height by increasing in width, since aboveground growth of neighboring plants was able to extend beyond the boundaries of the pot. Moreover, cutting may have resulted in the loss of apical dominance and promoted branching. In the case of *Paspalum*, much of its biomass is stored in rhizomes at the soil surface; these rhizomes were not affected by the cutting treatments. Additionally, cutting treatments were stopped 6-8 weeks before plants

were harvested. This time period corresponded with increased growth and flowering in *Paspalum* in fall-established plants, which may have been able to compensate for the loss of biomass imposed by cutting before the biomass harvest.

Contrary to the hypothesis, cutting did not increase the competitive ability of the target *Coreopsis*. An increase in disturbance can disrupt competitive exclusion by decreasing the number of occupied patches and by increasing light (Cordonnier et al. 2006). However, the cutting treatments in this study did not decrease occupied patches. Additionally, the ability of disturbance to prevent competitive exclusion is based on life-history and growth strategy trade-offs of the competing species. Since each species has limited resources to allocate to growth and reproduction, there is a trade-off between competitive ability and colonization success and/or stress tolerance (Cordonnier et al. 2006). In a short-term competition study where colonization space is restricted, the longer-term effects of disturbance and trade-offs may not be evident. Moreover, although cutting may have increased light, it simultaneously decreased the biomass of the target *Coreopsis*.

Initial Advantage

The absence of an initial advantage effect on interspecific competition in the present study may indicate that light was not a limiting factor during establishment. Consequently, seedling age may not have been a good surrogate for first arrival or earlier germination under field conditions. Although initial advantage has been shown to increase competitive ability, this increase was only important for seedling establishment (Weigelt et al. 2002). After seedling establishment, species-specific attributes (particularly allocation to biomass) determined the outcome of competitive interactions (Weigelt et al. 2002). Wilson (1988) found that initial advantage was only relevant in competition for light. In the present study, plugs (seedlings) were not competing for light at the beginning of the study because they were planted in pots

large enough to accommodate eight months of growth. Therefore, although the older seedlings were larger (taller and had more leaves) than the younger seedlings, the older seedlings did not shade the younger seedlings. Additionally, one of the assumptions of the founder effect model is that a species cannot invade a patch that is already occupied (Cordonnier et al. 2006). However, in this study, *Paspalum* frequently occupied additional patches by growing over *Coreopsis* plants. This suggests that competition in this experiment follows a hierarchical competition model, where species can be replaced (Cordonnier et al. 2006). In a hierarchical model, coexistence between species occurs if there is a trade-off between competition and colonization. Despite the lack of difference in initial advantage treatments, *Paspalum* decreased *Coreopsis* growth and fecundity within one growing season. This suggests that the lack of native forb establishment in communities dominated by *Paspalum* in the field is likely influenced by competition. However, it is not clear if initial advantage in the field increases *Paspalum* competitive advantage.

Although results of this study demonstrate competition between *Paspalum* and both *Coreopsis* species, applying these results to field conditions should be done with caution. The present study was conducted in an environment where nutrients and water were not limiting factors, but growth, especially belowground, was constricted by pots. In contrast, many of Florida's upland communities, where *Paspalum* is most often planted, are dry and nutrient poor. Different environmental conditions and nutrient availability can shift or reverse competitive interactions (Barbour et al. 1987). Dry and nutrient poor conditions would likely increase the intensity of belowground competition, which could increase the competitive ability of *P. notatum* due to its dense root system.

Conclusions

Based on results of this experiment, season of planting and species of *Coreopsis* greatly influenced competitive interactions with *Paspalum notatum*. *Coreopsis lanceolata* survivorship was greater than that of *C. leavenworthii*, especially in spring-established plants. However, biomass of *C. leavenworthii* was less affected by interspecific competition than *C. lanceolata*. Additionally, *C. leavenworthii* produced more flowers than *C. lanceolata*. Cutting treatments did not increase species coexistence, at least within the time limits of this experiment.

Competitive interactions between *Coreopsis* and *Paspalum* were strong regardless of initial advantage (as tested through seedling age). Intraspecific competition was as strong, or stronger, than interspecific competition in terms of biomass, but fitness of the overall population was not reduced by intraspecific competition as it was by interspecific competition. Based on these results, *C. lanceolata* may result in a more successful long-term establishment in a restoration context than *C. leavenworthii*. While intraspecific competition limits *Coreopsis* establishment more than interspecific competition, planting in the fall and limiting disturbance may increase *Coreopsis* survival.

Table 2-1. Effects of species (*Coreopsis leavenworthii*, *C. lanceolata*), cutting frequency (none, once/month, twice/month), planting treatment (see Figure 2-2), and their interactions on above- and belowground biomass of the target (central) *Coreopsis* in fall-established plants. Means were square root transformed for analysis.

Factor	df	Aboveground		Belowground	
		F	P	F	P
Species	1, 202	10.40	0.0015	33.74	<0.0001
Cutting	2, 202	27.23	<0.0001	6.16	0.0025
Planting	5, 202	18.76	<0.0001	14.08	<0.0001
Species X cutting	2, 202	1.39	0.2523	0.84	0.4348
Species X planting	5, 202	0.71	0.6182	1.08	0.3744
Cutting X planting	10, 202	0.48	0.9022	0.40	0.9464
Species X cutting X planting	10, 202	0.80	0.6281	1.27	0.2470

Table 2-2. Effects of species (*Coreopsis leavenworthii*, *C. lanceolata*), cutting treatment (none, once/month, twice/month), planting treatment (see Figure 2-2), and their interactions on flower number of the target (central) *Coreopsis* in fall-established plants. Flower numbers were log (x + 1) transformed for analysis.

Factor	df	<i>Coreopsis</i> flowers	
		F	P
Species	1, 272	17.54	<0.0001
Cutting	2, 272	96.20	<0.0001
Planting	5, 272	8.45	<0.0001
Species X cutting	2, 272	19.33	<0.0001
Species X planting	5, 272	2.45	0.0341
Cutting X planting	10, 272	1.98	0.0358
Species X cutting X planting	10, 272	0.54	0.8574
<i>Coreopsis leavenworthii</i>			
Cutting	2, 100	53.74	<0.0001
Planting	5, 100	2.92	0.0167
Cutting X planting	10, 100	1.06	0.4037
<i>Coreopsis lanceolata</i>			
Cutting	2, 172	28.56	<0.0001
Planting	5, 172	10.95	<0.0001
Cutting X planting	10, 172	1.42	0.1765

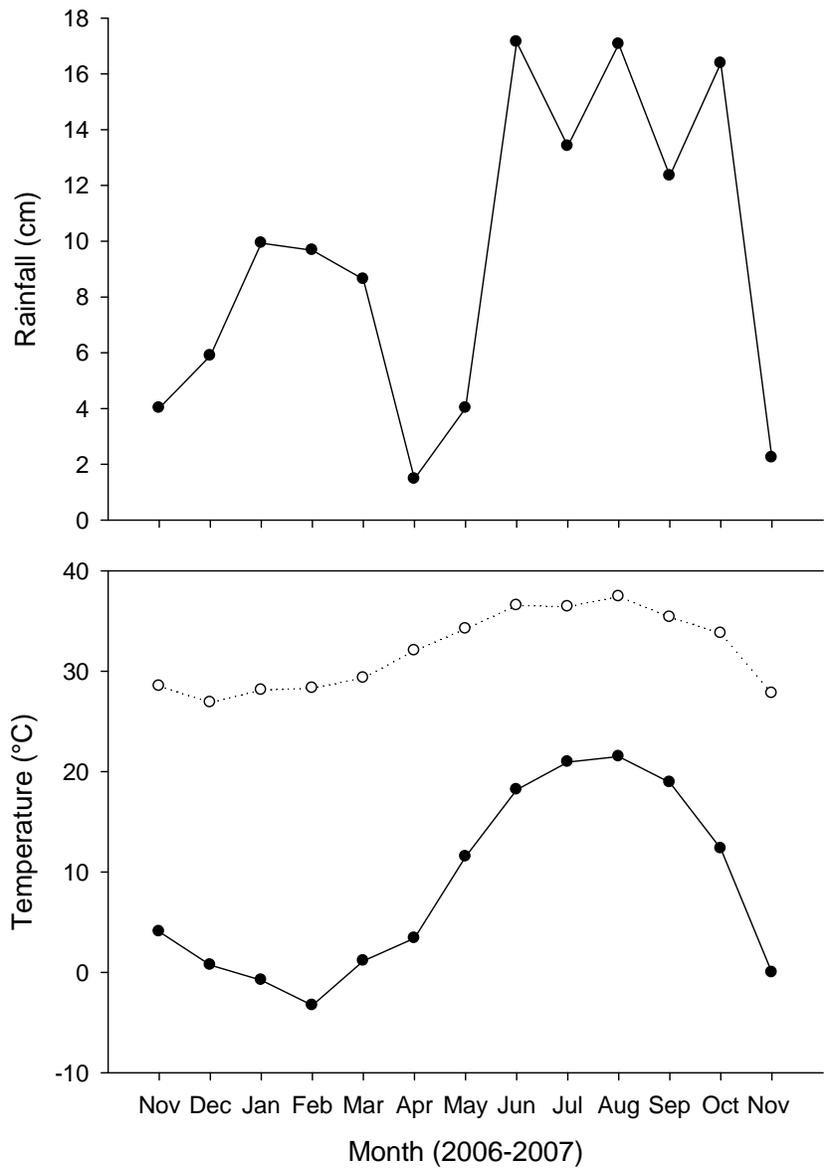


Figure 2-1. Total monthly rainfall and minimum and maximum temperatures at the study site during the experiment. Monthly rainfall from The University of Florida’s W4DFU Weather Station in Gainesville, FL, approximately 1.5 km from the study site, accessed through Weather Underground (<http://www.weatherunderground.com>, ID KFLGAIN10). Temperatures recorded on site with a HOBO® data logger (Onset Computer Corporation, Bourne, MA).

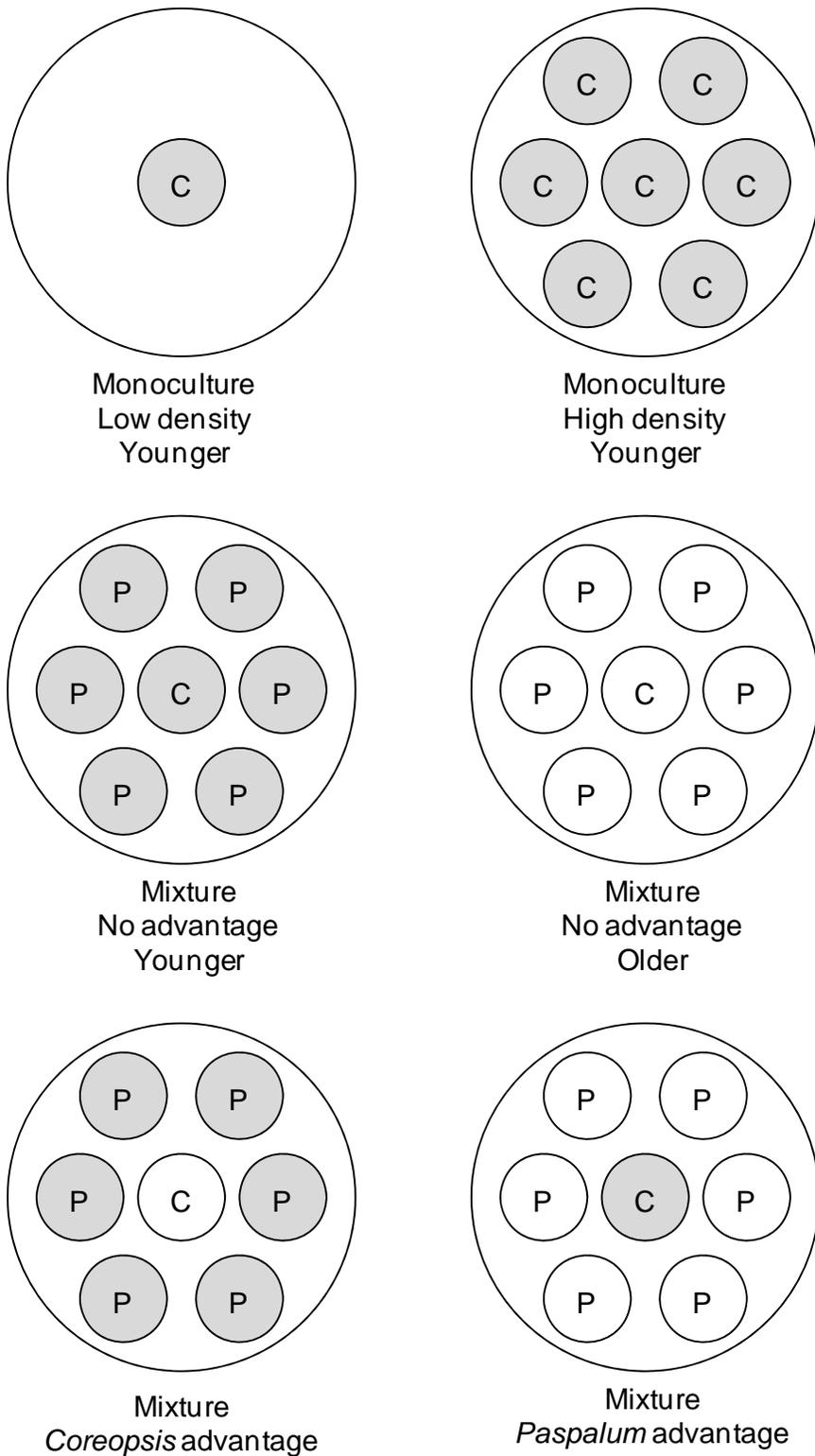


Figure 2-2. The two monocultures and four mixtures included in the planting treatments. “C” indicates *Coreopsis* and “P” indicates *Paspalum*. Shaded circles represent younger plants (10 ± 2 days old); white circles represent older plants (40 ± 7 days old). The

center plant in each pot is the target species (*C. leavenworthii* or *C. lanceolata*) while the surrounding plants are neighbor species (*Coreopsis* or *Paspalum*).

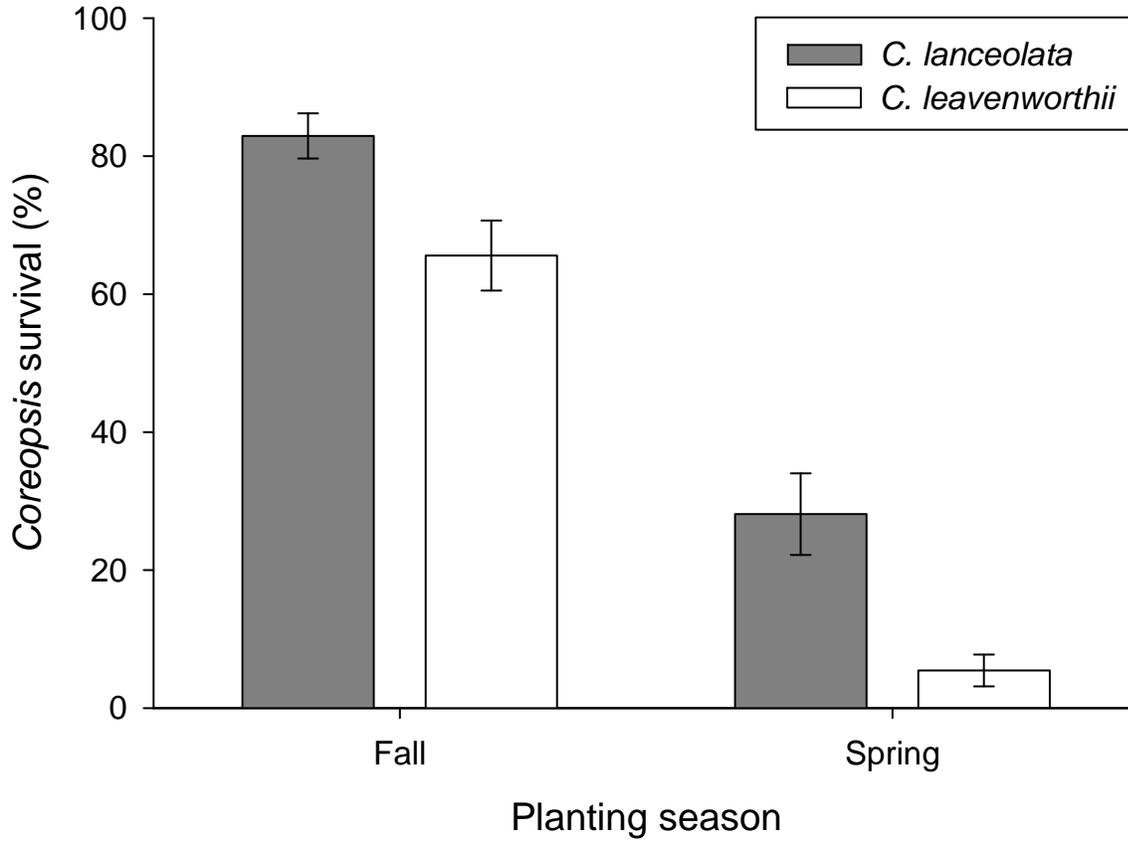


Figure 2-3. Effects of planting season (fall or spring) and species (*Coreopsis lanceolata* or *C. leavenworthii*) on mean (± 1 SE) *Coreopsis* survival (target plant) eight months after planting. Percent survival was averaged across planting and cutting treatments.

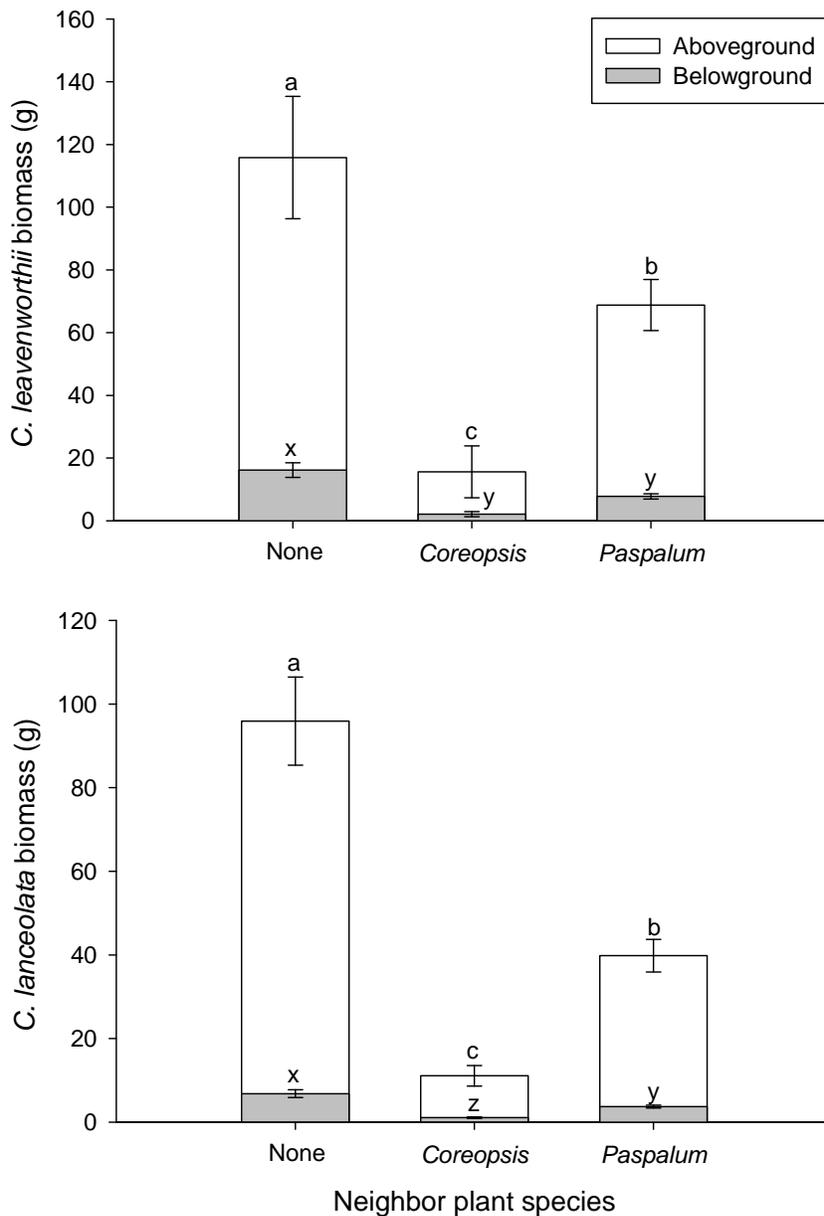


Figure 2-4. Effects of neighbor plant species (none, conspecific *Coreopsis*, or *Paspalum*) on above- and belowground biomass of the target (center) *Coreopsis* in fall-established plants. Means (± 1 SE) with different letters within a graph (target species) and above- and belowground biomass differ significantly ($P < 0.05$, Bonferroni correction). Above- and belowground biomass of the target *Coreopsis* were square root transformed for analysis; untransformed means are presented here. Means were averaged across cutting treatments.

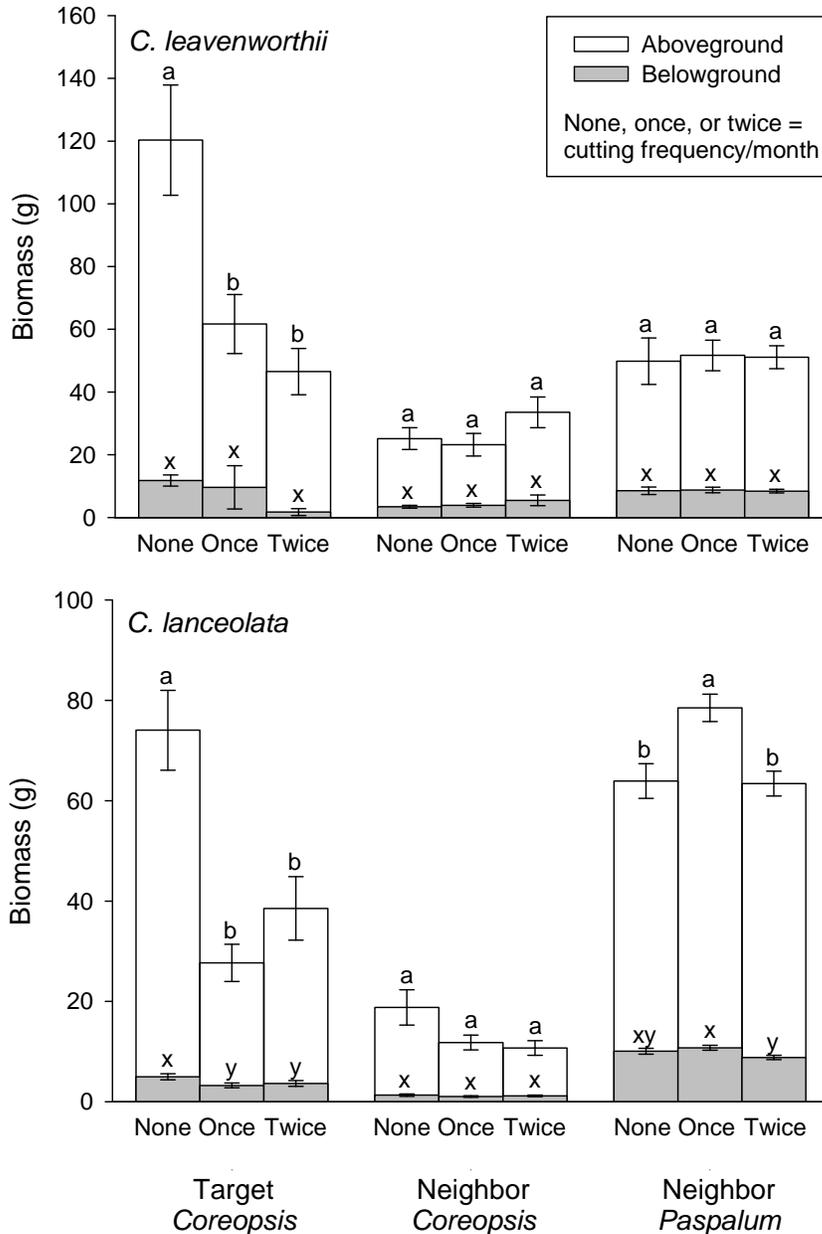


Figure 2-5. Effects of cutting frequency on above- and belowground biomass of the target (center) *Coreopsis*, neighboring *Coreopsis*, and neighboring *Paspalum* in fall-established plants. *Coreopsis* indicates *C. leavenworthii* in the top graph and *C. lanceolata* in the bottom graph. Means (± 1 SE) with different letters within a group (target, neighbor *Coreopsis*, or neighbor *Paspalum*) and above- and belowground biomass differ significantly ($P < 0.05$, Bonferroni correction). Above- and belowground biomass of the target *Coreopsis* were square root transformed for analysis; untransformed means are presented here. Total neighbor biomass per pot was divided by number of neighbors (generally six) to compare with target biomass on a per plant basis. Means for cutting frequencies were averaged across planting treatments.

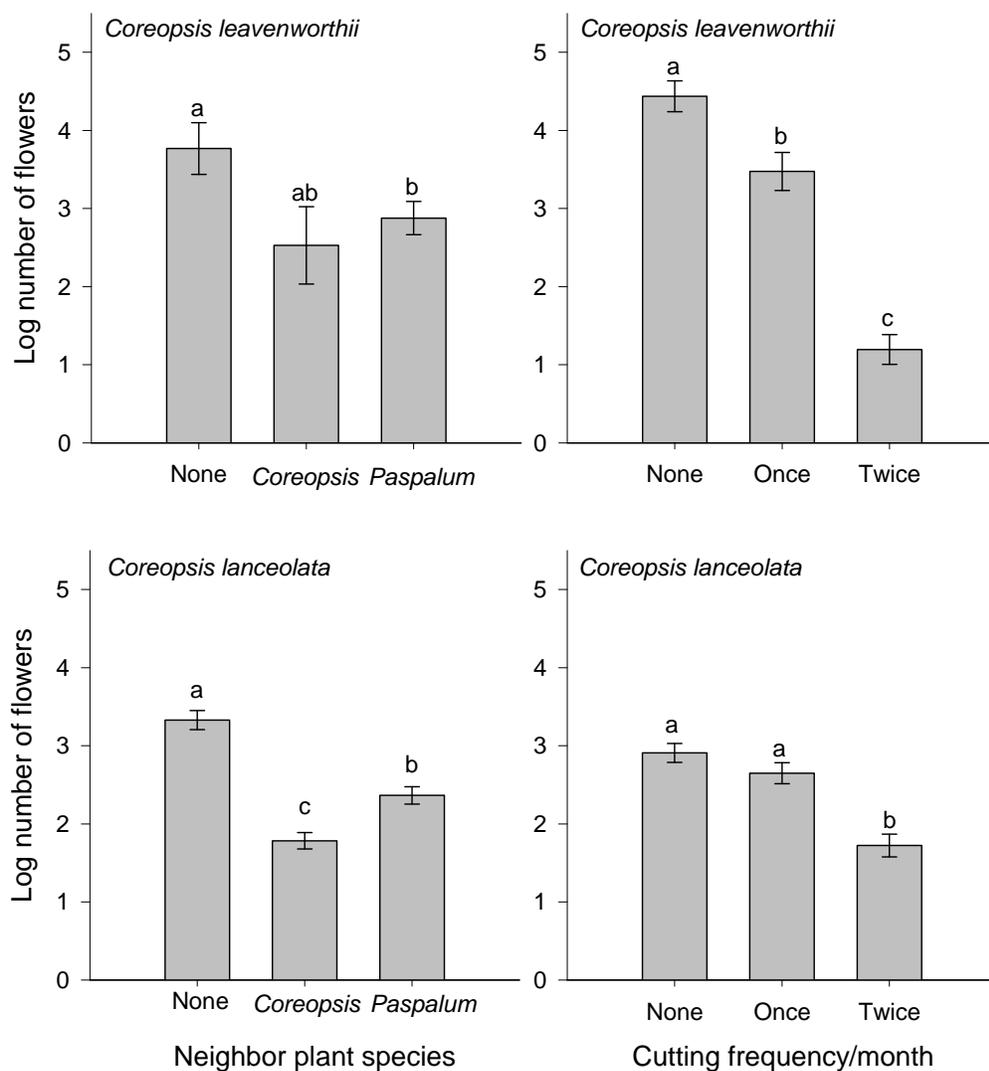


Figure 2-6. Effects of cutting frequency and planting treatment on the mean (± 1 SE) number of *Coreopsis lanceolata* (top graphs) and *C. leavenworthii* (bottom graphs) flowers. Means with different letters within a cutting or planting treatment differ significantly ($P < 0.05$, Bonferroni correction). Number of flowers was $\log(x + 1)$ transformed for analysis.

CHAPTER 3
EVALUATING SEED AND MICROSITE LIMITATION TO THE ESTABLISHMENT OF A
NATIVE WILDFLOWER IN A NON-NATIVE PASTURE GRASS

Introduction

Ecological restoration and roadside revegetation projects often require the introduction of desirable plant species. In Florida, *Paspalum notatum* Flügge var. *saurae* Parodi (bahiagrass) occurs on roadsides as well as on some pastures slated for restoration (Violi 2000). *Paspalum notatum* was originally introduced as a pasture grass but is also commonly planted on roadsides due to its effectiveness in controlling erosion (Violi 2000). Therefore, establishing native wildflowers (forbs) into *P. notatum* is a common goal of ecological restoration and roadside management projects. However, several barriers exist to establishing native plants in former pastures (Zimmerman et al. 2000). Abandoned agricultural areas often have altered hydrology and soil nutrients, which can affect plant productivity. The dominant species (usually a grass) may prevent the establishment of new species and may be difficult to eradicate (Stevenson and Smale 2005). Moreover, native plant propagules to recolonize the site may be lacking (Orrock et al. *in press*).

If the former pasture lacks native plant propagules to recolonize the site, introducing native plants may be necessary. Establishing native species at the time of pasture removal may also slow or prevent the invasion of undesirable ruderal and invasive species. Yet, introducing native plants does not guarantee their establishment. In order for a plant to become established at a new site, the seed (or propagule) must not only arrive at the site, but also germinate and survive the seedling stage of development. For this reason, plant establishment is limited by the availability of seeds, of areas suitable for emergence and growth, or of both (Stampfli and Zeiter 1999, Turnbull et al. 2000, Zobel et al. 2000, Holzel 2005).

Seed addition experiments test seed limitation by introducing seeds to a site and determining if the population increases as a result. Turnbull et al. (2000) distinguish between two types of seed limitation experiments. Seed augmentation involves adding seeds of species that are already part of the target community, whereas seed introduction involves adding seeds of non-resident species to the community. In a meta-analysis of seed limitation experiments, Clark et al. (2007) suggest testing the magnitude of seed addition effects, rather than simply detecting the occurrence of seed limitation. In a restoration setting, understanding the magnitude of seed addition effects could help determine criteria for establishment of a self-sustaining population.

Direct seeding of propagules into restoration sites is often the most economical approach to revegetation (Pfaff and Gonter 1999), yet there is limited information on the effects of seeding rate on establishment. Seeding rates are rarely based on parameters that ensure establishment of the restored population (e.g., Cole 2007) and are more often based on seed availability (Burton et al. 2006). For example, the Florida Department of Transportation uses the same bulk seeding rate, regardless of the wildflower species being seeded, because species-specific requirements are not yet known (Florida Department of Transportation 1998). However, given differences in viability of seed lots and differences in seed mass by species, the number of viable seeds used per project may vary widely. Seeding at deliberately high rates is practiced to increase the seeded species' competitive ability over existing vegetation. In a study on native grass restoration in California, doubling the seed density resulted in twice as many established grass plants (Orrock et al. *in press*). While increasing the seeding rate may increase overall emergence, Harkess and Lyons (1998) found that doubling the seeding rate did not affect the number of plants maturing to flower. Moreover, increasing the seeding rate of native legumes negatively affected individual plant establishment (Fischbach et al. 2006).

Plant establishment of introduced populations not only depends upon the appropriate seeding rate but also upon creating areas suitable for seedling emergence and survival, i.e., microsites, which are also known as safe sites or regeneration niches (Nathan and Muller-Landau 2000). I define microsite in a broad sense to include the environmental conditions necessary for germination and emergence as well as the absence of competitors, predators, and pathogens (Harper 1977, referred to as “safe site”). Microsites suitable for germination and seedling establishment are species-specific, but usually provide water and contact with the soil (Isselstein et al. 2002). Water availability on degraded sites may be different than on adjacent natural systems due to altered hydrology. Therefore, germination of introduced seeds on degraded sites may be limited by the lack of water at the soil surface. Moreover, seeding may occur in a different season than natural seed dispersal or when natural rainfall is limited. In these cases, supplemental irrigation can increase the seeded species’ survival and establishment (Harper-Lore and Wilson 2000, Cox et al. 2004).

Microsites for new species may be limited by the existing vegetation (Pfaff and Gonter 1999), which can prevent seed-to-soil contact and limit resources like water, light, and nutrients through competition (Tilman 1994). For example, increased productivity in grasslands can prevent seedling establishment of forbs by decreasing light levels (Foster and Gross 1998). Releasing competition by disturbing the existing vegetation often leads to increased seedling establishment (Holzel 2005, Martin and Wilsey 2006). The competitive effects of grasses on herbaceous species can be at least temporarily alleviated by removing the grass via herbicide (del-Val and Crawley 2005). Removing the topsoil has also been shown to increase native species establishment, especially in former agricultural areas, by decreasing artificially enhanced soil nutrient levels as well as removing dominant vegetation (Holzel 2005, Buisson et al. 2006,

Clark and Tilman 2008). Topsoil removal may also remove the majority of weed seeds in the soil seed bank (Roberts 1981, Dalrymple et al. 2003).

In Florida, *P. notatum* pastures occupy some of the area slated for restoration (Violi 2000). *Paspalum notatum* is a rhizomatous, mat-forming grass that can persist for decades and prevent native species establishment (Uridel 1994, Violi 2000). Applying glyphosate, a non-selective herbicide, to *P. notatum* increased the establishment of native species subsequently planted in *P. notatum* pastures (Uridel 1994). A combination of repeated herbicide application and sod removal through disking or plowing also can effectively control *P. notatum*; however, undesirable ruderal or non-native species then typically colonize the site (Violi 2000). Additionally, it is not clear if combining herbicide treatments with mechanical sod removal results in greater *P. notatum* control than mechanical treatments alone (Violi 2000).

Many species are often limited by both seed and microsite limitation (Stampfli and Zeiter 1999, Juenger and Bergelson 2000). Eriksson (1992) suggests that seed and microsite limitation represent extremes on a spectrum and that a simple dichotomy between the two does not describe the limitations of most species to establishment. Similarly, Clark et al. (2007) stress the relative importance of seed and microsite limitation to plant establishment. It is possible that seed and microsite availability can interactively affect establishment, where the availability of one may compensate for the lack of the other. For example, rolling or raking the soil after seeding increased establishment by improving seed-to-soil contact (Harkess and Lyons 1998, Gordon et al. 2000). This increase in establishment may allow for a reduction in seeding rate (Harkess and Lyons 1998, Harper-Lore and Wilson 2000, Grabowski 2005). A better understanding of the relative and interactive effects of seed and microsite limitation may help guide revegetation efforts that are limited by time and resources.

This study focuses on seed and microsite limitation to the establishment of a native wildflower species in a former pasture. Specifically, the objectives of the experiment were to determine the relative and interactive effects of supplemental irrigation, seeding rate, and disturbance on *C. lanceolata* establishment in a *P. notatum* pasture. By focusing on the establishment of one species, I was able to test several levels of both seed and microsite limitation simultaneously. I hypothesized that establishment would increase with increasing seed and microsite availability.

Methods

Study Site and Species

The study site was located at the University of Florida's Institute of Food and Agricultural Sciences Plant Science Research and Education Unit in Citra, Florida (lat 29 24' 35" N, long 82 08' 26" W; elevation 21 meters). Before its conversion to agriculture, the site was likely part of the sandhill ecosystem (Myers 1990), an open savanna dominated by *Pinus palustris* Mill. (longleaf pine), *Quercus laevis* Walter (turkey oak), and *Aristida stricta* Michx. var. *beyrichiana* (Trin. & Rupr.) D.B.Ward (wiregrass). A diverse assemblage of grasses and forbs generally comprises the groundcover of sandhills (Myers 1990). Rainfall averages 132 cm annually and average minimum and maximum temperatures are 14 and 27 °C, respectively (Figure 3-1). The soil is a Candler sand (0-5% slopes) with low nitrogen levels, both in the form of available nitrates and ammonium (Table 3-1).

The study area was a *P. notatum* pasture that had not been grazed or fertilized since 1995. *Paspalum notatum* was introduced to the United States from Brazil in 1913 (Scott 1920) and was estimated to occupy over 2 million ha in the southeastern U.S. by 1978 (Beatty and Powell 1978). While several cultivars have been developed since its introduction, 'Pensacola' is commonly used in Florida pastures and along roadsides and the cultivar planted at the study site

(Violi 2000). At the start of the study, *P. notatum* was the dominant species, with forbs and other graminoids comprising less than 5% of cover.

Coreopsis lanceolata L. (lanceleaf tickseed) is an evergreen, short-lived perennial that is native to much of eastern North America. Ranging from Florida west to New Mexico and north to Ontario, *C. lanceolata* typically occurs on sandy soils, ditches, roadsides, and disturbed sites and flowers from May through July (Flora of North America Editorial Committee 2006). In north-central Florida, *C. lanceolata* occurs in sandhills and disturbed sites and blooms in spring (from March through May, Wunderlin and Hansen 2003). Although *C. lanceolata* occurs in two counties adjacent to the study site (Wunderlin and Hansen 2008), *C. lanceolata* was not found at the study site at the start of the experiment. A seed bank study conducted in a nearby field confirmed that *C. lanceolata* was not present in the seed bank (data not presented). For this study, seeds of *C. lanceolata* (north Florida ecotype) were purchased from Florida's Wildflower Seed and Plant Growers Association, Inc. (2008). Seed viability was independently determined using a tetrazolium test (AOSA 2006).

Experimental Design

This experiment tested the effects of supplemental irrigation, seeding rate, and disturbance on *C. lanceolata* establishment in a *P. notatum* pasture. The experiment was arranged in a completely randomized split plot design with irrigation as the main plot treatment and seeding rate and disturbance regime as factorial sub plots. Each replicate sub plot was 5 X 5 m with 1-m and 9-m buffers between sub and main plots, respectively. The experiment was conducted in two adjacent fields and there were three replicates per field.

To test the sensitivity of seedling establishment due to seeding rate, plots were seeded at 100 (low), 600 (medium), and 1100 (high) live seeds/m² with a no-till, hydraulic seed drill on November 20, 2006. The medium seeding rate is recommended by the Florida Department of

Transportation for right-of-way plantings (pure live seed equivalent of recommended bulk rate 11.2 kg/ha, Florida Department of Transportation 1998).

Microsites were experimentally altered with two factors: irrigation and disturbance of existing vegetation. The irrigation treatment had three levels: no irrigation (none), a pre-seeding soak (pre), and pre- and post-seeding irrigation (full). For the pre-seeding soak, plots were irrigated to approximately 5 cm immediately before seeding. The pre- and post-seeding irrigation included the same pre-seeding soak plus 2.5 cm irrigation twice/week for 6 weeks following seeding (Figure 3-1).

The disturbance treatment had four levels, listed in increasing level of disturbance: no disturbance (control), sethoxydim herbicide (sethoxydim), glyphosate herbicide (glyphosate), and topsoil removal (scraped). To test competitive effects of *P. notatum* on the seedling stage of *C. lanceolata* development, sethoxydim (Poast®; BASF), a grass herbicide, was applied to actively growing *P. notatum* 23 and 30 weeks after seeding at 2.6 L/ha (with a surfactant of 83% paraffin base petroleum oil at 2.3 L/ha). Glyphosate (Roundup Original Max®; Monsanto) was applied 4 and 2 weeks prior to seeding at 2.3 L/ha, after which the vegetation was mowed to 5 cm (2 days prior to seeding). Both sethoxydim and glyphosate were applied with a Cushman® Spraytek™ (Jacobsen Co.) that delivered 281 L/ha at 310 kPa. The scraped treatment consisted of removing the top 13 cm of vegetation and soil one week prior to seeding. The soil surface was smoothed down with a turf roller a few days before planting.

I collected soil samples after implementing the disturbance treatments and just prior to seeding. I haphazardly collected one core (6 cm diameter X 5 cm depth) from each sub plot. Cores were aggregated by disturbance treatment within each main plot.

Data Collection and Analyses

I recorded percent cover and density data 10, 20, 39 and 46 weeks after seeding (WAS). Aboveground biomass was sampled 46 WAS (the end of the study). I categorized biomass into *C. lanceolata*, *P. notatum*, forbs (excluding *C. lanceolata*), or graminoids (excluding *P. notatum*). Percent cover categories included those of biomass as well as standing dead, bare ground, and an estimate of the cover occupied by *C. lanceolata* flowers. To visually estimate percent cover, I randomly placed three 1 X 1-m subsamples within each plot. Density was counted for *C. lanceolata* only in 0.25 X 0.25-m subsamples nested within the meter squared subsamples for percent cover. Biomass was collected from circular 0.15-m² (diameter 0.44 m) subsamples nested within the meter squared cover subsamples but not overlapping with the density subsamples. Aboveground vegetation rooted in each biomass subsample was cut at ground level, categorized, and dried at 60 °C for one week.

I analyzed data using mixed models with restricted maximum likelihood methodology (PROC MIXED, version 9.1; SAS Institute, Cary North Carolina, USA). The fixed effects were seeding rate (low, medium, high), irrigation (none, pre, full), disturbance (control, sethoxydim, glyphosate, scraped), and the interactions among them. The random effects were block (for field), main plots within blocks, and main plot by sub plot within blocks. Degrees of freedom were approximated with Kenward-Roger's method. Response variables included density, percent cover, and biomass as explained above. To identify changes in percent cover and density over time, a repeated measures analysis was added to the model with an exponential spatial covariance structure (SP(EXP)). Means were separated using least squares means (with PDIFF option) as part of the mixed models analyses; *P* values were adjusted using the Bonferroni method. Percent cover and density data were averaged by subplot for the repeated measures analysis and biomass data were averaged by subplot and converted to a per meter squared basis

before analysis. Density data were $\log(x + 1)$ transformed, percent cover data were arcsine square root transformed and biomass of *P. notatum*, forbs, and graminoids were square root transformed to meet assumptions of normality and homogeneity of variance.

Results

Coreopsis lanceolata Changes Over Time

Increasing seeds and microsites resulted in greater *C. lanceolata* establishment. However, the effects of irrigation, seeding rate, and disturbance on *C. lanceolata* density and percent cover changed over time (Figure 3-2). In general, density decreased while cover increased; however, the extent of these temporal changes depended on the treatment (Figure 3-2). Between 10 and 46 WAS, density decreased 50% at the high seeding rate and 39% in glyphosate treated plots but did not decrease at the low seeding rate or in scraped plots. Percent cover increased eight-fold in the glyphosate treated plots compared to a five-fold increase in the control and scraped plots.

Different temporal responses by treatment resulted in significant interactions between WAS and each of the main effects so main effects were analyzed separately within each time period (Table 3-2). There were a number of significant interactions among seeding rate, irrigation, and disturbance treatments for both density and percent cover 10 WAS (Table 3-2). By 46 WAS, each of the main effects significantly affected *C. lanceolata* density and cover but there were no significant interactions. Therefore, means of density and cover over time are presented separately for each main effect (Figure 3-2).

At 10 WAS, density and cover differences among irrigation treatments varied by seeding rate (Table 3-2). Density and cover were twice as high in the full irrigation treatment as in the no- and pre-irrigation treatments, but only at the medium and high seeding rates. At the low

seeding rate, density and cover were equally low among irrigation treatments, resulting in significant rate by irrigation interactions ($P = 0.0116$ for density, $P < 0.0001$ for cover, Table 3-2). Similarly, density in the scraped plots was lower than in the other three disturbance treatments at the medium and high seeding rates. However, at the low seeding rate, density was equally low among disturbance treatments, resulting in significant rate by disturbance interaction ($P = 0.0023$, Table 3-2). The full irrigation treatment increased percent cover compared to the no-and pre- irrigation treatments (Figure 3-2). However, this increase was more pronounced in the glyphosate treated plots than in the other disturbance treatments leading to a significant irrigation by disturbance interaction ($P = 0.0004$, Table 3-2).

***Coreopsis lanceolata* Establishment**

Despite significant interactions among main effects at the beginning of the study, disturbance treatments resulted in the largest differences in *C. lanceolata* cover and biomass by the end of the study. While percent cover was greatest in the glyphosate treated plots throughout the study, by 46 WAS, cover in glyphosate treated plots was more than double that of the control, sethoxydim, and scraped plots (Figure 3-2). Effects on biomass mirrored those of cover; biomass in glyphosate treated plots was 7, 6, and 2.5 times greater than in control, sethoxydim, and scraped plots, respectively (Figure 3-3). At 46 WAS, density in glyphosate treated plots was 17% greater than in control plots but there was no difference in density between glyphosate and control plots at 10 and 20 WAS (Figure 3-2).

The scraped treatment affected *C. lanceolata* density, biomass, and cover differently. Density in the scraped plots remained low throughout the study. In contrast, biomass (at 46 WAS) in the scraped plots was more than double that of the control and sethoxydim treated plots (Figure 3-3). Cover in the scraped plots was greater than the control 20 and 39 WAS. However,

by 46 WAS, cover in the scraped plots was equal to the control and lower than the sethoxydim-treated plots (Figure 3-2).

In general, the sethoxydim treatment did not increase *C. lanceolata* establishment. While the sethoxydim treatment increased cover slightly compared to the control at 39 WAS, there was no difference by 46 WAS (Figure 3-2). Density in the sethoxydim treatment remained equal to that of the control throughout the study (Figure 3-2). At 46 WAS, there was no difference in biomass between the sethoxydim and control treatments (Figure 3-3).

Coreopsis lanceolata density and cover increased with each increase in seeding rate (Figure 3-2). The difference between the low and medium seeding rates was larger than the difference between the medium and high seeding rates. For cover, this trend became more apparent over time. Effects of seeding rate on biomass varied by disturbance treatment, resulting in a significant rate by disturbance interaction (Figure 3-3; $P = 0.024$). In glyphosate treated plots, biomass was greater at the mid and high seeding rates compared to the low rate. However, seeding rate did not result in biomass differences among the other three disturbance treatments (Figure 3-3).

The full irrigation treatment resulted in the highest density, with no difference between the no- and pre- irrigation treatments (Figure 3-2). This difference was consistent throughout the study, despite the decline in density over time. Percent cover was greatest with the full irrigation treatment at 10 and 46 WAS but there was no difference among irrigation treatments at 20 and 39 WAS (Figure 3-2). Irrigation treatments did not affect *C. lanceolata* biomass at 46 WAS (data not presented).

***Coreopsis lanceolata* Fitness**

The percent cover of *C. lanceolata* flowers was recorded 20 WAS, which was estimated to be peak bloom in glyphosate treated plots and in a nearby planted population. Percent cover

of flowers ranged from 2.8% in the low seeding rate to 4.2% in the high seeding rate in glyphosate treated plots (Figure 3-4). In the scraped plots, flower cover ranged from 0.8% in the low seeding rate to 3.1% in the high seeding rate (Figure 3-4). Percent cover of *C. lanceolata* flowers was less than 0.5% in the control and sethoxydim treatments regardless of seeding rate (Figure 3-4).

Between 20 and 39 WAS, the *C. lanceolata* population consisted of adult plants originating from the fall seeding. However, between 39 and 46 WAS, I observed recruitment (emerged seedlings). At 46 WAS, the number of seedlings (per 0.25 X 0.25-m quadrat) averaged 2.5 in scraped plots but less than 1 in control, sethoxydim, and glyphosate treatments (Figure 3-5). Seedlings likely represent new recruitment from the planted population because 1) no seeds were observed on the soil surface 10-20 WAS and 2) numerous seeds were visible on the soil surface following seed maturation and dispersal from the adult plants. However, it is possible that some of the seedlings originated from dormant seeds from the fall seeding.

Community Vegetation

The percent cover of *P. notatum*, forbs, and graminoids changed significantly over the experiment. However, these changes over time varied by treatment factor, resulting in significant interactions between main effects and WAS (data not presented). Therefore, percent cover results were analyzed separately within each time period (WAS).

Paspalum notatum cover in glyphosate and scraped treatments remained significantly lower than control and sethoxydim treatments throughout the study. At 10 WAS, *P. notatum* cover was less than 1% in glyphosate and scraped treatments compared to 79% in control plots (Table 3-3). By week 46, *P. notatum* cover was less than 4% in glyphosate and scraped treatments compared with greater than 81% in control and 75% in sethoxydim treatments, respectively (Table 3-3). Similarly, *P. notatum* biomass was more than 20 times greater in the

control and sethoxydim treatments as compared to the glyphosate and scraped plots (Figure 3-3). While the sethoxydim treatment significantly reduced *P. notatum* cover by approximately 7% compared to the control 46 WAS, this reduction was slight when compared to the effects of the glyphosate and scraped treatments on *P. notatum* cover (Table 3-3). Increases in *C. lanceolata* seeding rate decreased *P. notatum* cover and biomass 46 WAS (Table 3-3). The decrease in biomass was only significant in the control and glyphosate treatments which led to a significant rate by disturbance interaction ($P < 0.05$; Figure 3-3). *Paspalum notatum* cover was lower with the full irrigation treatment compared to no irrigation 46 WAS (Table 3-3).

Disturbance treatments resulted in the greatest differences in forb cover. At 10 WAS, forb cover was greater in glyphosate treated plots than control and scraped plots (Table 3-3). However, by 46 WAS, forb cover was 58% in scraped plots, much greater than in all other disturbance treatments. The low seeding rate resulted in greater forb cover than the high rate at 10 WAS (Table 3-3). This trend continued 46 WAS, but only in the glyphosate treatment. There was no difference in forb cover or biomass among seeding rates in the control, sethoxydim, and scraped treatments (Figure 3-3), resulting in significant rate by disturbance interactions for both cover and biomass of forbs 46 WAS ($P < 0.01$, for both). In the scraped plots, forb cover and biomass were lowest with the full irrigation treatment at 46 WAS. However, there was no difference in forb cover among irrigation treatments in the control, sethoxydim, and glyphosate treatments, resulting in a significant irrigation by disturbance interaction 46 WAS ($P < 0.0001$ for cover, $P < 0.05$ for biomass).

Graminoids, excluding *P. notatum*, occupied a small percentage of the community vegetation (Table 3-3). The scraped treatment resulted in the greatest graminoid cover and biomass compared to the control, sethoxydim, and glyphosate treatments (Table 3-3, Figure 3-3,

$P < 0.0001$ for cover at 10 WAS and cover and biomass at 46 WAS). In the scraped treatment, graminoid cover and biomass were greatest with the full irrigation treatment compared to the no- and pre-irrigation treatments (Table 3-3). However, there were no differences among irrigation treatments in the control, sethoxydim, and scraped treatments, resulting in significant irrigation by disturbance interactions for cover at 10 and 46 WAS ($P < 0.001$ and $P < 0.0001$, respectively). Averaged over disturbance and irrigation treatments, graminoid biomass was greater in the low seeding rate than the medium and high rates ($P < 0.01$; Figure 3-3).

Soil Characteristics

Removing the topsoil resulted in decreased pH and organic matter and increased potassium as compared to the control, sethoxydim, and glyphosate treatments (Table 3-1). There was no difference in nitrogen (as available nitrates and ammonium) or phosphorus levels among disturbance treatments (Table 3-1).

Discussion

Interactive Effects of Seed and Microsite Availability

Seed and microsite availability interactively affected *C. lanceolata* emergence and seedling growth as observed 10 WAS. While increases in seeding rate generally increased *C. lanceolata* establishment, differences in microsite availability (i.e., disturbance and irrigation treatments) were often apparent only at the medium and high seeding rates. Hence, microsite limitation may only become biologically relevant when a minimum number of seeds is present.

Although seed and microsite limitations interactively affected *C. lanceolata* establishment at the beginning of the study, the relative importance of microsite limitation was greater than that of seed limitation by the end of the study. When the extant vegetation was not disturbed, seeding at the high rate (essentially eliminating seed limitation) did not increase *C. lanceolata* biomass as compared to the medium or low rates (Figure 3-3). This study provides

further support that increasing seed availability may not necessarily lead to increased recruitment if microsites are not available (Holl et al. 2000).

Disturbance Effects on Microsite Quality

C. lanceolata establishment was limited by the extant pasture vegetation (*P. notatum*), and not surprisingly, disturbance treatments increased *C. lanceolata* establishment compared to the control. However, the three disturbance treatments affected *C. lanceolata* establishment differently. Treating *P. notatum* pastures with glyphosate resulted in the greatest *C. lanceolata* establishment, regardless of seeding rate or irrigation treatment (Figure 3-2). Additionally, percent cover of flowers was greater in plots where *P. notatum* had been removed compared to plots where *P. notatum* was present (Figure 3-4). In other studies, *P. notatum* was a strong competitor (Rich et al. 2003) and limited establishment of native forbs (Uridel 1994, Violi 2000).

Contrary to my hypothesis, the scraped plots did not result in the greatest *C. lanceolata* establishment. Both the glyphosate and scraped disturbance treatments reduced *P. notatum* biomass; however, this decrease alone did not result in an equivalent increase in wildflower cover or biomass (Figures 3-2 and 3-3). Most studies on sessile organisms equate microsites with available space for growth (Eriksson 2005). However, the differences in *C. lanceolata* establishment between the glyphosate and scraped treatments suggest that microsite requirements are more complex than providing adequate space and likely include abiotic as well as biotic components (Tilman 1994).

The difference in *C. lanceolata* establishment between glyphosate and scraped treatments was largely due to lower emergence in the scraped plots. Removing the topsoil resulted in greater than 90% cover of bare ground, compared with 5% in the glyphosate treatment. While seed-to-soil contact generally increases establishment, multiple, small gaps result in greater establishment than fewer, large gaps (Burke and Grime 1996). Topsoil removal also likely

exposed native sandhill soils, which are deep, well-drained deposits of sand. Sandhill soils generally do not have horizon layers; organic matter, if present, is superficial and associated with existing vegetation (Myers 1990). The topsoil removal resulted in a harsh environment with little substrate stability and reduced organic matter. In fact, the sandhill environment has been likened to a desert for establishing seedlings (Myers 1990). In arid environments, seedling survivorship has been shown to be greater under shrub cover than in open areas (De Jong and Klinkhamer 1988). In a study on pasture restoration in Puerto Rico, removal of pasture vegetation resulted in decreased germination of four species and increased soil surface temperature (Zimmerman et al. 2000).

While topsoil removal may be an effective way to remove *P. notatum*, glyphosate was as equally effective in removing *P. notatum* and much more effective in establishing *C. lanceolata*. The glyphosate treatment effectively killed *P. notatum* but left a layer of “litter,” comprised of dead thatch and *P. notatum* stems. The litter present in glyphosate treated plots seemed to provide better microsites for germination and emergence than the bare sand present in scraped plots. Because of the litter layer, microsite characteristics in glyphosate treated plots may not have been different than control plots. Soil characteristics of glyphosate treated plots were equivalent to control plots, and both had higher organic matter than in scraped plots (Table 3-1). Additionally, there was no difference in percent cover of litter or of bare ground between the glyphosate and control treatments (data not presented). Existing vegetation can actually facilitate germination in some species by buffering relative humidity and temperature on the soil surface (Holmgren et al. 1997, Kennedy and Sousa 2006). The litter left by the glyphosate treatment may also have ameliorated the low moisture and nutrient levels characteristic of sandhills (Foster and Gross 1998).

Reducing *P. notatum* through a grass herbicide treatment at the rate applied did not increase *C. lanceolata* establishment. While sethoxydim decreased *P. notatum* cover by approximately 7%, the reduction resulted in only a small and short-lived increase in *C. lanceolata* cover. Despite the small reduction in cover, *P. notatum* was still the dominant species in the sethoxydim treatment. Most grass herbicides, including sethoxydim, work best when applied during active growth of the target species. In this study, *P. notatum* was not actively growing until approximately 20 WAS, at which point *C. lanceolata* was already flowering in glyphosate plots. Existing vegetation may serve as an effective nurse crop, helping to control undesirable ruderals while desirable natives become established (Ewel and Putz 2004). Although *P. notatum* suppressed the growth of unwanted ruderals in this case, it also suppressed the growth and flowering of the desirable native species. Reducing *P. notatum* cover after *C. lanceolata* was established was not as effective as removing *P. notatum* prior to seeding.

By the end of the study, supplemental irrigation did not result in large increases in *C. lanceolata* cover or biomass, but this result may be confounded by the particularly wet winter during which this study was conducted (El Niño year with high rainfall). Effects of irrigation on cover were apparent at 10 and 46 WAS but not between 10 and 46 WAS (Figure 3-3). Perhaps differences between the full irrigation treatment compared to the pre- and no-irrigation treatments were too small to be detected. At 46 WAS, differences in cover may have been more apparent than at 20 and 39 WAS due to increased rain following a drought (Figure 3-2). *Coreopsis lanceolata* has thick, leathery leaves that curl in response to drought, resulting in decreased cover. Plants may have recovered by 46 but not 39 WAS. Although the full irrigation treatment did not result in large increases in *C. lanceolata* cover compared to the no- and pre-

irrigation treatments, *C. lanceolata* density was consistently higher in the full irrigation treatment than the other two irrigation treatments.

Requirements for Emergence Versus Establishment

Different responses of *C. lanceolata* density and cover by treatment and over time indicate different requirements for seedling emergence versus subsequent growth. *Coreopsis lanceolata* emergence occurred within 10 weeks of seeding, from which point density decreased over time (Figure 3-2). However, percent cover increased throughout the experiment. The decrease in density coupled with the increase in cover indicates that increases in stand establishment through time resulted from emerged seedlings increasing in size rather than number. While growth of *C. lanceolata* was limited by *P. notatum*, emergence was not. At 10 WAS, there were no differences in density between the control and glyphosate treatments; however, cover was greater in glyphosate than control treatments (Figure 3-2). These results indicate that *C. lanceolata* was able to germinate in *P. notatum* but the resulting seedlings were smaller than those in the glyphosate treated plots. Plants are often more sensitive to environmental conditions and competition during the seedling stage than during germination or as adults (Isselstein et al. 2002, Holzel and Otte 2003). A study focusing on the establishment of annuals in an arid environment found that plant-plant interactions shifted from facilitation in the seedling stage to competition during the reproductive stage (Schiffers and Tielborger 2006). In this study, *P. notatum* had a neutral effect on *C. lanceolata* emergence but a competitive effect on seedling and adult growth.

While adding seeds and supplemental irrigation did not compensate for the lack of microsites created by the glyphosate treatment by the end of the study, the significant interactions among treatments 10 WAS suggest a greater interplay between seed and microsite limitation early in *C. lanceolata* establishment. Changes to microsite availability have been

shown to affect different growth stages of the same plants differently. The present study supports these results, but also suggests a more complex relationship. The differences in *C. lanceolata* establishment between the glyphosate and scraped treatments and between the full and no- or pre-irrigation treatments suggest that microsites represent a complex interaction of factors, not just the availability of space, water, or nutrients.

Effects on Community Vegetation

Treatments that improved wildflower establishment affected other vegetation in the community positively and negatively. For example, increasing the seeding rate not only resulted in increased *C. lanceolata* cover, but also decreased cover of *P. notatum*, forbs, and graminoids. The full irrigation treatment increased *C. lanceolata* cover and density but also increased graminoids and decreased *P. notatum*. Since *P. notatum* is dormant during winter, the decrease in *P. notatum* due to irrigation appears to be a result of increased wildflower density.

Removing the topsoil did not prevent colonization of weedy forbs in the scraped plots. Although not tested for this site, several studies have demonstrated that the majority of the seed bank is found in the top 5 cm of soil (Roberts 1981). In this study, the top 13 cm was removed but forb establishment was still high, especially 46 WAS. Although some forbs were native species representative of sandhill communities like *Asimina* Adans sp. (paw paw) and *Asclepias* L. sp. (milkweed), the majority of forbs were agricultural weeds like *Rumex* L. sp. (dock) and *Indigofera hirsuta* L. (rough hairy indigo). Most of the weedy forbs that colonized the scraped plots occurred in nearby agricultural fields. Removing topsoil creates large patches of bare ground where colonizing plants can quickly become established. In agricultural and heavily-fragmented areas, propagule pressure from undesirable ruderal or invasive species can be high. Therefore, topsoil removal in these settings may not be as beneficial as in less disturbed settings, where recruitment from desirable natives is more likely.

Graminoids (other than *P. notatum*) comprised a small percentage of the community vegetation and were mostly represented by common sedges (*Cyperus* spp.) This indicates that native grasses, which are an essential component of the native understory, were largely absent from the study site. These results suggest that while introducing a single forb species may be a short term solution in converting pasture grass to native habitat, seed introductions of a suite of native grasses and forbs would be necessary to develop this site into a species rich native community.

Conclusions

While seed and microsite limitations interactively affected *C. lanceolata* establishment at the beginning of the study, the relative importance of microsite limitation was greater than that of seed limitation by the end of the study. Alleviation of microsite limitation depended strongly on the quality of microsite. Specifically, disturbing the extant vegetation with glyphosate herbicide prior to seeding resulted in greater establishment than any other disturbance treatment. Removing the topsoil increased *C. lanceolata* somewhat compared to the control but also increased colonization by weedy forbs. By the end of the study, *C. lanceolata* establishment was not affected by supplemental irrigation. *Coreopsis lanceolata* establishment was limited when seeded at 100 live seeds/m² but not at 600 live seeds/m². Seeding at 1100 live seeds/m² provided little additional benefits to overall *C. lanceolata* establishment compared to seeding at 600 live seeds/m². Different treatment responses between *C. lanceolata* density and percent cover, at the beginning and end of the study, suggest that requirements for seedling emergence are less stringent than those for plant establishment.

Table 3-1. Disturbance treatment effects (control, sethoxydim, glyphosate, scraped) on soil chemistry before seeding *Coreopsis lanceolata* in a former pasture in Citra, FL.

Disturbance treatment	Soil characteristics					
	pH	Organic matter (%)	NO ₃ -N (mg·kg ⁻¹)	NH ₄ -N (mg·kg ⁻¹)	P (mg·kg ⁻¹)	K (mg·kg ⁻¹)
Control	5.89a	2.02a	<1.00	0.95	31.62	37.12a
Sethoxydim	5.91a	2.01a	<1.00	0.96	30.08	39.53a
Glyphosate	5.88a	1.88a	<1.00	0.95	31.21	43.44a
Scraped	5.62b	1.37b	<0.10	1.00	30.17	46.65b

Means with different letters within soil characteristics differ significantly as determined by ANOVA ($P < 0.0001$, Bonferroni correction); no means comparison was performed if a soil characteristic was not significant. Analysis was not performed on NO₃-N because values were too low to be detected with greater accuracy.

Table 3-2. Effects of irrigation (none, pre, full), seeding rate (low, medium, high), disturbance (control, sethoxydim, glyphosate, scraped), and time (weeks after seeding) on density and percent cover of *Coreopsis lanceolata* in a former pasture in Citra, FL. Analysis was performed on log (x +1) transformed density data and arcsine square root percent cover data.

Model Factor	df	Density		Percent cover	
		F	P	F	P
Repeated measures model					
Irrigation	2, 14	26.47	<0.0001	8.89	0.0032
Seeding rate	2, 165	244.75	<0.0001	142.07	<0.0001
Disturbance	3, 165	28.69	<0.0001	153.08	<0.0001
Weeks after seeding	3, 540	43.90	<0.0001	960.09	<0.0001
Irrigation X rate	4, 165	2.69	0.0330	0.90	0.4650
Irrigation X disturbance	6, 165	1.04	0.3982	0.79	0.5802
Rate X disturbance	6, 165	2.47	0.0256	0.48	0.8225
Irrigation X rate X disturbance	12, 165	0.68	0.7693	0.29	0.9909
Irrigation X weeks	6, 540	6.60	<0.0001	3.16	0.0047
Rate X weeks	6, 540	20.7	<0.0001	24.36	<0.0001
Disturbance X weeks	9, 540	7.38	<0.0001	69.66	<0.0001
Irrigation X rate X weeks	12, 540	1.80	0.0453	0.73	0.7184
Irrigation X disturbance X weeks	18, 540	0.64	0.8696	0.91	0.5706
Rate X disturbance X weeks	18, 540	1.95	0.0110	1.57	0.0624
Irrigation X rate X disturbance X weeks	36, 540	0.68	0.9226	0.77	0.8310
Ten weeks after seeding					
Irrigation	2, 14	21.47	<0.0001	48.53	<0.0001
Seeding rate	2, 165	130.94	<0.0001	152.16	<0.0001
Disturbance	3, 165	29.43	<0.0001	35.55	<0.0001
Irrigation X rate	4, 165	3.34	0.0116	6.51	<0.0001
Irrigation X disturbance	6, 165	0.86	0.5263	4.42	0.0004
Rate X disturbance	6, 165	3.58	0.0023	1.79	0.1050
Irrigation X rate X disturbance	12, 165	0.49	0.9208	1.22	0.2705
Forty six weeks after seeding					
Irrigation	2, 14	14.15	<0.0001	5.62	0.0161
Seeding rate	2, 165	134.03	<0.0001	83.51	<0.0001
Disturbance	3, 165	26.81	<0.0001	118.46	<0.0001
Irrigation X rate	4, 165	2.30	0.0608	0.59	0.6725
Irrigation X disturbance	6, 165	0.69	0.6543	0.91	0.4888
Rate X disturbance	6, 165	1.15	0.3349	0.80	0.5738
Irrigation X rate X disturbance	12, 165	0.62	0.8261	0.49	0.9167

Table 3-3. Effects of irrigation (none, pre, full), seeding rate (low, medium, high), and disturbance (control, sethoxydim, glyphosate, scraped) on percent cover of *Paspalum notatum*, forbs, and graminoids 10 and 46 weeks after seeding *Coreopsis lanceolata* in a former pasture in Citra, FL.

Factor level	Vegetation category					
	<i>Paspalum notatum</i>		Forbs		Graminoids	
	Weeks after seeding		Weeks after seeding		Weeks after seeding	
	10	46	10	46	10	46
Irrigation	ns	**	ns	ns	ns	*
None	38.8	42.8 a	3.2	19.9	0.5	1.5 ab
Pre	39.9	40.9 ab	3.7	20.3	0.6	1.2 a
Full	40.7	38.9 b	4.3	15.9	0.9	2.2 b
Rate (live seeds/m ²)	ns	***	**	***	ns	+
100	40.1	45.7 a	4.7 a	24.6 a	0.8	1.8
600	39.3	40.1 b	3.7 ab	15.8 b	0.7	1.7
1100	39.9	36.8 c	2.8 b	15.8 b	0.6	1.3
Disturbance	***	***	***	***	***	***
Control	79.0 a	81.6 a	2.3 a	2.5 a	0.6 a	1.6 a
Sethoxydim	79.4 a	75.1 b	2.0 a	3.9 a	0.7 a	1.7 a
Glyphosate	0.5 b	3.4 c	7.3 b	11.0 b	0.3 a	1.1 a
Scraped	0.3 b	3.5 c	3.3 a	57.5 c	1.1 b	2.1 b
Significance of F-test						
Irrigation*rate	ns	ns	ns	ns	ns	ns
Irrigation*disturbance	**	ns	ns	***	**	***
Rate*disturbance	ns	ns	ns	**	ns	ns
Irrigation*rate*disturbance	ns	ns	+	ns	ns	ns

Significant main effects and interactions are indicated by: *** ($P < 0.0001$), ** ($P < 0.01$), * ($P < 0.05$). Marginally significant effects ($0.10 > P > 0.05$) are indicated by +. Means with different letters within vegetation categories are significantly different ($P < 0.05$, Bonferroni correction). Analysis was performed on arcsine square root transformed data; untransformed means are presented here.

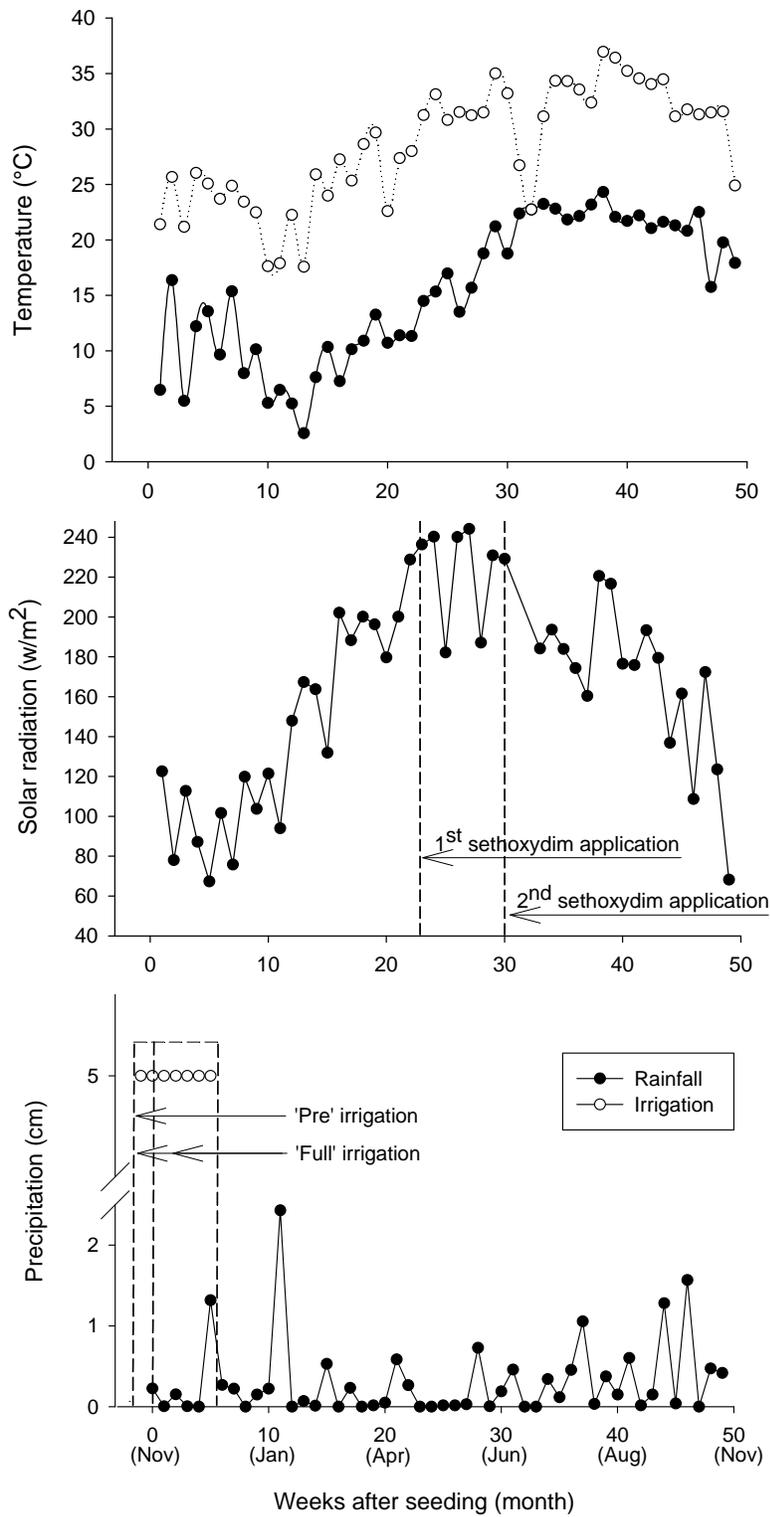


Figure 3-1. Minimum and maximum temperatures at 60 cm, solar radiation, and precipitation at the study site in north-central Florida from November 2006 to November 2007. Data from FAWN, Florida Automated Weather Network (<http://fawn.ifas.ufl.edu>).

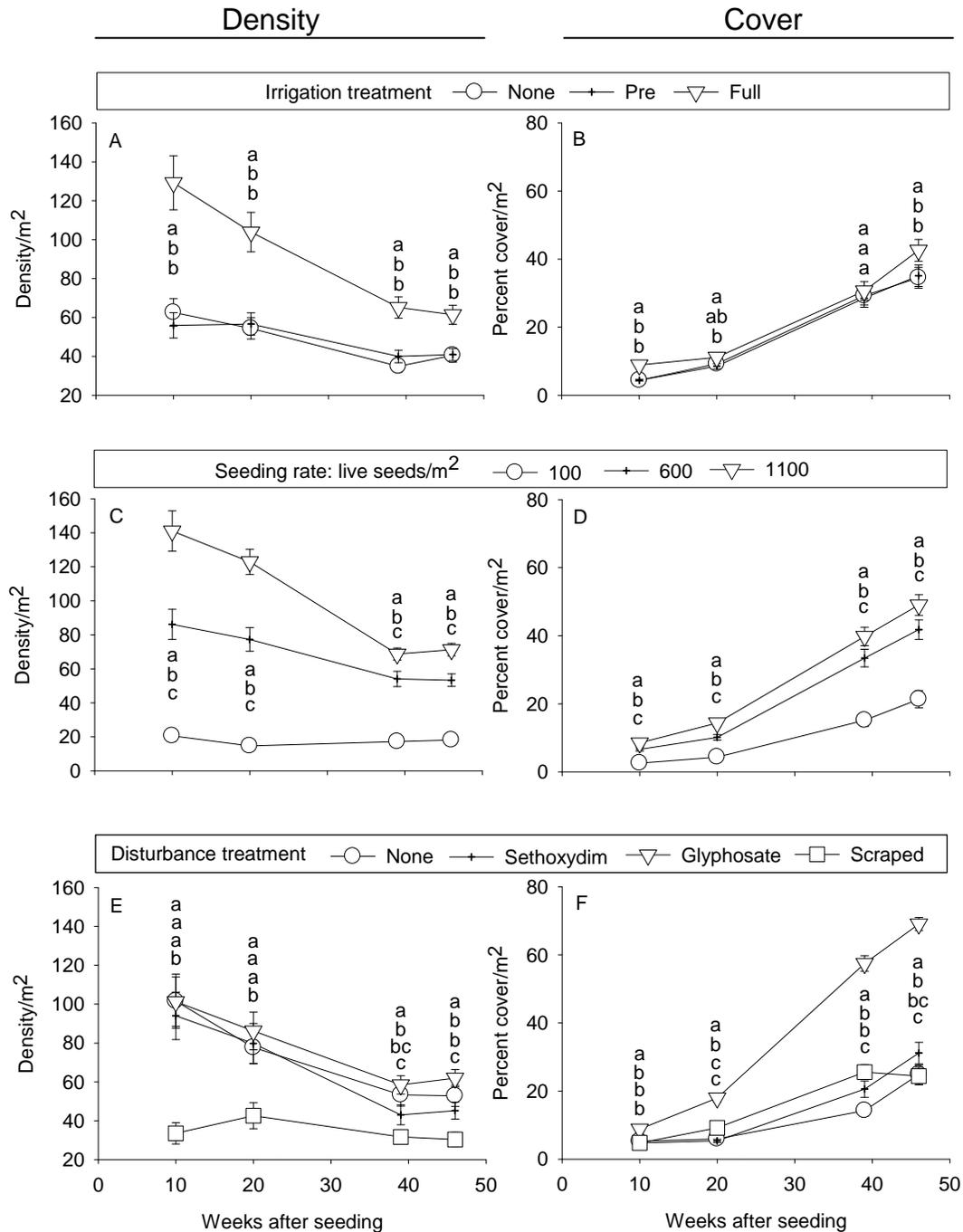


Figure 3-2. Effects of irrigation (graphs A and B), seeding rate (graphs C and D), and disturbance (graphs E and F) treatments on mean (\pm SE) *Coreopsis lanceolata* density (individuals/m²; graphs A, C, E) and percent cover (graphs B, D, F). Different letters within each column indicate significant differences ($P < 0.05$; Bonferroni correction). Analysis was performed on $\log(x + 1)$ transformed density data and arcsine square root cover data; untransformed means are presented here. Means are presented separately for each main effect because there were no significant interactions by the end of the study (see Table 3-2).

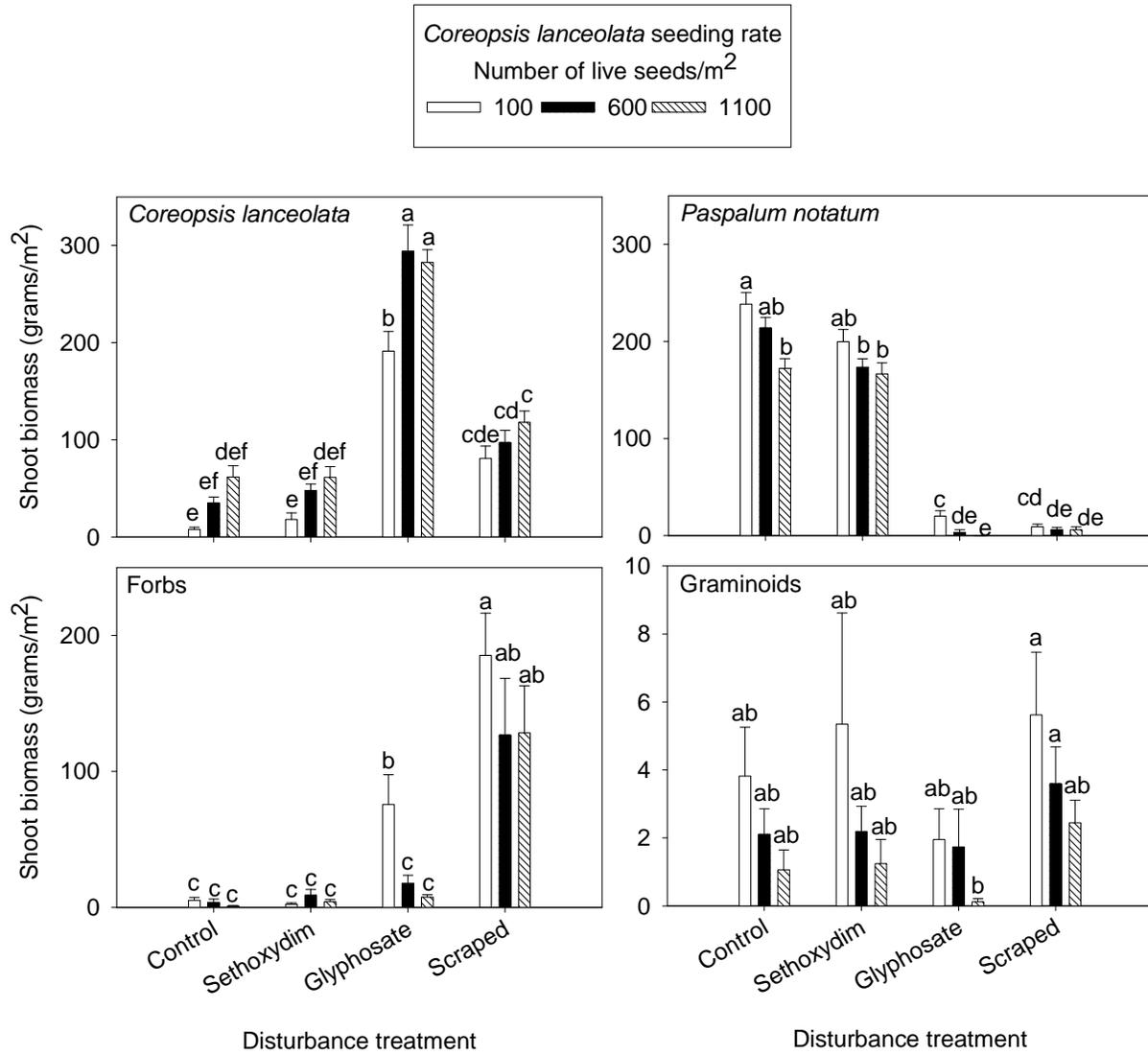


Figure 3-3. Effects of seeding rate and disturbance treatment on mean (+ SE) shoot biomass of *Coreopsis lanceolata*, *Paspalum notatum*, forbs, and graminoids 46 weeks after seeding. Means with different letters within each species/guild indicate significant differences ($P < 0.05$; Bonferroni correction). Analysis of all response variables except *Coreopsis lanceolata* was performed on square root transformed data; untransformed means are presented here. Note differences in y-axis scale for forbs and graminoids.

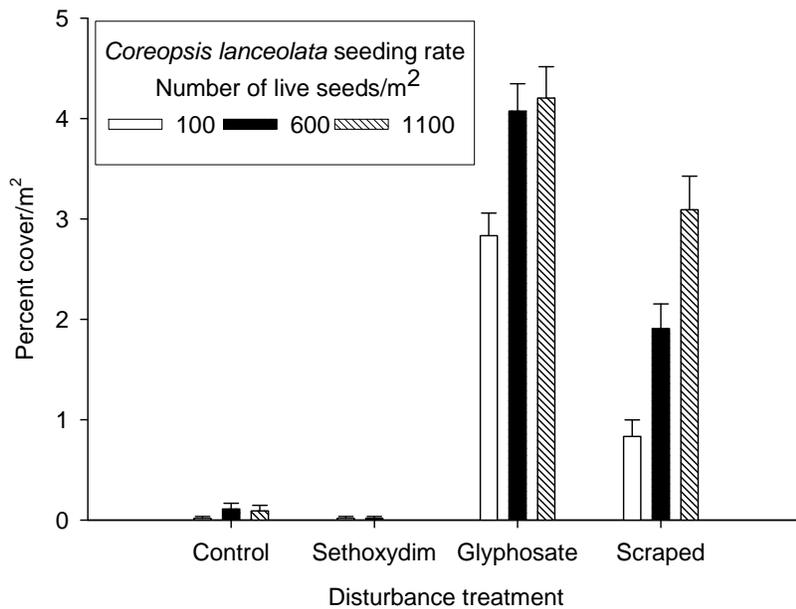


Figure 3-4. Effects of seeding rate and disturbance treatment on mean (+ SE) percent cover of *Coreopsis lanceolata* flowers 20 weeks after seeding. Means were not compared statistically due to the high proportion of zero values.

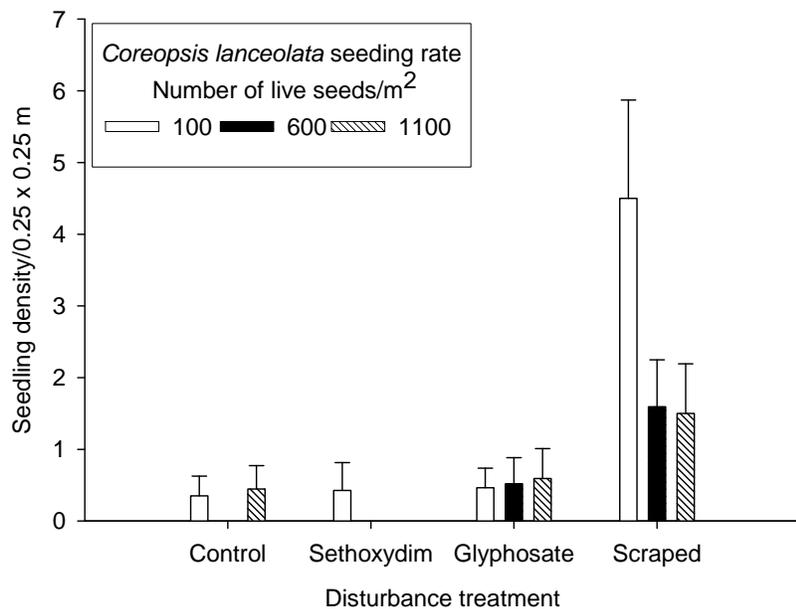


Figure 3-5. Effects of seeding rate and disturbance treatment on mean (+ SE) number of *Coreopsis lanceolata* seedlings 46 weeks after seeding. Means were not compared statistically due to the high proportion of zero values.

CHAPTER 4
MOWING FREQUENCY AND HERBICIDE EFFECTS ON ESTABLISHING NATIVE
WILDFLOWER POPULATIONS ON SIMULATED ROADSIDES

Introduction

Roads have become a ubiquitous part of our landscape, comprising more than 4 million ha of land in the United States (Forman and Alexander 1998, Harper-Lore and Wilson 2000). Roads cause habitat fragmentation (Heilman et al. 2002) and provide corridors for invasive, non-native species to expand their range (Gelbard and Belnap 2003, Hansen and Clevenger 2005). However, since the 1970s, there has been more of an ecological approach to roadside management, with increased efforts to increase biodiversity and manage for wildlife (Harper-Lore and Wilson 2000). Increasing native wildflower populations on roadsides can decrease the occurrence of non-native, invasive species as well as improve aesthetics (Florida Department of Transportation 1998, Harper-Lore and Wilson 2000). Moreover, roadside maintenance costs can be reduced when wildflower populations are managed appropriately (Markwardt 2005). Hence, roadside vegetation managers are becoming increasingly interested in planting native wildflowers along roadsides (Harper-Lore and Wilson 2000).

Roadsides are often planted with grass monocultures that effectively control erosion and can tolerate frequent mowing (Forman et al. 2003). However, the establishment of new species into established grass monocultures may be limited by competition (Forman et al. 2003). In Florida, roadsides are commonly planted with *Paspalum notatum* Flüggé var. *saurae* Parodi (bahiagrass), a non-native pasture grass introduced to the United States from Brazil (Violi 2000). *Paspalum notatum* forms dense mats of vegetation, often preventing native plant establishment (Violi 2000). Applying herbicide to extant vegetation (postemergence) before seeding may increase wildflower establishment (del-Val and Crawley 2005). The application of glyphosate, a non-selective herbicide, to *P. notatum* increased establishment of native species subsequently

planted in *P. notatum* pastures (Uridel 1994). When applied at the time of wildflower seeding, imazapic, a selective herbicide, decreased the density and growth rate of existing vegetation while not substantially impacting the establishment of some wildflower species (Beran et al. 1999, Norcini et al. 2003). However, the tolerance of wildflowers to imazapic varies considerably according to wildflower species, ecotype, and rate of application (BASF Corporation 2003, Norcini et al. 2003).

Limited information is available on the establishment and management of local ecotypes of native wildflowers on Florida roadsides. Seeds have been traditionally purchased from nonlocal sources (Florida Department of Transportation 1998), but local ecotype seeds have recently become available via Florida's Wildflower Seed and Plant Growers Association Inc. (2008). Local ecotypes may be better adapted to the area in which they occur than more distant ecotypes (Norcini et al. 2001). For example, Norcini et al. (2001) found that local ecotypes of *Coreopsis lanceolata* in Florida bloomed earlier and had higher survivorship than nonlocal ecotypes. However, environmental conditions on roadsides are altered and often do not mimic the biotic and abiotic characteristics of native habitats (Forman and Alexander 1998, Trombulak and Frissell 2000, Jenkins et al. 2004). Although Florida ecotypes are adapted to Florida's climate, establishment and management practices may be different than those for nonlocal seed sources and on altered landscapes such as roadsides.

Roadsides are managed to meet several objectives including driver safety, road stabilization, and maintenance access. Mowing of roadside vegetation is the most common and widespread form of roadside management, and is primarily utilized for driver safety. The frequency, timing, and height of mowing can influence plant species composition on roadsides. Mowing can increase species diversity (Parr and Way 1988, Collins et al. 1998, Hofmann and

Isselstein 2004). In a long-term study comparing mowing frequencies, the diversity of roadside vegetation was greater in areas mowed two times per year than once per year or not at all, and the lowest diversity was found in areas that were not mowed (Parr and Way 1988). In addition to increasing diversity, mowing and removing litter can increase germination and establishment of seedlings (Jensen and Meyer 2001, Jutila and Grace 2002). However, the time of year an area is mowed can significantly impact the growth and recruitment of a species, especially if mowing precedes seed set (Brys et al. 2004).

The objective of this study was to determine the effects of pre-seeding herbicide application and mowing frequency on native wildflower establishment on simulated roadsides in Florida. I hypothesized that a moderate amount of disturbance (mowing twice per year) and reduced competition through herbicide treatments would result in increased wildflower establishment.

Methods

Study Sites and Species

To examine treatment effects across a range of climate and soil types, the experiment was conducted in three different regions of Florida (Table 4-1, Figure 4-1). Sites were located in north (Quincy), north-central (Citra), and south-central (Fort Pierce) Florida (Table 4-1). All sites are research centers of the University of Florida's Institute of Food and Agriculture Sciences. Conducting the experiments at research centers allowed for more controlled conditions and easier access to equipment than would be possible on roadsides.

The study areas were planted in *P. notatum*, approximately 10-20 years before the beginning of the study. Selected for its drought tolerance and lack of pest problems, *P. notatum* was originally introduced as a pasture grass (Scott 1920). *Paspalum notatum* is now commonly planted on roadsides due to its effectiveness in controlling erosion through the formation of a

dense root system (Violi 2000). While several cultivars have been developed since its introduction, 'Pensacola' is the cultivar planted at all three study sites and frequently planted on pastures and roadsides in Florida (Violi 2000).

Native wildflowers in this study include three species in the Asteraceae: *Gaillardia pulchella* Foug. (firewheel), *Coreopsis lanceolata* L. (lanceleaf tickseed), and *Coreopsis leavenworthii* Torr. & A. Gray (Leavenworth's tickseed) (United States Department of Agriculture 2008). *Gaillardia pulchella* is an annual to short-lived perennial commonly occurring throughout Florida in disturbed uplands (Wunderlin and Hansen 2003). It blooms from spring to summer in north Florida and year-round in south Florida (Osorio 2001). *Coreopsis lanceolata* is an evergreen, short-lived perennial that occurs throughout much of the United States and blooms in spring (Flora of North America Editorial Committee 2006, United States Department of Agriculture 2008). In Florida, *C. lanceolata* occurs in northern and north-central regions in sandhill and disturbed habitats (Wunderlin and Hansen 2003). *Coreopsis leavenworthii* is an annual to short-lived perennial and a facultative wetland species (Wunderlin and Hansen 2008). Previously thought to be endemic to Florida, *C. leavenworthii* is now known to occur in Alabama (United States Department of Agriculture 2008). *Coreopsis leavenworthii* is common throughout Florida and occurs in depression marshes, disturbed wetland, marl prairie, pine rockland, wet flatwood, and wet prairie habitats (Gann et al. 2008). Flowers may be produced year-round in south Florida, but most flowers are produced in spring and early to mid-summer (Osorio 2001).

Local ecotype seeds of each wildflower species were mixed with moistened sand and hand broadcast into *P. notatum* pastures in early October 2005. The seeding rate (pure live seed) varied by species: *C. leavenworthii* – 3.1 kg/ha (~2007 seeds/m²); *C. lanceolata* – 6.2 kg/ha

(~554 seeds/m²); and *G. pulchella* – 1.9 kg/ha (~121 seeds/m²). All three wildflower species were seeded in Citra and Quincy; only *C. leavenworthii* was seeded in Fort Pierce. (*C. lanceolata* is not native to south-central Florida and local ecotype *G. pulchella* seeds were not available for this ecoregion.) Within three weeks of seeding, Hurricane Wilma made landfall near the Fort Pierce site and study plots were inundated for several days.

Experimental Design

I evaluated the effects of mowing regime and establishment methods on three native Florida wildflower species for two years at three sites in Florida. Treatment effects were assessed separately for each species and there were four replicates per site. Replicate plots were 12 m² (3 X 4 m) with 1-m perimeter buffers within each plot, 1-m alleys between each plot, and a 10-m buffer strip between each experiment.

Two mowing regimes and three establishment methods were evaluated in a split plot design, with mowing regime as the main plot treatment and establishment method as the sub plot treatment. The two mowing regimes differed in the number of times each plot was mowed, either two or six times per year. The timing of mowing treatments was adjusted for flowering and seeding phenology of each wildflower species (Table 4-2).

The three establishment methods evaluated the use of herbicides (glyphosate, imazapic, and an untreated control) on extant vegetation. Glyphosate (Roundup®, Monsanto) was applied at 2.3 L ai/ha approximately 4 and 2 weeks before seeding. Imazapic (Plateau®, Impose™, Panoramic 2SL, BASF) was applied at 0.07 kg ai/ha within one day of seeding. In Citra, herbicide was applied with a Cushman® Spraytek™ (Jacobsen Co.) that delivered 281 L/ha at 310 kPa. In Quincy and Fort Pierce, herbicide was applied with a compressed air backpack sprayer (Teejet® flat fan nozzle, Spraying Systems Co.) that delivered 374 L/ha at 138 kPa.

Sites were prepared by mowing the extant vegetation to 5 cm and removing thatch from the plots within one week before seeding. Because *P. notatum* was especially dense in Fort Pierce, vegetation was scarified with a conservation planter before seeding. After seeding, plots were rolled with a turf roller to increase seed-to-soil contact and irrigated overhead for approximately two weeks. At the start of the study, *P. notatum* was the dominant species with greater than 70% cover at each site. Forbs comprised less than 2% and 9% cover in Citra and Quincy, respectively. In Fort Pierce, forbs comprised 32% cover mainly due to the occurrence of *Arachis glabrata* Benth. (perennial peanut, a forage crop) that was previously planted. None of the planted wildflower species were growing at the study sites prior to seeding. A preliminary seed bank study conducted in fall 2005 confirmed that wildflower species were not present in the seed bank prior to the experiment.

Research plots were evaluated in fall (November/December), spring (April/May), and summer (August/September) from 2005 through 2007. Density and percent cover were evaluated in the center square meter of each plot. Density counts were for all individuals (adults and seedlings) of the wildflower species. Percent cover was visually estimated (to the nearest percent) by the same observer at each data collection to minimize observer bias (Korb et al. 2003). Percent cover categories included the wildflower species, forbs (excluding the wildflower species), graminoids, bare ground, and standing dead/litter. To allow for future evaluations, only nondestructive sampling was conducted.

Seed Bank Study

In fall 2006, eight soil cores (6 cm diameter by 5 cm deep, 141.3 cm³) were randomly sampled from each plot (excluding the center square meter), aggregated, and a subsample (282.6 cm³) was selected for the seed bank study. Soil samples were spread evenly, to no more than 2 cm deep, over a soilless medium (Fafard #2 Mix, Conrad Fafard, Inc.) in pots (18 cm diameter

by 11 cm high). Initially, soil was misted until saturated and subsequently irrigated by drip lines placed underneath the top 2 cm of soil. Pots were arranged in a randomized complete block design in a greenhouse at the University of Florida in Gainesville. A control pot filled only with a soilless medium was included within each block. After 2 months, emerged seedlings were removed from each pot and counted into groups of wildflower species, forbs, and graminoids. The surface soil was stirred in the pots and irrigated. After another 2 months, all emerged seedlings were counted again. The first and second data collections were combined for analysis.

Statistical Analysis

I analyzed aboveground vegetation data using mixed models with restricted maximum likelihood methodology (PROC MIXED, version 9.1; SAS Institute, Cary North Carolina, USA). Preliminary results indicated significant differences among seasons of data collection; therefore, each season was analyzed separately. Within each season, the fixed factors were mowing regime, establishment method, site, and year of data collection. Random factors were block (from split plot design), block by mowing regime, and block by site. To identify changes in wildflower percent cover and density over time, a repeated measures analysis was added to the model. Density data were $\log(x + 1)$ transformed and percent cover data were arcsine square root transformed to meet assumptions of normality and homogeneity of variance. Treatment effects on the seed bank (emerged seedlings) were determined as above, but without the repeated measures analysis. Counts of emerged seedlings were converted from cm^3 to m^2 (McBurney 2005), and $\log(x + 1)$ transformed to meet assumptions of normality and homogeneity of variance. Means were separated using least squares means (with PDIFF option) as part of the mixed models analyses; P values were adjusted using the Bonferroni method.

Results

Mowing frequency did not affect the percent cover or seed bank density of any of the wildflower species (Tables 4-3, 4-4, and 4-5). However, establishment method was significant for every species during every season of data collection ($P < 0.0001$, Tables 4-3, 4-4, and 4-5). In most cases, the glyphosate treatment increased wildflower cover and seed bank density compared to the control, but results varied by wildflower species and site. Therefore, results of each species are presented separately.

Gaillardia pulchella

Mowing frequency had no effect on *G. pulchella* emergence or growth; however, establishment treatment significantly affected percent cover, density, and seed bank density. The glyphosate treatment resulted in greater *G. pulchella* cover compared to the control and imazapic treatments (Table 4-3, Figure 4-2). Cover was less than 3% in the control and imazapic treatments and did not differ between the two treatments. During spring, cover was greater in 2007 than 2006 in the glyphosate treatment but showed no response by year in the control and imazapic treatments (Table 4-3, Figure 4-2). During fall, cover decreased in the glyphosate treatment as a result of *G. pulchella* mortality (or aboveground dieback) following the growing season. The seasonal reduction in cover was greater in Citra than in Quincy in 2006, resulting in a significant establishment by site by year interaction (Table 4-3, Figure 4-2).

I observed no difference in density among establishment treatments the first year after seeding. However, in the second year of the experiment (starting fall 2006 in Quincy and spring 2007 in Citra), density was greater in the glyphosate treatment than in the control and imazapic treatments ($P < 0.001$; data not presented). Similarly, the number of seedlings emerging from the soil seed bank was greater in the glyphosate treatment than the control and imazapic treatments in Citra (Table 4-6, Figure 4-3, based on results of seed bank study). However, there was no

difference in seedling emergence in Quincy, resulting in a significant site by establishment interaction (Table 4-6, Figure 4-3). Regardless, *G. pulchella* contributed less than 4% to the overall seed bank density (Figure 4-3).

The establishment treatment affected both the above- and belowground composition of forbs and graminoids (Figure 4-3). The glyphosate treatment decreased graminoid cover but increased forb cover in spring 2007 (Figure 4-3). Graminoids generally dominated the aboveground vegetation, yet only comprised a small percentage of the seed bank. The majority of seeds in the seed bank consisted of forbs, which comprised less than 13% of aboveground cover in the control and imazapic treatments and up to 40% cover in the glyphosate treatment (Figure 4-3).

Coreopsis lanceolata

Similar to *G. pulchella*, *C. lanceolata* was significantly affected by establishment treatments but not mowing treatments. *Coreopsis lanceolata* cover in the glyphosate treatments was greater than the control and imazapic treatments in all seasons (Table 4-4, Figure 4-2). The imazapic treatment increased *C. lanceolata* cover compared to the control treatment in Quincy but not in Citra (Figure 4-2), resulting in significant ($P < 0.05$) establishment by site interactions for spring and summer (Table 4-4). Until one year after seeding, *C. lanceolata* cover generally increased (Figure 4-2). However, the extent of the increase was affected by site, establishment treatment, and season, resulting in several significant interactions (Table 4-4). In the glyphosate treatment, *C. lanceolata* cover did not change in the second year of the experiment (Figure 4-2, fall 2006-fall 2007). In the control and imazapic treatments, however, cover increased from 2006 to 2007 in Citra but there was no change in cover in Quincy (Figure 4-2).

During the second year of the experiment (starting fall 2006), density was consistently greater in the glyphosate treatment than the control and imazapic treatments ($P < 0.0001$; data not

presented). In the glyphosate treatment, density averaged 44 and 491 individuals/m² in Citra and Quincy, respectively. Density in the control and imazapic treatments averaged 13 and 75 individuals/m² in Citra and in Quincy, respectively (averages include fall 2006 and spring and fall 2007). While *C. lanceolata* seed bank density was greater in the glyphosate treatment than the control and imazapic treatments, *C. lanceolata* only comprised a small proportion of the overall seed bank (Table 4-6, Figure 4-4).

Establishment treatments affected both above- and belowground community composition (Figure 4-4). *Coreopsis lanceolata* dominated the aboveground vegetation in the glyphosate treatment while graminoids dominated the aboveground vegetation in the control and imazapic treatments (Figure 4-4). The glyphosate treatment decreased graminoid cover but did not affect seed bank density compared to the control and imazapic treatments ($P < 0.001$, Figure 4-4). Moreover, graminoid cover was lower in the imazapic treatment than the control in fall and spring, regardless of year ($P < 0.05$, Figure 4-4). In all establishment treatments, forbs comprised the majority of the seed bank but a small minority of aboveground vegetation (Figure 4-4).

Coreopsis leavenworthii

Effects of establishment on *C. leavenworthii* cover varied by site, season, and year (Table 4-5). In general, *C. leavenworthii* cover decreased over time, despite seasonal fluctuations (Figure 4-2). Additionally, cover was typically greater in the glyphosate treatment than in the control and imazapic treatments, but this varied considerably by site (Figure 4-2). In Quincy, cover in the glyphosate treatment was greater than the control and imazapic treatments, except in fall 2006 when there was no difference between the glyphosate and imazapic treatments ($P < 0.05$ for all seasons and years, Figure 4-2). In Citra, *C. leavenworthii* cover was greater in glyphosate treated plots than in control and imazapic treated plots in summer and fall 2006 (P

<0.05 for all treatments) but there was no difference in cover among establishment treatments before or after this time period (Figure 4-2). There was no difference in cover between the imazapic and control treatments in Quincy or Citra.

In Fort Pierce, cover was greater in the glyphosate treatment than the control and imazapic treatments from fall 2005 through summer 2006 ($P < 0.05$ for all seasons and treatments, Figure 4-2). *Coreopsis leavenworthii* cover remained below 1% in imazapic treated plots in Fort Pierce throughout the study (Figure 4-2), significantly lower than control and glyphosate treated plots from fall 2005 through spring 2007 ($P < 0.05$ for all seasons and treatments). In summer and fall 2007, wildflower cover in control and glyphosate treated plots decreased, resulting in no differences among any establishment treatment (Figure 4-2).

Mowing frequency alone did not affect cover of *C. leavenworthii*; however, there was a mowing by site interaction during summer ($P = 0.0064$, Table 4-5). This resulted from a difference in mowing treatment in Fort Pierce only. During summer 2006, cover was estimated within two weeks of a mowing treatment, resulting in a short-term difference between mowing treatments.

Coreopsis leavenworthii density fluctuated widely, varying by site, season, and establishment treatment. For example, density averaged 3,146 individuals/m² in the glyphosate treatment in Quincy in fall 2006 compared to 1,127 and 285 individuals/m² in control and imazapic treatments, respectively. Despite this increase in density, cover decreased in glyphosate treated plots during the same time period due to mortality (or aboveground dieback) of adults following the growing season (Figure 4-2). At all sites, the glyphosate treatment increased *C. leavenworthii* seed bank density compared to the control and imazapic treatments (Table 4-6, Figure 4-5). In Quincy, there was no difference in the *C. leavenworthii* seed bank

density between the control and imazapic treatments. However, the imazapic treatment increased the seed bank density in Citra and decreased the seed bank density in Fort Pierce compared to the control treatment (establishment by site interaction, Table 4-6, Figure 4-5).

Effects of establishment treatments on the above- and belowground community composition varied by site (Figure 4-5). In general, graminoids dominated the aboveground vegetation. However, in Quincy, *C. leavenworthii* was dominant in the glyphosate treated plots. In Fort Pierce, forbs dominated the imazapic treated plots. *Coreopsis leavenworthii* comprised the majority of the seed bank in the glyphosate treatment in Fort Pierce and Quincy (Figure 4-5). However, in Citra, forbs dominated the glyphosate treatment, despite a high density of *C. leavenworthii* in the seed bank (Figure 4-5), resulting in significant site by establishment interactions (Table 4-6). Forbs also dominated the seed bank in the control and imazapic treatments (Figure 4-5).

Discussion

Species-Specific Responses

Treating *P. notatum* with glyphosate in the early fall before wildflower seeds were sown increased establishment of all three wildflower species compared to the control and imazapic treatments. However, overall wildflower establishment varied by species. *Coreopsis lanceolata* was able to establish without any disturbance to the extant vegetation, and the cover of the established population generally increased over time. *Coreopsis lanceolata* cover in the glyphosate treated plots remained high throughout the study, and *C. lanceolata* was often the dominant species. *Coreopsis lanceolata* cover was also consistently high throughout the study, with few seasonal fluctuations (Figure 4-2).

Although the glyphosate treatment increased *G. pulchella* cover, establishment of this species was lower than that of the other two wildflower species. Cover of *G. pulchella* remained

below 25% throughout the study. This may have been caused by seeding at a lower seeding rate than the other two species. Although the *G. pulchella* population was small, it did not appear to decrease over time, aside from seasonal fluctuations in cover (Figure 4-2).

Coreopsis leavenworthii establishment varied by site and over time. Establishment was lower in Citra than in Quincy and Fort Pierce. *Coreopsis leavenworthii* is a facultative wetland species and Citra is part of an upland, xeric habitat. Despite sufficient seedling emergence in the second year of the study, *C. leavenworthii* cover decreased over time. *Coreopsis leavenworthii* is an annual to short-lived perennial that often dies after flowering. The seasonal mortality of this species may have created gaps that were colonized by *P. notatum* and ruderal species from the seed bank. These species, in turn, likely limited the growth (and increase in cover) of *C. leavenworthii* seedlings.

The results from the seed bank study provide further evidence of species-specific responses to establishment treatments. Species that maintain viable seeds in the soil seed bank may be more likely to maintain stable populations over time (Yates and Ladd 2005), provided that the seed bank serves as a source rather than a sink of new individuals (Rees 1997). However, in this study, the aboveground vegetation differed markedly from the seed bank composition. One year after initial seeding, *C. leavenworthii* seeds dominated the seed bank in the glyphosate treatment (Figure 4-5). However, this was not expressed in aboveground growth for *C. leavenworthii* in Fort Pierce or Citra. Conversely, in glyphosate treated plots, *C. lanceolata* was the dominant species aboveground but did not comprise the majority of seeds in the seed bank (Figure 4-4). *Gaillardia pulchella* neither dominated the seed bank community nor the aboveground vegetation (Figure 4-3). Studies on the establishment of perennial native

forbs in grass-dominated communities also found differential effects by species (Fenner 1978, Brown and Bugg 2001).

Effects of Imazapic

In contrast to the hypothesis and other studies (Beran et al. 1999, Washburn and Barnes 2000), imazapic resulted in minimal wildflower establishment over the control treatment. Applied at low rates, imazapic reduces *P. notatum* vegetative growth and seedhead development (Baker et al. 1999, BASF Corporation 2003). Although *P. notatum* seed production was not measured in this study, imazapic did not reduce *P. notatum* cover or seed bank density, except in Fort Pierce (Figures 4-3, 4-4, and 4-5). However, the effects of imazapic on wildflower establishment varied by site and species. For example, *C. lanceolata* cover was greater in imazapic treated plots in Quincy but not in Citra (Figure 4-2). *Coreopsis lanceolata* may be more tolerant to imazapic than the other wildflower species. In a study by Norcini et al. (2003), imazapic stunted the growth of *G. pulchella* more than *C. lanceolata*. In Fort Pierce, *C. leavenworthii* did not establish in the imazapic treatment. Seedlings emerged within a few days of seeding but died shortly thereafter. Imazapic can cause stand-thinning, which may be corrected by increasing the seeding rate (although not tested in this study) (BASF Corporation 2003, Norcini et al. 2003). Moreover, tolerance to imazapic has been shown to vary according to local soil and environmental conditions (BASF Corporation 2003). In a study on imazethapyr, an herbicide in the same family as imazapic, persistence in the soil increased as soil pH decreased (Loux and Reese 1993). While soil pH in Fort Pierce was lower than the other two sites, it is not clear why the effect of imazapic on *C. leavenworthii* was different in Fort Pierce than in Quincy and Citra.

Mowing Treatments

Mowing frequency did not affect cover, density, or number of seedlings emerging from the seed bank of any of the wildflower species in this study (Table 4-6). This result contrasts with other studies in which diversity increased in response to mowing or grazing (Hofmann and Isselstein 2004, Williams et al. 2007); however, mowing was typically more frequent than six times per year. Additionally, mowing in the present study was adjusted for the flowering and seeding phenology of each of the wildflower species, likely reducing the effects of mowing. For example, because *C. lanceolata* blooms in early spring, plots were not mowed from March 1 through May 15 in the mow six times per year treatment (Table 4-2). The time of year an area is mowed can significantly impact the growth and survival of a species (Brys et al. 2004). In both annual and perennial species, if mowing precedes the seed maturation of a species, recruitment will be limited and the population will decrease in size. If the species is an annual, the population would only continue at that site if viable seeds were stored in the soil (Rees 1997, Norcini et al. 2003). Several studies have shown that mowing and removing litter can increase germination and establishment of seedlings (Jensen and Meyer 2001, Jutila and Grace 2002). Although litter was not removed in this study, mowing frequency had no effect on wildflower germination or seedling establishment.

***Paspalum notatum* Dominance**

Establishment of wildflowers was likely limited by competition from *P. notatum* (Chapter 2, Violi 2000). The ability of *P. notatum* to limit establishment of other species is evident by comparing the above- and belowground community composition. In undisturbed plots, graminoids (the majority of which were *P. notatum*) dominated the aboveground vegetation, yet forbs comprised the majority of the seed bank. When *P. notatum* was disturbed by glyphosate, wildflower and forb establishment generally increased. *Paspalum notatum* is a

rhizomatous, fast-growing, tropical grass that often forms a dense, monotypic stand (Violi 2000). In contrast, most grasses native to this region are slow growing bunchgrasses that leave more patches of bare ground for other species to establish (Myers 1990). Moreover, the small proportion of graminoids emerging from the seed bank suggests that regeneration of graminoids, and in particular *P. notatum*, after glyphosate treatment occurs vegetatively rather than through seeds. Forbs occupied the majority of the seed bank, reinforcing the benefits of a no-till system on roadsides or simulated roadsides. While tilling would decrease *P. notatum* competition, it would also increase competition from weedy forbs emerging from the seed bank.

Conclusions

Reducing extant vegetation through glyphosate resulted in the greatest establishment of native wildflowers. Seeding wildflowers into *P. notatum* without disturbing the extant vegetation resulted in little to no establishment for *G. pulchella* and *C. leavenworthii* (except at Fort Pierce) and a moderate amount of cover for *C. lanceolata*. An imazapic treatment at the time of seeding did not increase establishment of *G. pulchella* and *C. leavenworthii* but did result in increased cover of *C. lanceolata* in Quincy. Differences in establishment by species suggest that perennials, particularly evergreen species, may persist longer in a competitive environment than annuals.

Mowing frequency did not affect the percent cover or seed bank density of any of the wildflower species; however, the timing of mowing was adjusted for the phenology of each wildflower species at each site. Since roadside mowing in Florida is timed typically to control the height of the dominant grass species rather than to facilitate wildflower seeding, it is unclear whether the mowing frequencies in this study would have the same effect on roadside wildflower populations.

Table 4-1. Soil characteristics and types before seeding native wildflowers (*Gaillardia pulchella*, *Coreopsis lanceolata*, *C. leavenworthii*) at the study sites located in Quincy, Citra, and Fort Pierce, FL. Means for soil chemistry are presented with standard errors in parentheses.

Site characteristic	Site		
	Quincy	Citra	Fort Pierce
Location in Florida (Lat, Long)	North (30°32'27"N, 84°35'17"W)	North-central (29°24'23"N, 82°08'39"W)	South-central (27°25'54"N, 80°24'40"W)
Elevation (m)	70	20	6
Soil type	Norfolk loamy fine sand (0-5% slopes)	Candler sand (0-5% slopes)	Ankona sand (0-2% slopes)
pH	5.78 (0.02)	6.62 (0.04)	5.16 (0.05)
Organic matter (%)	2.56 (0.12)	2.21 (0.07)	1.25 (0.02)
NO ₃ -N (mg/kg)	0.16 (0.02)	0.39 (0.02)	6.39 (0.86)
NH ₄ -N (mg/kg)	4.12 (0.12)	4.86 (0.46)	2.08 (0.20)
P (mg/kg)	3.11 (0.25)	35.67 (1.52)	10.79 (0.56)
K (mg/kg)	53.38 (3.57)	31.26 (2.07)	11.13 (0.55)

Table 4-2. Dates of mowing treatments used at each site (Quincy, Citra, Fort Pierce, FL) for each wildflower species (*Gaillardia pulchella*, *Coreopsis lanceolata*, *C. leavenworthii*). The timing of mowing treatments was adjusted to allow for flowering and seeding of each wildflower species. Mowing dates were adjusted slightly for *C. leavenworthii* in Fort Pierce because of earlier flowering due to the warmer climate.

Mowing Treatment Year	Species Site			
	<i>Gaillardia pulchella</i> Quincy & Citra	<i>Coreopsis lanceolata</i> Quincy & Citra	<i>Coreopsis leavenworthii</i> Quincy & Citra	Fort Pierce
Mow 2 times/ year				
2006	Mar 15 Oct 15	Mar 1 Oct 15	Apr 1 Oct 15	Mar 1 Oct 1
2007	Mar 15 Oct 15	Mar 1 Oct 15	Apr 1 Oct 15	Mar 1 Oct 1
Mow 6 times/ year				
2005	Dec 1		Nov 15	Nov 15
2006	Jan 1 Feb 15 Mar 15 Jul 1 Oct 15 Nov 15 Dec 15	Jan 1 Mar 1 May 15 Jul 15 Sep 1 Oct 15	Jan 1 Mar 1 Apr 1 Aug 1 Oct 15 Dec 1	Jan 1 Mar 1 Jul 15 Aug 21 Oct 1 Dec 1
2007	Feb 15 Mar 15 Jul 1 Oct 15	Jan 1 Mar 1 May 15 Jul 1 Sep 1 Oct 15	Jan 1 Mar 1 Apr 1 Aug 1 Oct 15	Jan 1 Mar 1 July 15 Aug 21 Oct 1

Table 4-3. Effects of establishment treatment (pre-seeding herbicide: control, glyphosate, and imazapic), mowing frequency (two or six times/year), and their interactions on wildflower percent cover (arcsine square root transformed) of *Gaillardia pulchella* in Quincy and Citra, FL. Fall season included three years of data collection; spring and summer included two years.

Treatment factors	Season								
	Fall			Spring			Summer		
	df	F	P	df	F	P	df	F	P
Mowing	1, 3	0.23	0.6659	1, 3	1.35	0.3288	1, 3	0.02	0.9018
Establishment	2, 99	131.69	<0.0001	2, 63	116.54	<0.0001	2, 63	188.96	<0.0001
Site	1, 3	0.16	0.7145	1, 3	3.38	0.1635	1, 3	1.67	0.2867
Year	2, 99	11.78	<0.0001	1, 63	0.68	0.4124	1, 63	0.33	0.5653
Mow X estab	2, 99	0.70	0.4971	2, 63	0.18	0.8321	2, 63	0.15	0.8613
Mow X site	1, 99	1.71	0.1945	1, 63	0.30	0.5828	1, 63	1.91	0.1716
Mow X year	2, 99	0.47	0.6272	1, 63	1.11	0.2954	1, 63	0.01	0.9405
Estab X site	2, 99	0.13	0.8821	2, 63	2.69	0.0758	2, 63	2.68	0.0762
Estab X year	4, 99	20.57	<0.0001	2, 63	16.50	<0.0001	2, 63	0.28	0.7543
Site X year	2, 99	26.05	<0.0001	1, 63	1.99	0.1629	1, 63	0.07	0.7966
Mow X estab X site	2, 99	0.32	0.7243	2, 63	0.62	0.5394	2, 63	1.51	0.2285
Mow X estab X year	4, 99	0.44	0.7802	2, 63	0.78	0.4611	2, 63	0.57	0.5665
Mow X site X year	2, 99	0.79	0.4578	1, 63	0.11	0.7464	1, 63	0.05	0.8258
Estab X site X year	4, 99	12.25	<0.0001	2, 63	0.25	0.7775	2, 63	1.12	0.3314
Mow X estab X site X year	4, 99	0.34	0.8492	2, 63	1.12	0.3315	2, 63	0.11	0.8919

Table 4-4. Effects of establishment treatment (pre-seeding herbicide: control, glyphosate, and imazapic), mowing frequency (two or six times/year), and their interactions on wildflower percent cover (arcsine square root transformed) of *Coreopsis lanceolata* in Quincy and Citra, FL. Fall season included three years of data collection; spring and summer included two years.

Treatment factors	Season								
	Fall			Spring			Summer		
	df	F	P	df	F	P	df	F	P
Mowing	1, 3	0.06	0.8256	1, 3	0.46	0.5460	1, 3	0.02	0.8949
Establishment	2, 98	97.81	<0.0001	2, 63	89.99	<0.0001	2, 63	123.71	<0.0001
Site	1, 3	2.01	0.2515	1, 3	23.48	0.0168	1, 3	5.27	0.1054
Year	2, 98	484.10	<0.0001	1, 63	91.99	<0.0001	1, 63	20.17	<0.0001
Mow X estab	2, 98	0.28	0.7589	2, 63	0.36	0.6997	2, 63	0.48	0.6183
Mow X site	1, 98	0.12	0.7296	1, 63	0.65	0.4233	1, 63	0.42	0.5218
Mow X year	2, 98	0.23	0.7952	1, 63	1.93	0.1695	1, 63	0.66	0.4183
Estab X site	2, 98	1.90	0.1550	2, 63	4.29	0.0179	2, 63	7.81	0.0009
Estab X year	4, 98	18.15	<0.0001	2, 63	4.46	0.0155	2, 63	5.46	0.0065
Site X year	2, 98	23.97	<0.0001	1, 63	1.80	0.1850	1, 63	6.71	0.0119
Mow X estab X site	2, 98	0.02	0.9777	2, 63	0.16	0.8546	2, 63	0.69	0.5046
Mow X estab X year	4, 98	0.76	0.5515	2, 63	0.39	0.6766	2, 63	0.00	0.9995
Mow X site X year	2, 98	0.43	0.6486	1, 63	0.11	0.7436	1, 63	0.08	0.7773
Estab X site X year	4, 98	4.23	0.0033	2, 63	2.11	0.1296	2, 63	0.80	0.4544
Mow X estab X site X year	4, 98	0.19	0.9442	2, 63	0.16	0.8509	2, 63	0.28	0.7596

Table 4-5. Effects of establishment treatment (pre-seeding herbicide: control, glyphosate, and imazapic), mowing frequency (two or six times/year), and their interactions on wildflower percent cover (arcsine square root transformed) of *Coreopsis leavenworthii* in Quincy, Citra, and Fort Pierce, FL. Fall season included three years of data collection; spring and summer included two years.

Treatment factors	Season								
	Fall			Spring			Summer		
	df	F	P	df	F	P	df	F	P
Mowing	1, 3	0.09	0.7809	1, 3	0.21	0.6760	1, 3	1.33	0.3323
Establishment	2, 150	81.55	<0.0001	2, 96	103.04	<0.0001	2, 96	235.23	<0.0001
Site	2, 6	8.16	0.0194	2, 6	28.04	0.0009	2, 6	22.21	0.0017
Year	2, 150	23.55	<0.0001	1, 96	31.37	<0.0001	1, 96	288.86	<0.0001
Mow X estab	2, 150	0.50	0.6059	2, 96	0.55	0.5794	2, 96	0.28	0.7587
Mow X site	2, 150	0.77	0.4658	2, 96	1.82	0.1683	2, 96	5.32	0.0064
Mow X year	2, 150	0.06	0.9464	1, 96	0.85	0.3581	1, 96	3.30	0.0725
Estab X site	4, 150	8.66	<0.0001	4, 96	38.96	<0.0001	4, 96	30.16	<0.0001
Estab X year	4, 150	1.32	0.2669	2, 96	0.49	0.6131	2, 96	63.43	<0.0001
Site X year	4, 150	19.67	<0.0001	2, 96	0.20	0.8222	2, 96	7.41	0.0010
Mow X estab X site	4, 150	0.14	0.9660	4, 96	1.22	0.3071	4, 96	2.15	0.0811
Mow X estab X year	4, 150	0.08	0.9873	2, 96	0.08	0.9201	2, 96	0.96	0.3861
Mow X site X year	4, 150	0.11	0.9792	2, 96	2.28	0.1074	2, 96	1.13	0.3258
Estab X site X year	8, 150	5.70	<0.0001	4, 96	8.68	<0.0001	4, 96	8.03	<0.0001
Mow X estab X site X year	8, 150	0.79	0.6162	4, 96	1.03	0.3942	4, 96	1.38	0.2471

Table 4-6. Effects of establishment treatment (pre-seeding herbicide: control, glyphosate, and imazapic), mowing frequency (two or six times/year), and their interactions on emerged wildflower seedlings from the soil seed bank (per meter squared) in fall 2006 in Quincy, Citra, and Fort Pierce, FL.

Factor level	Species						
	Site						
	<i>Gaillardia pulchella</i>		<i>Coreopsis lanceolata</i>		<i>Coreopsis leavenworthii</i>		
	Quincy	Citra	Quincy	Citra	Quincy	Citra	Ft. Pierce
Establishment							
Control	0 a	0 a	133 a	199 a	686 a	199 a	4,313 a
Glyphosate	88 a	1,327 b	2,565 b	3,118 b	30,786 b	26,362 b	31,980 b
Imazapic	22 a	22 a	265 a	177 a	929 a	973 c	376 c
Significance of F-test							
Establishment	***		***			***	
Mowing	ns		ns			ns	
Site	*		ns			ns	
Establishment x mowing	ns		ns			ns	
Establishment x site	***		ns			***	
Mowing x site	ns		ns			ns	
Establishment x mowing x site	ns		ns			ns	

Significant main effects and interactions are indicated by: *** ($P < 0.0001$) and * ($P < 0.05$). Means with different letters within a species and site are significantly different ($P < 0.05$, Bonferroni correction). Analysis was performed on log transformed data; untransformed means are presented here.

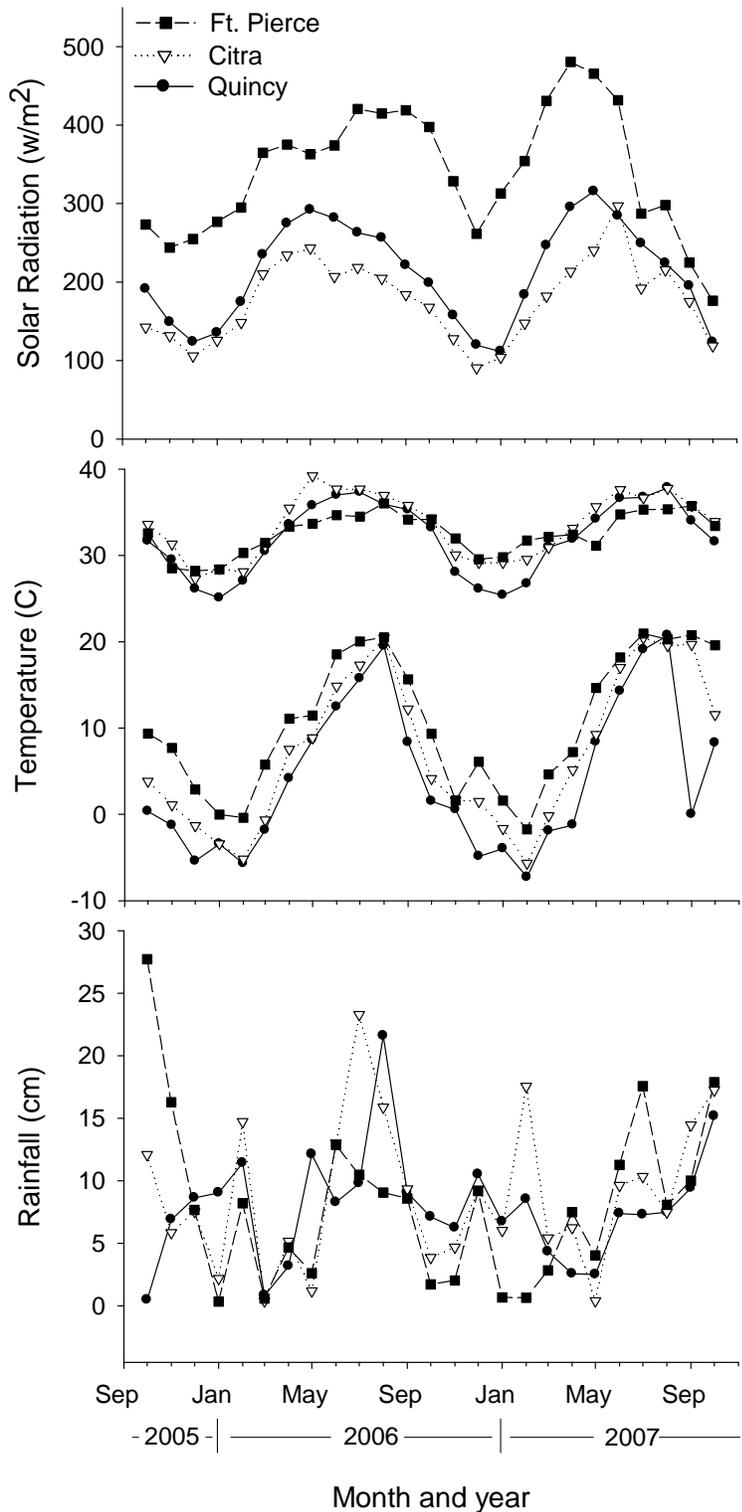


Figure 4-1. Solar radiation (monthly average), temperature (monthly average minimum and maximum), and rainfall (monthly total) in Fort Pierce, Citra, and Quincy, FL during the study period. Data from FAWN, Florida Automated Weather Network (<http://fawn.ifas.ufl.edu>).

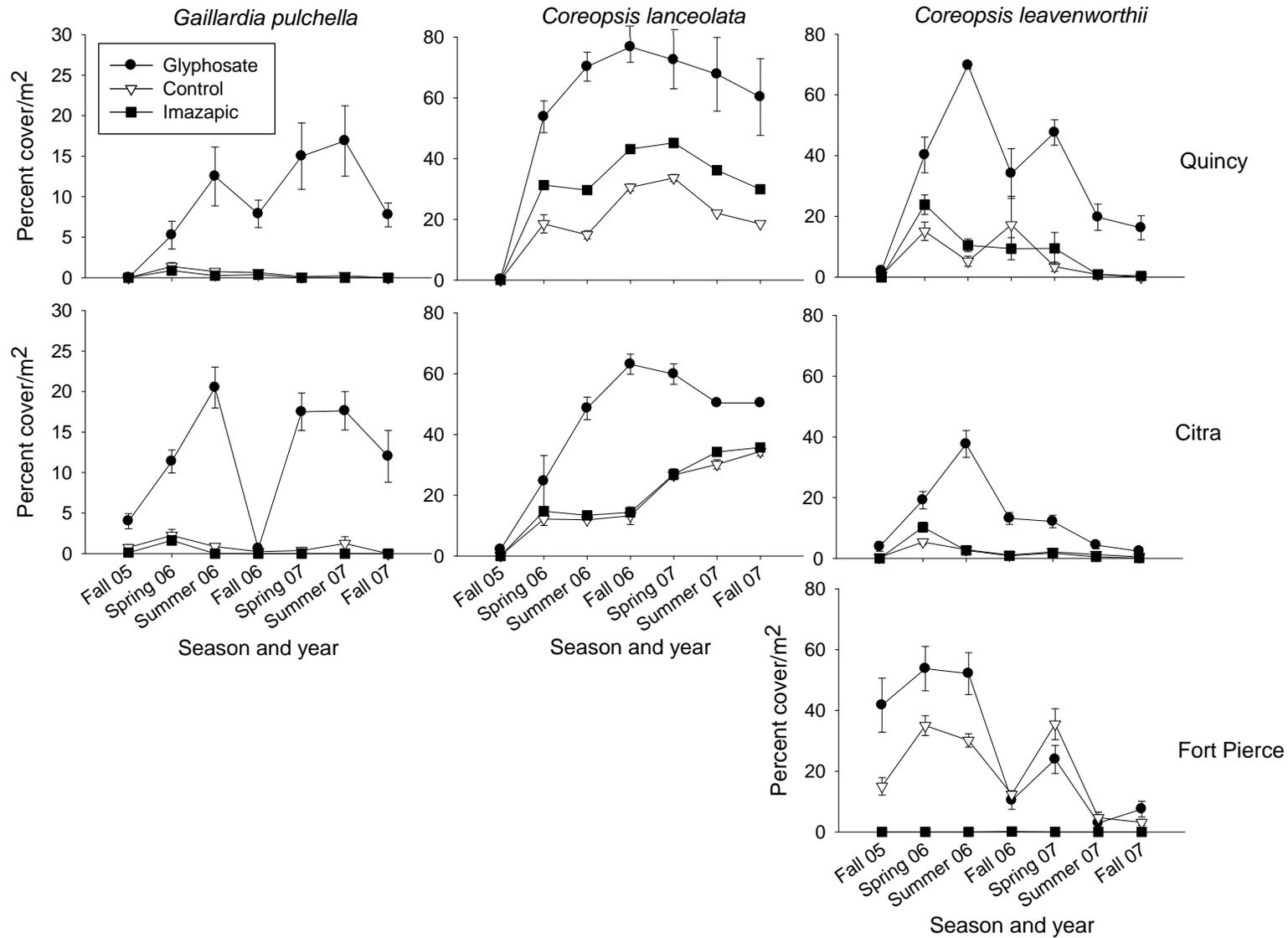


Figure 4-2. Effects of establishment treatment (pre-seeding herbicide: control, glyphosate, and imazapic) on mean (± 1 SE) percent cover of *Gaillardia pulchella*, *Coreopsis lanceolata*, and *C. leavenworthii* by site, season, and year.

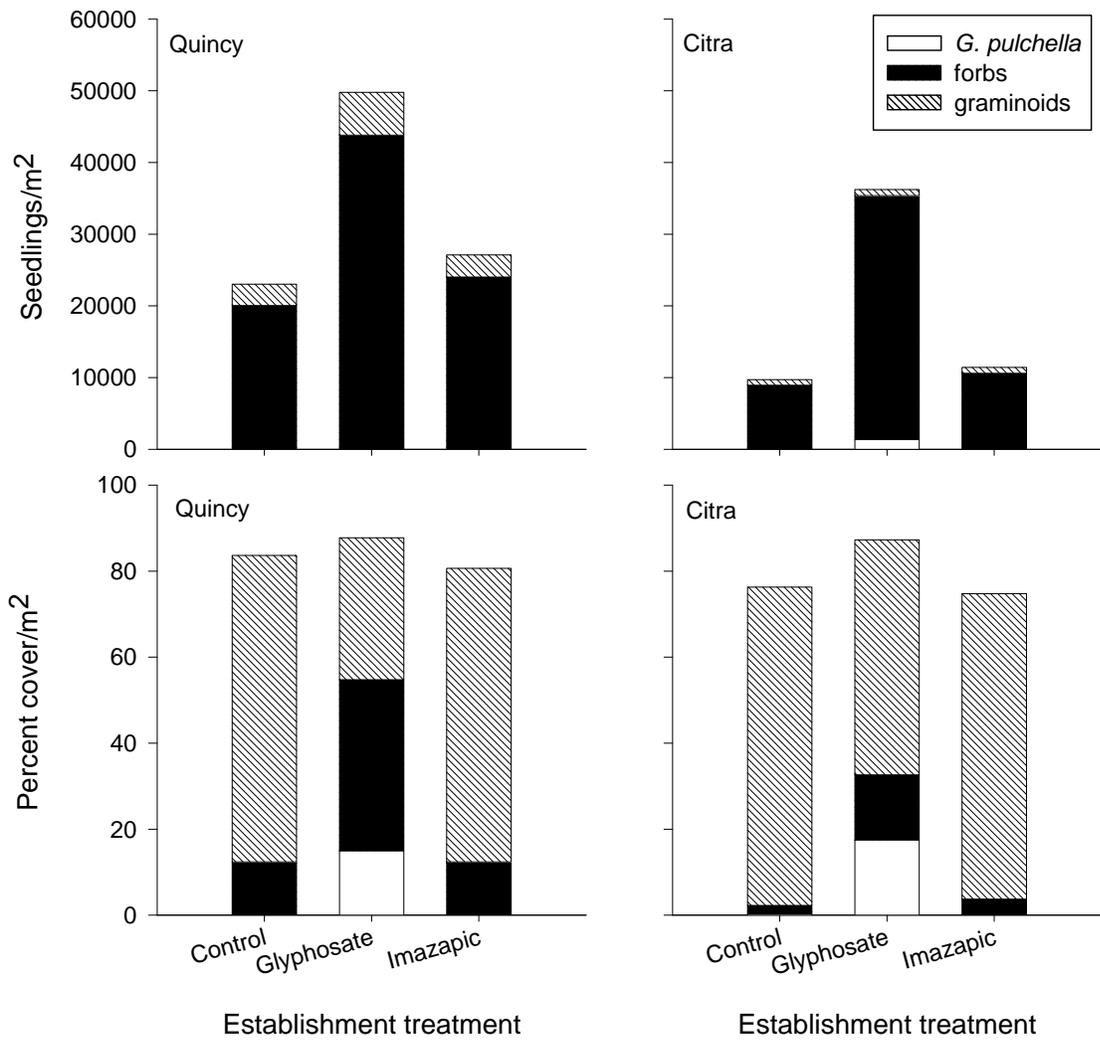


Figure 4-3. Composition of *Gaillardia pulchella*, forbs, and graminoids in the seed bank in fall 2006 (emerged seedlings/m², top graphs) and as aboveground vegetation in spring 2007 (percent cover/m², bottom graphs) in Quincy and Citra, FL.

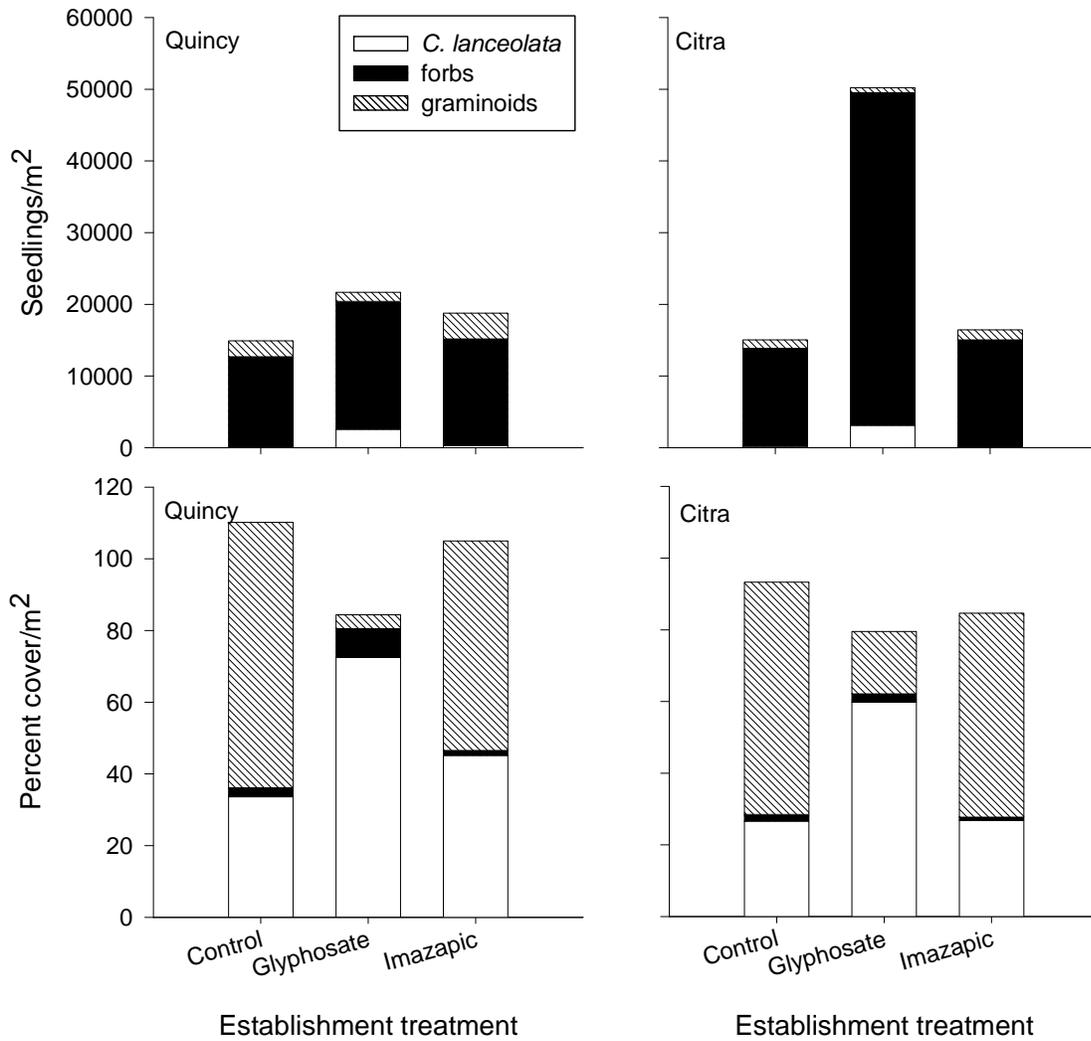


Figure 4-4. Composition of *Coreopsis lanceolata*, forbs, and graminoids in the seed bank in fall 2006 (emerged seedlings/m², top graphs) and as aboveground vegetation in spring 2007 (percent cover/m², bottom graphs) in Quincy and Citra, FL.

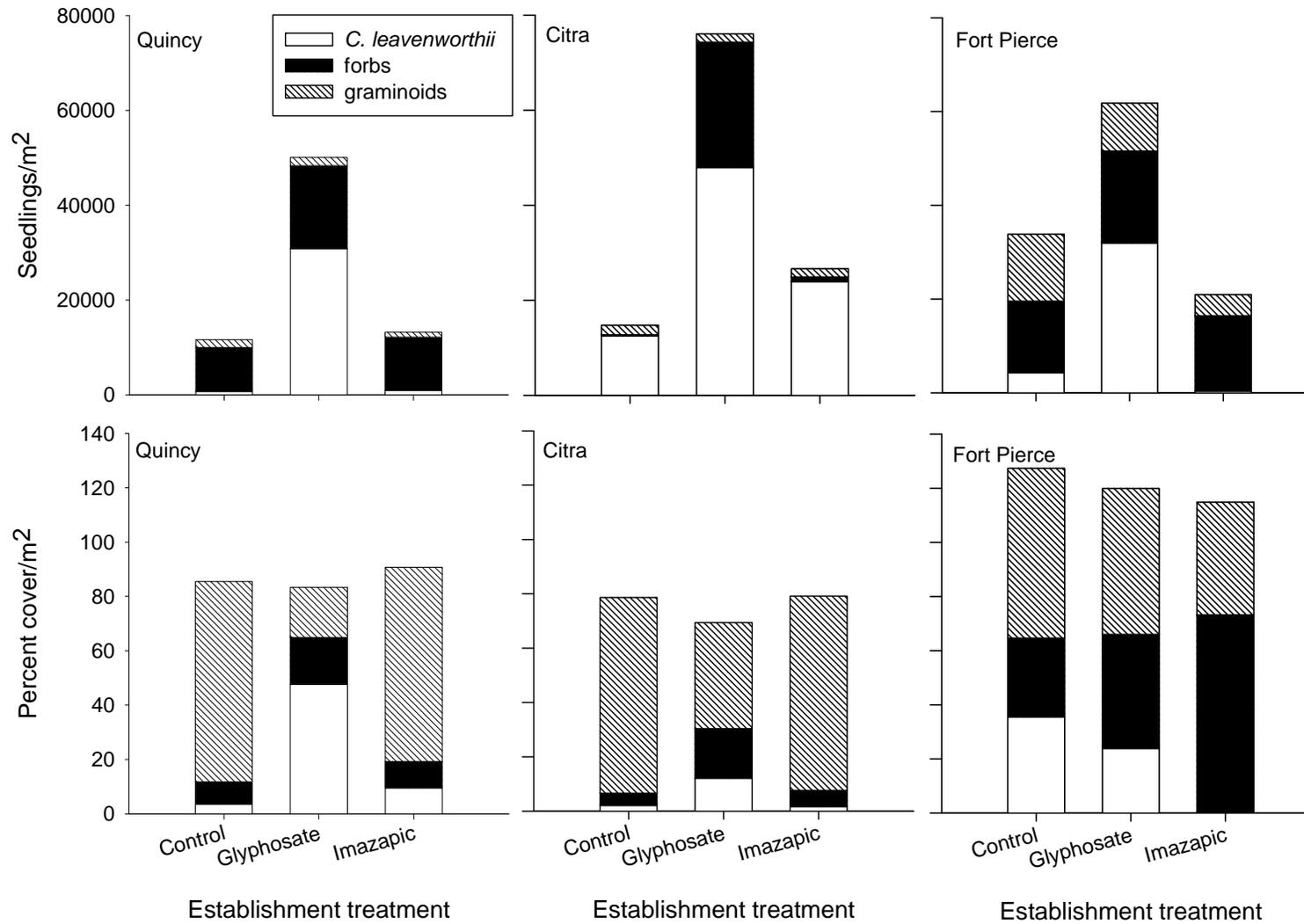


Figure 4-5. Composition of *Coreopsis leavenworthii*, forbs, and graminoids in the seed bank in fall 2006 (emerged seedlings/m², top graphs) and as aboveground vegetation in spring 2007 (percent cover/m², bottom graphs) in Quincy, Citra, and Fort Pierce, FL.

CHAPTER 5 CONCLUSIONS

Results from this study indicate that native wildflower establishment on roadsides and pastures dominated by *P. notatum* is limited by competition (Chapter 2). Disturbing *P. notatum* with glyphosate herbicide prior to wildflower seeding greatly improved establishment of all species (Chapters 3 and 4). Other herbicide treatments, including applying imazapic at the time of wildflower seeding and applying sethoxydim post wildflower emergence, resulted in no to little increase in wildflower establishment in most cases. A moderate amount of post-planting disturbance (mowing two or six times per year) did not affect the short-term sustainability of wildflower populations, perhaps because the timing of disturbance was adjusted for the phenology of each wildflower species (Chapter 4). However, frequent disturbance (cutting 12 or 24 times per year) that was not adjusted to each wildflower species' phenology reduced the growth and fitness of wildflower populations (Chapter 2). Although overall effects of establishment and management were similar among the wildflower species, some species-specific differences were noteworthy and may help to guide future research.

While competition from *P. notatum* limited wildflower establishment and growth, aboveground competition did not account for the total reduction in growth. In Chapter 3, both the glyphosate and scraped disturbance treatments reduced *P. notatum* biomass; however, this decrease alone did not result in an equivalent increase in wildflower cover or biomass. Most studies on sessile organisms equate microsites with available space for growth (Eriksson 2005). However, the differences in *C. lanceolata* establishment between the glyphosate and scraped treatments suggest that microsite requirements are more complex than providing adequate space and likely include abiotic as well as biotic components (Tilman 1994). Moreover, in Chapter 2, intraspecific competition resulted in greater reduction of *Coreopsis* biomass than interspecific

competition, yet conspecific neighbor biomass was smaller than that of *Paspalum* neighbors. In the field experiment in Chapter 3, scraped plots had less organic matter than glyphosate treated plots. Additionally, although not measured in the study, there was likely less moisture at the soil surface of scraped plots than glyphosate treated plots. In the study presented in Chapter 2, fertilizer and supplemental irrigation were applied so that resources would not be limiting. However, because conspecific individuals have the same resource needs, those resources were likely depleted more quickly with intraspecific rather than interspecific competition.

Wildflower establishment was affected by seasonal differences. *Coreopsis* species planted in the fall had greater survivorship, biomass, and number of flowers compared to *Coreopsis* planted in spring (Chapter 2). Although wildflowers were seeded only in fall in the field experiments, wildflower establishment did not seem to be limited in glyphosate treated plots following seeding. Seasonal differences in wildflower establishment appeared related to *P. notatum* phenology. *P. notatum* is a long-day plant that is dormant during the short days of winter and initiates flowering when day length exceeds 13.5 hours (Marousky and Blondon 1995). Wildflowers planted in fall are able to establish when *P. notatum* is dormant, which likely limits competition. Seasonal differences may also help to explain species-specific responses of wildflowers. The fitness and perhaps subsequent recruitment of species that bloom in spring, prior to *P. notatum* flower initiation, may be greater than species that bloom later due to decreased competition from *P. notatum*. The continued recruitment of *Phlox drummondii* Hook. and *C. basalis* (A.Dietr.) S.F.Blake, both of which bloom in spring (Wunderlin and Hansen 2003), may also be due to their production of flowers while *P. notatum* is dormant. Although neither *P. drummondii* nor *C. basalis* is native to Florida (Wunderlin and Hansen 2003), they are both commonly planted on Florida roadsides.

Seeding rates can greatly influence wildflower establishment, although this was only explicitly tested for one wildflower species in this study (*C. lanceolata*, Chapter 3). Seeding at too low of a rate results in low levels of establishment while seeding at too high of a rate provides no benefit for the additional resources expended (Chapter 3, Burton et al. 2006). Pure live seed rates are often expressed as seed mass per unit area seeded (e.g., kg/ha). Although this type of pure live seed rate accounts for differences in viability, it does not take into account differences in seed mass by species. Therefore, even if the same pure live seed rate is used for different species, the number of viable seeds per unit area may vary widely among species. For example, because the mass of *C. leavenworthii* seeds is smaller than *C. lanceolata*, seeding at 6 kg pure live seed/ha results in more *C. leavenworthii* seeds/ha than *C. lanceolata* seeds/ha. For species like *C. leavenworthii* that have small seeds and are short-lived, it may be more cost-effective to seed at lower rates for consecutive years than at a high rate only once. To avoid seeding at too high of a rate, species-specific recommendations for seeding rates can be developed (e.g., Texas Department of Transportation, Markwardt 2005). Until species-specific seeding rates are established for Florida ecotype seeds, the number of live seeds per unit area can be approximated using the pure live seed rate and the seed mass (Burton et al. 2006). Using the appropriate seeding rate for each species may increase wildflower establishment and also decrease costs.

The establishment of *C. lanceolata* was affected by both seed and microsite limitation. While there were interactive effects of seeding rate, irrigation, and disturbance treatment early in wildflower establishment, by the end of the study, lack of disturbance to the existing vegetation (i.e., microsite limitation) proved to be the factor most limiting to establishment (Chapter 3). Although increasing the seeding rate and providing supplemental irrigation may improve

establishment, these practices did not compensate for lack of disturbance. While *P. notatum* did not limit wildflower emergence, it did limit subsequent growth and reproduction of wildflowers (Chapters 3 and 4). Due to the possibility of increased erosion on roadsides, complete eradication of *P. notatum* with glyphosate may not be desirable. Eradication of *P. notatum* after wildflower establishment but still early in the wildflower life cycle may result in established wildflower populations with little erosion. However, the selective herbicides in this study were not effective in increasing wildflower establishment.

Results from the herbicide treatments in Chapters 3 and 4 provide further evidence that *P. notatum* is a competitive, dominant species that restricts growth of other species. The ability of *P. notatum* to limit establishment of other species was evident by comparing the above- and belowground plant community composition (Chapter 4). In undisturbed plots, graminoids (the majority of which were *P. notatum*) dominated the aboveground vegetation, yet forbs comprised the majority of the seed bank. When *P. notatum* was disturbed by glyphosate, a non-selective herbicide, wildflower and forb establishment increased. The limited effectiveness of imazapic and sethoxydim, both selective herbicides, in increasing wildflower establishment demonstrate that a slight reduction in *P. notatum* growth does not result in competitive release (Chapters 3 and 4). *Paspalum notatum* is a rhizomatous, fast-growing, tropical grass that often forms a dense, monotypic stand (Violi 2000). In contrast, most grasses native to Florida are slow growing bunchgrasses that leave more patches of bare ground in the landscape (Myers 1990). Native wildflowers may be able to coexist better with native grasses than with *P. notatum* because patches of bare ground often provide suitable microsites in which native wildflowers can become established.

The effectiveness of the glyphosate treatment may have been related to seasonal effects on *P. notatum* phenology, although season of application was not tested in this study. Since glyphosate is applied as a spray application to aboveground plant growth, foliar absorption is required for glyphosate activity. Because of this, rapidly growing plants are the most sensitive (Monaco et al. 2002). However, the timing of glyphosate application can affect the efficacy of the herbicide (Adams and Galatowitsch 2006). Although rapidly growing plants are the most sensitive, better control of perennial plants may be achieved when plants are not rapidly growing. Many perennial plants, including *P. notatum*, invest resources in stored carbohydrates, often in roots or rhizomes. For this reason, perennial plants are often able to resprout the season following glyphosate application. Because plant resource allocation to stored carbohydrates often follows a seasonal pattern, applying glyphosate when plants move carbohydrates to stored reserves may help to increase translocation of the herbicide itself (Adams and Galatowitsch 2006). This may result in greater control over the long-term.

Post-planting disturbance (mowing two or six times per year) did not affect the short-term sustainability of wildflower populations, perhaps because the timing of disturbance was adjusted for the phenology of each wildflower species (Chapter 4). However, frequent disturbance (cutting 12 or 24 times per year) that was not adjusted to each wildflower species' phenology reduced the growth and fitness of wildflower populations (Chapter 2). There were no interactive effects of mowing or cutting on wildflower establishment (Chapter 4) or growth (Chapter 2), suggesting that the effects of mowing and competition are additive. Wildflower establishment would be expected to increase with either reduced competition, less frequent disturbance, or both. Moreover, mowing too frequently can not only negatively impact newly-established wildflowers but also can reduce the sustainability of long-established wildflower

populations. Therefore, mowing of roadside vegetation in areas with wildflower populations should be carefully timed to adjust for the flowering and seeding phenology of each wildflower species at each site. Although similar guidelines are included in the Florida Department of Transportation's *Wildflowers in Florida* (1998), these guidelines appear to be followed inconsistently in Florida (personal observation, Gordon et al. 2000). Management practices on Florida roadsides include mowing frequently and close to the ground (personal observation), although this is not beneficial to grasses or wildflowers. Regardless of wildflower establishment, it seems that the Florida Department of Transportation could reduce mowing frequency without affecting driver safety (personal observation, Gordon et al. 2000), which would likely result in decreased maintenance costs.

Native wildflowers responded differently to establishment and management practices in this study. For example, *C. lanceolata* became established without any disturbance to the extant vegetation, and the cover of the established population generally increased over time. *Coreopsis leavenworthii* establishment varied by site but tended to decrease over time, while establishment of *G. pulchella* was lower than that of the other two wildflower species (Chapter 4). Moreover, the imazapic treatment increased establishment of *C. lanceolata* only (Chapter 4). The results from the seed bank study provide further evidence of species-specific responses to establishment treatments. One year after initial seeding, *C. leavenworthii* seeds dominated the seed bank in the glyphosate treatment. However, this was generally not expressed in aboveground growth. The seasonal mortality of *C. leavenworthii* may have created gaps that were colonized by *P. notatum* and ruderal species, which likely limited the growth of *C. leavenworthii* seedlings. Conversely, in glyphosate treated plots, *C. lanceolata* was the dominant species aboveground but did not comprise the majority of seeds in the seed bank. Due to its evergreen, perennial nature, *C.*

lanceolata may have been better able to compete for space than *C. leavenworthii* (Chapter 4). Species-specific responses were also evident in response to competition from *P. notatum* (Chapter 2). Although survivorship of *C. lanceolata* was greater than that of *C. leavenworthii*, *C. lanceolata* produced less biomass and fewer flowers than *C. leavenworthii* (Chapter 2). These results suggest that *C. lanceolata* may persist longer in a community dominated by *P. notatum* than its congener.

Although this study was limited to three wildflower species, results suggest that evergreen, perennial wildflower species may be stronger competitors with *P. notatum* than annual species or perennials with seasonal growth fluctuations. Moreover, species that bloom in the spring while *P. notatum* is dormant may persist for longer on roadsides planted with bahiagrass. In areas where it is necessary to maintain aggressive mat-forming grasses on roadsides (i.e., for erosion control), native wildflowers that are evergreen and/or bloom early in the spring may compete better than other wildflower species. However, many of Florida's native wildflowers are not evergreen or spring-bloomers. Therefore, where possible, limiting the planting and expansion of aggressive grasses will not only benefit native wildflowers, but will likely be necessary to establish new populations of many species of native wildflowers.

While a fall application of glyphosate effectively increased the establishment of native wildflowers, the resulting plant community was rarely diverse. This study focused on the introduction of a single wildflower species into a *P. notatum* pasture because 1) the Florida Department of Transportation typically plants wildflower monocultures and 2) the source of competition between species is more apparent in two-species models than multi-species models. However, native plant communities in Florida are generally diverse and contain a suite of interacting species, especially in the understory. From a restoration perspective, introducing one

native species to the site would likely not fulfill the goals of the restoration project. An alternative to introducing wildflower monocultures for beautification is to restore a diverse native plant community to roadsides. Other states have successfully incorporated restoration into roadside management (Houseal and Smith 2000, Brown and Bugg 2001, Markwardt 2005). There are ecological benefits to this approach (Ries et al. 2001), but there may be practical benefits as well. For example, diverse plant communities tend to be more resilient to disturbance and stable over the long-term than less diverse communities or monocultures (Tilman et al. 2006).

The lack of diversity observed in glyphosate treated plots in Chapters 3 and 4 is also likely due to the lack of propagules at the study sites, which had been under agricultural production before the study. In areas depauperate of native propagules, introducing a suite of native species in addition to treating with glyphosate will likely be necessary to establish a diverse native plant community. In addition, eradicating *P. notatum* without subsequently establishing desirable species may result in the colonization by weedy, or possibly, invasive species (as seen in the scraped plots in Chapter 3). Re-establishing the dominant native groundcover species seems essential to the establishment of an herbaceous, native community. In Florida, the dominant native groundcover species is usually a grass (Myers 1990). However, native grasses are rarely used in roadside plantings in Florida (Jenkins et al. 2004). Harper-Lore (2000) recommends including native grasses with wildflowers to “visually compliment and physically give structure to the wildflower planting”. While many state wildflower programs include grasses in wildflower plantings (Harper-Lore 2000), grasses and wildflowers are usually not seeded or planted at the same time in Florida (Florida Department of Transportation 1998).

Based on the results of this study, recommendations for native wildflower establishment and management include: 1) limiting *P. notatum* establishment and occurrence to areas where erosion control is absolutely necessary, like areas closest to the road, 2) removing *P. notatum* where it is not necessary or beneficial, with two glyphosate applications in the fall, and 3) carefully timing roadside mowing or other post-planting disturbance for the phenology of each wildflower species. In addition, recommendations for future research include: 1) studies on native wildflowers that can compete with aggressive grasses including evergreen perennials and/or species that bloom in early spring, 2) species-specific seeding rates based on the number of live seeds per unit area as well as species life history traits, 3) continued research on native grasses appropriate for roadsides and restoration (see Jenkins et al. 2004), 4) restoration approaches to roadside management, and 5) studies that include long-term results of establishment and management methods.

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BIOGRAPHICAL SKETCH

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