INFLUENCE OF SOIL DISTURBANCE AND FIRE ON CAESAR'S WEED (*URENA LOBATA*) INVASION IN PINE FLATWOODS

By

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This thesis was prepared under the direction of the candidate's thesis advisor, Dr. Brian Benscoter, Department of Biological Sciences, and has been approved by the members of his supervisory committee. It was submitted to the faculty of the Charles E. Schmidt College of Science and was accepted in partial fulfillment of the requirements for the degree of Master of Science.

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ABSTRACT

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Title: Influence of Soil Disturbance and Fire on the Distribution of Caesar's Weed (*Urena Lobata*) in Pine Flatwoods

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Novel disturbances can increase the vulnerability of pine flatwoods to exotic species such as Caesar's weed (*Urena lobata*), a plant that has invaded many ecosystems. To understand Caesar's weed response to disturbance, a factorial field manipulation was used to quantify invasion success. Influence of feral swine (*Sus scrofa*) on the presence of seeds in the area was analyzed. The effect of heat on Caesar's weed germination was also quantified. A winter fire and mechanical soil disturbance had no statistical effect on the spread of Caesar's weed. However, in feral swine disturbed soils Caesar's weed was more likely to be husked and experience less competition from seeds of other species. Low levels of seed heating increased germination. This data can provide information about the influences of fire and soil disturbances on the spread of Caesar's weed, as well as how fire intensity levels can affect the spread of invasive Caesar's weed.

INFLUENCE OF SOIL DISTURBANCE AND FIRE ON CAESAR'S WEED (*URENA LOBATA*) INVASION IN PINE FLATWOODS

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1. GENERAL INTRODUCTION

Invasive species, defined as an alien species whose introduction does or is expected to inflict harmful effects on the environment or human well-being (Executive Order 13112. 1999), present problems to natural ecosystems. Invasive plant and animal species are known to have direct detrimental effects on native species richness, diversity and evenness (Hejda et al. 2009, Siemann et al. 2009), as well as ecosystem functions such as soil and water nutrient levels and fire regimes (Brooks et al. 2004, Jordan et al. 2008, Barrios-Garcia and Ballari 2012). The vast majority of natural habitats on Earth have been invaded by introduced species (Mack et al. 2000), presenting challenges for the conservation of native ecosystems and biodiversity.

Many plant invasions have occurred due to human alterations of natural disturbance regimes (Turner 2010). Natural disturbances, such as fire, influence many terrestrial ecosystems. Disturbances are discrete incidents that disrupt structure and alter resources, substrate availability, or the physical environment (Pickett and White 1985). Through this influence on proximate drivers of composition and function, natural disturbances are an integral component of ecosystem ecology, shaping and maintaining the dynamics of ecosystems throughout the world (Turner 2010, Banks et al. 2013). Humans have greatly altered the occurrence of many natural disturbances due to population growth, changes in land use, and through efforts to prevent harmful impacts of disturbance (e.g., flooding, fire) on human resources. Suppressing or mitigating natural disturbances can cause those disturbances to occur at a greater magnitude or severity (Turner 2010).

Fire plays an important role in the ecology of most terrestrial ecosystems, particularly through its influence on plant communities. Ecosystems depend on fire for clearing overgrown brush, assisting in nutrient cycling and availability, and facilitating seed germination of some plants (Abrahamson and Hartnett 1990, Schafer and Mack 2013, Dean et al. 2015). Fire has occurred naturally for millions of years and has been an evolutionary force that has created many fire-adapted ecosystems (Pausas and Keeley 2009). Natural fire regimes have been shown to promote growth of native plants while suppressing invasive plants (Clark and Wilson 2001). Plants within their respective fire-adapted ecosystems have not adapted to fire in general but to specific fire regimes that they have been exposed to over extended periods of time (Keeley and Brennan 2012).

Due to human presence, many natural fire regimes have been altered. Alterations to fire regimes can allow invasive plant species to spread and negatively affect ecosystem functions (Keeley and Brennan 2012). Shortened return intervals result in less intense fires, preventing invasive species from being killed and allowing rapidly establishing invasive species to outcompete and replace native woody plants that depend on longer time between fires to become established (Clark and Wilson 2001). Conversely, lengthened fire return intervals due to fire suppression allow monocultures of competitive, invasive woody species to replace diverse communities of herb species (Clark and Wilson 2001).

A fire-adapted ecosystem of particular concern is the pine flatwoods; distributed throughout the southeastern U.S.A., pine flatwoods are found in low-lying topography with relatively poorly drained acidic sandy soils and an open pine canopy that allows for a diverse understory of shrubs and herb species (Abrahamson and Hartnett 1990, Cronan et al. 2015). They are the dominant terrestrial ecosystem in Florida, covering approximately 50% of the land area (Monk 1968, Abrahamson and Hartnett 1990). Pine flatwoods depend on fire to mediate many ecosystem processes, such as nutrient cycling and species composition and density (Abrahamson and Hartnett 1990). Prior to human influence, fire was estimated to have occurred every 2.2-3.2 years in pine flatwoods with shorter fire return intervals favoring a diverse understory of herb species (Abrahamson and Hartnett 1990). Specific fire regimes also dictate what tree species are present in an area (Abrahamson and Hartnett 1990). The dominant trees that characterize pine flatwoods are pond pine (*Pinus serotina*), longleaf pine (*P. palustris*), typical slash pine (*P. elliottii* var. *elliottii*), and South Florida slash pine (*P. elliottii* var. *densa*), with geographic location, soils, fire regime, and history of human influences dictating which tree species will be the most abundant (Abrahamson and Hartnett 1990). Pond pine has the furthest northern range of the dominant pines, found from Maryland to central Florida (Kirkman et al. 2007). Pond pine depends on periodic fire and dominates in the wettest areas of pine flatwoods. (Abrahamson and Hartnett 1990). Longleaf pine has the second furthest northern range, from West Virginia to central Florida, and is the most fire resistant of the pine species, found in well-drained frequently burned areas (Abrahamson and Hartnett 1990, Kirkman et al. 2007). Slash pine ranges from South Carolina to parts of south Florida and is predominant in frequently burned areas with poorly-drained soils. South Florida slash pine has the most southern range of the dominate pine species, found from central Florida to the Florida Keys, and is more fire resistant and drought tolerant than slash pine (Abrahamson and Hartnett 1990). Similar to other pine flatwoods characteristics, the proportion of shrubs to herbs is driven by specific fire regimes that are required to maintain high biodiversity (Abrahamson and Hartnett 1990, Wilcox and Giuliano 2010). Common shrub species include saw palmetto (*Serenoa Repens*), gallberry (*Ilex glabra*), fetterbush (*Lyonia lucida*), and wax myrtle (*Myrica cerifera*). Herb species include wiregrass (*Aristida stricta*), blue maidencane (*Amphicarpum muhlenbergianum*), and beaksedges (*Rhynchospora chapmanii, R. latifolia, R. compressa*) **(**Abrahamson and Hartnett 1990).

Human modification of the fire regime and conversion of land for human uses are the main factors in what has caused modern day pine flatwoods to be one of the most human affected landscapes in the United States (Abrahamson and Hartnett 1990). Human fire suppression has led to longer fire return intervals and a decrease in plant diversity (Abrahamson and Hartnett 1990). Lowered plant diversity results in decreased availability of habitat and forage for many native animal species, including species of special concern such as the gopher tortoise (*Gopherus polyphemus*) and the red cockaded woodpecker (*Picoides borealis*) (Wilcox and Giuliano 2010, Cronan et al. 2015). Forest management techniques use prescribed (Rx) fire in an attempt to mimic historic fire regimes, but once present invasive plants can alter fire regimes by affecting fuel properties (e.g., fuel load, moisture level; Brooks et al. 2004) and after dense stands are formed fire is generally not enough to remove them from an ecosystem and costlier mixed-management options may be required (Paynter and Flanagan 2004).

Altered fire regimes and novel disturbances (e.g., agriculture, altering hydrology, clearcutting) reduce the overall self-regulating capacity of pine flatwoods, lowering resistance to exotic species invasion. One invasive species of growing concern is Caesar's weed (*Urena lobata*), a recently upgraded Category I Invasive that has been increasingly spreading and displacing native species in recent years (The Florida Exotic Pest Plant Council 2015). The ecology of Caesar's weed is poorly understood, providing little information for managing the spread of this noxious species that is found in most subtropical and tropical regions (Austin 1999, Awan et al. 2014). Caesar's weed is a perennial herb or small shrub in the Malvaceae family that can tolerate a wide range of soil types and grow up to 2 meters in its first year (Langeland et al. 2008). It can quickly establish in disturbed areas like those found throughout pine flatwoods and create dense stands that replace native vegetation (Francis 2004). A single mature plant can create 600 seeds per year. The seeds are encapsulated by burs that cling to fur-bearing animals and humans, which serve as vectors for dispersal (Wang et al 2009). The hard seed coat, or bur, is the major limiting factor in Caesar's weed germination and allows the seed to lie dormant until scarified (Wang et al 2009, Awan et al 2014).

Fire has been shown to promote the germination of many species in the Malvaceae family, but the effect of fire on Caesar's weed germination is unknown (Awan et al. 2014). Increases in the presence of Caesar's weed has been linked to a variety of disturbance, making the heavily disturbed pine flatwood landscape an optimal habitat for residency. Agriculture and construction have been some of the main contributors to widespread novel disturbances that create open soils and altered resource availability that increases opportunity for invasion in pine flatwoods (Abrahamson and Hartnett 1990). Disturbances related to fire management (e.g., tilled firebreaks, roads) have also created extensive areas of increased vulnerability where dense stands of Caesar's weed have been observed.

The creation of optimal habitat for invasion within pine flatwoods can also be attributed to activity of another invasive species, the destructive feral swine (*Sus scrofa*) that has been increasing throughout the SE United States (Bevins et al. 2014). Feral swine are one of the most significant vertebrate modifiers of plant communities (Bratton 1975) and are believed to have first been introduced to the continental United States in Florida by Spanish explorers in the 1500s (Bevins et al. 2014). Rapid expansion of populations in the past 30 years has been facilitated by swine escaping from farms and the significant reduction of native predators coupled with feral swine's ability to flourish in human-altered areas (i.e., croplands) (Bevins et al. 2014). Feral swine are omnivores that consume above ground plant matter and conduct below ground foraging (i.e., rooting) and wallowing, which can reduce understory plant cover and species diversity by as much as 80% (Barrios-Garcia and Ballari 2012). Feral swine effects on soil properties and hydrology can be comparable to tillage treatments in agroecosystems (Barrios-Garcia and Ballari 2012) and their defecation and urination can affect nutrient inputs into the soil and surrounding water sources (Siemann et al. 2009). These novel disturbances created by feral swine have been linked to the spread of invasive plant species (Siemann et al. 2009) and may also be increasing Caesar's weed presence in pine flatwoods because of Caesar's weed ability to rapidly establish in newly disturbed soils and its bur encapsulated seed that depends on mammals for dispersal (Austin 1999). As feral swine populations increase and spread throughout native ecosystems in the United States they create direct threats associated with their own presence, as well as indirect threats by potentially facilitating the spread of invasive plant species.

In this study, I investigated the effects of fire and soil disturbance on the dispersal and establishment success of Caesar's weed in a pine flatwoods landscape. To better inform land management practices for native ecosystem conservation, I examined the vulnerabilities of managed pine flatwoods ecosystems to Caesar's weed invasion. Through observational and experimental studies in field and laboratory settings I assessed 1) the influence of a winter prescribed burn and mechanical soil disturbance on the incidence of Caesar's weed, 2) the effect of heating on Caesar's weed seed germination success, and 3) the effect of feral swine soil disturbance on the composition of the soil seed bank. Due to heat induced increases in germination of other plant species in the Malvaceae family (Awan et al. 2014) and Caesar's weed ability to rapidly colonize disturbed areas (Francis 2004), I hypothesized exposure to prescribed fire or mechanical soil disturbance would increase the presence of Caesar's weed within vegetation communities and exposure to a combination of prescribed fire and mechanical soil disturbance would cause the greatest increase in Caesar's weed presence with in vegetation communities. I anticipated the threshold for Caesar's weed seed survival would be lower than typical flame front intensities found in pine flatwoods fires. However, I anticipated that lower heating levels that did not consume seeds would create a significant increase in germination rates by weakening the hard seed coat of the Caesar's weed seeds. As found in previous studies, I expected feral swine disturbed soils to have reduced overall seed bank species richness and seed abundance (Siemann et al. 2009), but that the presence and activity of the swine would deposit Caesar's weed seeds due to their bur seed coat and increase the relative abundance of Caesar's weed seeds in the seed bank compared to native plant species.

2. EFFECT OF DISTURBANCES ON CAESAR'S WEED (*URENA LOBATA*) INVASION IN PINE FLATWOODS

Introduction

Invasive plant species, like the exotic Caesar's weed (*Urena lobata*), present issues for the management of natural ecosystem especially when invasion may be facilitated by traditional prescribed fire practices or non-native animals like feral swine. Biological invasions have dramatically increased as human populations have grown and caused the majority of natural habitats on Earth to be invaded by introduced species (Mack et al. 2000). The impacts of invasive species are one of the most influential disturbances in natural ecosystems, having negative effects on native species richness, evenness and diversity (Hejda et al. 2009), soil structure and processes (Jordan et al. 2008, Barrios-Garcia and Ballari 2012), and fire regimes (i.e., changing fuel properties; Brooks et al. 2004).

Natural disturbance is a vital component of ecosystem ecology, shaping and maintaining the dynamics of ecosystems throughout the world (Turner 2010, Banks et al. 2013). Disturbances (e.g., fire, flood) assist in creating heterogeneity in a landscape, which forms a wider array of habitats that allow for a higher diversity of plant and animal species (Abrahamson and Hartnett 1990, Turner 2010). Fire is a naturally occurring disturbance that has been shown to promote the growth of native plants and suppress invasive plant species (Clark and Wilson 2001). Many terrestrial ecosystems depend on fire to clear overgrown brush, assist in nutrient cycling and availability, and facilitate seed germination of some plants (Abrahamson and Hartnett 1990, Schafer and Mack 2013, Dean et al. 2015). Fire has occurred naturally (e.g., lighting strikes) long before humans were present and has been an evolutionary force that has created many fire-adapted ecosystems with plants that have become adapted to specific fire regimes (Keeley and Brennan 2012).

Increases in human populations and novel disturbances have caused many natural fire regimes to be altered, which can allow invasive plant species to spread and negatively affect ecosystem functions (Keeley and Brennan 2012). Forest management techniques use prescribed (Rx) fire in an attempt to mimic historic fire regimes, but once present invasive plants can alter fire regimes by affecting fuel properties (i.e., fuel load, moisture level, etc.; Brooks et al. 2004). After dense invasive stands are formed fire is generally not enough to remove them from an ecosystem and costlier mixed-management options may be required (Paynter and Flanagan 2004).

A human influenced fire-adapted ecosystem of particular concern is pine flatwoods, which depend on fire to mediate habitat structure and species composition (Abrahamson and Hartnett 1990, Cronan et al. 2015, Dean et al. 2015). The pine flatwoods landscape is found throughout the southeastern U.S., makes up approximately 50% of the land area in Florida, and can generally be characterized by low-lying topography, relatively poorly drained acidic sandy soils and open pine canopies with a diverse understory (Abrahamson and Hartnett 1990, Cronan et al. 2015). Naturally, a fire return internal of 2-3 years occurs in pine flatwoods (Abrahamson and Hartnett 1990). These low-intensity high-frequency fires support a high diversity of herb and shrub species and provide a heterogeneous habitat for a wide variety of animals including species of concern such as the gopher tortoise (*Gopherus polyphemus*) and the red cockaded woodpecker (*Picoides borealis*) that are historically indicative of pine flatwoods (Abrahamson and Hartnett 1990, Wilcox and Giuliano 2010).

Present-day pine flatwoods have been vastly diminished by land conversion to support growing human populations (Abrahamson and Hartnett 1990). Humans have suppressed fire to protect assets and subsequently lowered biodiversity in pine flatwoods (Wilcox and Giuliano 2010). Human influences have increased remaining pine flatwoods' susceptibility to exotic species by creating novel open spaces for colonization, altering resource availability, and depleting native soil seed banks (Abrahamson and Hartnett 1990, Davis et al. 2000).

An exotic species of particular pressing concern in Florida pine flatwoods is Caesar's weed (*Urena* lobata). Caesar's weed is a rapidly sprouting annual herb or small shrub in the Malvaceae family that can tolerate a wide range of soils and grows up to 2 meters in its first year (Langeland et al. 2008). It can readily invade disturbed areas, particularly following fires or in areas with novel soil disturbance, and can create dense stands that replace native vegetation (Francis 2004). A single plant can produce 600 burred seeds a year that cling to fur-bearing animals and humans for dispersal and persist in soil seed banks until the seed coat is removed (i.e., husked) (Wang et al 2009, Awan et al 2014). Fire has been shown to break the dormancy of many seeds with hard seed coats, but the effect of fire on Caesar's weed seeds is unknown (Awan et al. 2014). Caesar's weed has displayed increasing invasion rates in recent years, making it a growing threat to native communities by displacing native species and lowering biodiversity (FLEPPC

2015). Due to its growing threat to native ecosystems, Caesar's weed has been upgraded to a top priority Category I Invasive by the Florida Exotic Pest Plant Counsel (FLEPPC) suggesting there is an urgent need to understand what is facilitating the spread of this exotic species.

The concurrent spread of soil disturbing feral swine (*Sus scrofa*) may also accelerate the spread of Caesar's weed. Feral swine display aggressive characteristics that have allowed them to flourish in human-altered landscapes (Bevins et al. 2014). With swine escaping from farms and a reduction of native predators swine have spread to 21 new states in the past 30 years (Bevins et al. 2014). Feral swine are one of the most significant vertebrate modifiers of plant communities (Bratton 1975) and can reduce understory plant diversity and cover by as much as 80% by conducting below ground foraging (i.e., rooting) and wallowing (Barrios-Garcia and Ballari 2012). These activities also effect water quality and soil properties (i.e., nutrient cycling and decomposition rates), similarly to tillage treatments in agroecosystems (Barrios-Garcia and Ballari 2012). Novel soil disturbances created by feral swine have been linked to the spread of invasive plant species and are a growing threat to native ecosystems as feral swine populations increase (Martin et al. 1996, Siemann et al. 2009). Therefore, animals like feral swine that serve as dispersal vectors and disturb soils could facilitate the spread of Caesar's weed.

In this study, I investigated the effects of fire and soil disturbance on the dispersal and establishment success of Caesar's weed in a pine flatwoods landscape. To better inform land management practices for native ecosystem conservation, I examined the vulnerabilities of managed pine flatwoods ecosystems to Caesar's weed invasion.

Through observational and experimental studies in field and laboratory settings I assessed 1) the influence of a winter prescribed burn and mechanical soil disturbance on the incidence of Caesar's weed, 2) the effect of heating on Caesar's weed seed germination success, and 3) the effect of feral swine soil disturbance on the composition of the soil seed bank. Due to heat induced increases in germination of other plant species in the Malvaceae family (Awan et al. 2014) and Caesar's weed ability to rapidly colonize disturbed areas (Francis 2004), I hypothesized exposure to prescribed fire or mechanical soil disturbance would increase the presence of Caesar's weed within vegetation communities and exposure to a combination of prescribed fire and mechanical soil disturbance would cause the greatest increase in Caesar's weed presence with in vegetation communities. I anticipated the threshold for Caesar's weed seed survival would be lower than typical flame front intensities found in pine flatwoods fires. However, I anticipated that lower heating levels that did not consume seeds would create a significant increase in germination rates by weakening the hard seed coat of the Caesar's weed seeds. As found in previous studies, I expected feral swine disturbed soils to have reduced overall seed bank species richness and seed abundance (Siemann et al. 2009), but that the presence and activity of the swine would deposit Caesar's weed seeds due to their bur seed coat and increase the relative abundance of Caesar's weed seeds in the seed bank compared to native plant species.

Methods

Study site

This research was conducted in the DuPuis Management Area (DMA; Figure 2.1). The DMA is a 21,785-acre multi-use natural area located in northwest Palm Beach and southwest Martin countries in central Florida (27° 0'3.99"N, 80°33'20.60"W) managed by the South Florida Water Management District (SFWMD). Previously a livestock ranch, the DMA is predominantly a restored mesic pine flatwoods landscape with flat low-lying topography, relatively poorly drained acidic sandy soils, and a vegetation assemblage of South Florida slash pine (*Pinus elliottii* var. *densa*), cabbage palm (*Sabal palmetto*), saw palmetto (*Serenoa repens*), bahia grass (*Paspalum notatum*), and various sedge species (e.g., *Cyperus sp*., *Rhynchospora sp*.). The DMA is managed with a 2-year rotation prescribed burning regiment and targeted removal of exotics (David 1991, DuPuis Area Management Plan 2008-2013) to maintain open-understory flatwood forests and control exotic plants. There is a large population of feral swine at the DMA that disturb significant expanses of soil throughout the region. In recent years, land managers have observed increased presence of Caesar's weed, particularly in hog disturbed areas and shortly after prescribed burns, both within burn units and along constructed (i.e., mechanically tilled) perimeter fire breaks.

My sites were located in DMA management units 1, 2, 3, and 18 (Figure 2.1). Units 3 and 18 were used for a manipulative field experiment and Units 1 and 2 were used to assess the influence of feral swine on soil seed banks (described below). Unit 3 was burned by SFWMD in January 2016, while the other Units were unburned during this study.

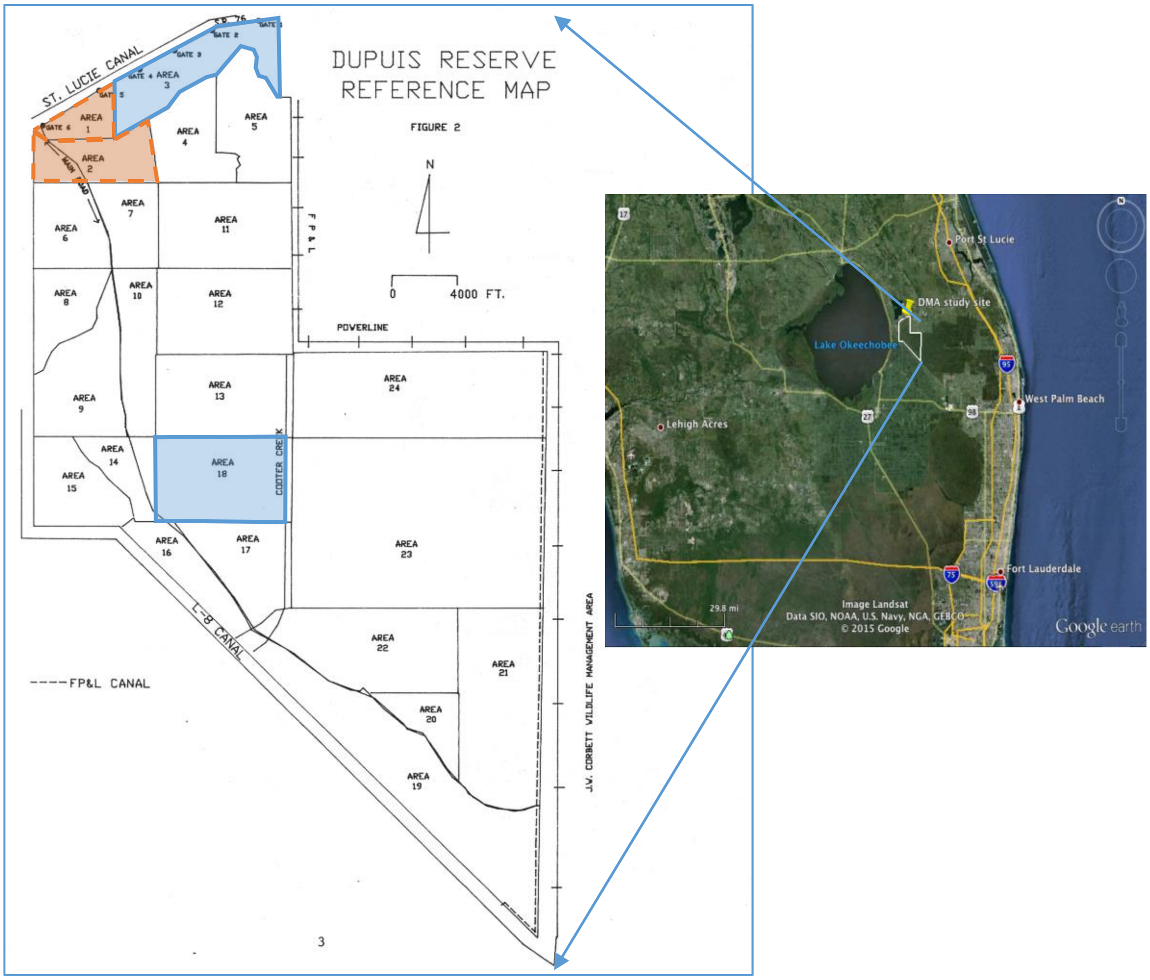

Figure 2.1: Map of DuPuis Management Area with management land Units 3 and 18 shaded in blue with a solid line outline and management land Units 1 and 2 shaded in orange and outlined with a dashed line.

Effect of prescribed burning and soil disturbance on Caesar's weed

To evaluate the effect of fire and soil disturbance on the frequency and abundance of Caesar's weed, we used a factorial combination of dormant season prescribed burning and mechanical soil disturbance. In January 2016, twenty randomly located 2x2 meter plots were established in Units 3 and 18. To assess environmental similarity at the onset of the study, surface soil moisture was measured non-destructively using a soil moisture probe (ThetaProbe, Delta-T Devices) and soil temperature was measured at a 2cm depth using a thermocouple probe (Omega Engineering) in three locations within each plot (Table 2.1). Additionally, surface litter layer thickness, maximum understory vegetation height, and over story canopy closure (via concave spherical densitometer) were measured for each plot (Table 2.1). Pretreatment environmental conditions and Caesar's weed abundance were compared between land units using one-way ANOVAs. Within each land unit, 10 plots were randomly assigned to either a disturbed or undisturbed soil treatment. Disturbed soil treatment plots were tilled with a hand operated Mantis 2-cycle Gas Powered Tiller/Cultivator to soil depths of 5–15cm to mimic the effects of swine rooting (Boughton and Boughton 2014) or tilled fire breaks, while the undisturbed treatment plots were left un-tilled. Within two days of establishing the soil disturbance treatment, Unit 3 was burned on January 13, 2016, by SFWMD personnel while Unit 18 was left unburned, establishing a factorial combination of burning (burned vs unburned) and soil disturbance (tilled vs. un-tilled). However, the Unit 18 plots comprising the 'unburned' treatment were subsequently burned by a prescribed fire on April 26, 2016, restricting the factorial assessment of burning and tilling on Caesar's weed abundance to a 3-month dataset; continued monitoring of the Unit 3 'burned' plots allowed assessment of soil disturbance effects on Caesar's weed in burned flatwoods.

Immediately following the prescribed burn, the plots were evaluated for species percent ground cover and then reevaluated biweekly to quantify vegetation recovery and incidence of Caesar's weed. To examine the effect of treatments on the spread of Caesar's weed the change in number of plots with Caesar's weed present was also compared using contingency tables with fisher's exact tests. Plots within Unit 3 were monitored for 16 months to evaluate the effects of burning with and without soil disturbance using a one-way ANCOVA to compare Caesar's weed abundance with pretreatment Caesar's weed abundance cover used as the covariate. Caesar's weed stem count was only counted after treatments so a Kruskal-Wallis test was used to compare Caesar's weed stem count 16 months post-treatment due to the collected stem counts not meeting the assumptions of a parametric ANOVA.

Effect of feral swine on the soil seed bank

In March 2016, the soil seed bank composition was assessed to characterize the seed bank and evaluate the effect of feral swine soil disturbance. I used land units (Units 1 and 2) outside those used for the manipulative experiment in order to 1) avoid impact to the manipulative experiment and 2) target locations with recent feral swine soil disturbance. Five surface soil samples (11.5cm dia., 9cm deep) were randomly collected from newly rooted soils at three different locations within each land unit. An additional five samples were collected from undisturbed (unrooted) soils within a 5m perimeter of the rooted soils. No mature Caesar's weed plants were observed within 5m of any sample. In the lab, each soil sample was sieved twice with a 2.5mm wire mesh sieve to separate the seeds from the soil. The seed species richness, total abundance of seeds (pooled for all species), and abundance of Caesar's weed seeds were recorded, as well as the condition (i.e., intact vs. husked) of Caesar's weed seeds. Species richness was based on seeds grouped by appearance but the exact species of seeds was not identified (with the exception of Caesar's weed). All seeds were then grouped by their respective soil samples, planted in pots (11.5cm dia., 9cm deep) with the original soil collected from the DMA, and placed in the FAU-Davie greenhouse, where emergence of Caesar's weed seeds was monitored for two months. Two-way ANOVA showed there was no site effect on the abundance of seeds created by site or the combination of site and soil condition (disturbed and undisturbed). Therefore, the data were pooled and contingency tables were created and chi-squared and fisher's exact tests, as well as nonparametric ANOVA analysis with a Kruskal-Wallis test, were used to compare results from disturbed and undisturbed soils (n=15).

To quantify seed rain in the rooted and undisturbed soil sites, I used seed traps (11.5cm dia., 9cm deep plastic pots filled with an autoclaved mixture of commercial topsoil and sand) inserted into the 15 previous sample locations. The contents of the seed traps were collected after 8 weeks (May 2016) and again after 4 weeks (June 2016) for a total of 12 weeks of collection time in the field. Seed trap samples were sieved twice with a 2.5mm wire mesh sieve and the isolated seeds quantified and analyzed as described previously for the in-situ soil seed bank to determine if there were differences in background Caesar's weed dispersal that could influence observed seed bank differences between rooted and undisturbed soils.

Effect of seed heating on Caesar's weed germination

We quantified the seed-heating threshold of Caesar's weed germination success by exposing seeds to a factorial range of heating duration and intensity (temperature) mimicking observed pine flatwoods prescribed fire conditions. Caesar's weed seeds were collected from approximately 30 mature plants at DMA in May 2016; the collected seeds were pooled and visually inspected to be free from damage or abnormality (e.g., insect damage, seed rot, etc.) before being assigned to heating treatments in batches of 100 seeds. Heating intensities and exposure times were based on maximum fireline temperatures (MaxT) and flame residence times (RT; defined as seconds with temperature above 300 ^{o}C) based on data from 16 prescribed burns in northern Florida pine flatwoods (Cronan et al. 2015; Table 2.2) and a single prescribed burn at DMA (this study; Table 2.2). Prior to a January 2016 burn in DMA Unit 3, six K-type fine-wire thermocouples and single-channel dataloggers (Omega Engineering, Inc.) were placed in a triangular array near the middle of the target burn unit. Three thermocouples were placed at a height of one meter (representing the height of seeds on a mature Caesar's weed plant) and three were buried 2 cm in the soil (representing seeds in the soil seed bank). During the prescribed burn, temperature was logged at one-second intervals to quantify fireline intensity and flame residence time. Preliminary tests demonstrated any temperatures over 400 ^{o}C for as little as 5 seconds resulted in complete combustion of the seeds, so the heating intensity ranged from 200-400 ^{o}C in 50 ^{o}C increments with heating durations from 10-60 seconds in 10 sec intervals. To simulate flame front-heating in a laboratory setting, seeds were exposed individually to varying positions (i.e., heights) within a Bunsen burner flame for the assigned duration using fine point forceps to achieve the desired heating scenario. Temperature during each trial was measured with an exposed-junction K-type thermocouple held in place at the seed insertion height.

After heating, seeds were germinated in 10 cm-diameter petri dishes between two pieces of medium-fine porosity filter papers (Fisher Scientific) moistened with 5 ml of deionized water and wrapped in Parafilm to retain moisture. The dishes were placed in an incubator at 25 ^{o}C in continuous dark conditions for 14 days (Wang et al. 2009, Awan et al. 2014), after which each seed was scored for germination (success vs failure). Germination success was defined by the presence of a visible live radicle. Multiple logistic regression was used to analyze the effect of heating intensity and duration on seed germination success.

Table 2.1: Mean (±SE) pre-treatment environmental characteristics and Caesar's weed abundance in the DMA study plots in land units 3 and 18 (n=20). Statistically significantly differences (t-test; $p<0.05$) indicated with an asterisk.

	Unit 3		***Unit 18***
Soil moisture (%)	16.0±0.6		17.3±0.6
Soil temperature (^oC)	22.5±0.1	>	21.5±0.1*
Litter layer thickness (cm)	7.6±1.0		5.4±0.8
Understory height (cm)	129.0±12.1	>	97.6±9.4*
Over story canopy cover (%)	20.0±6.2		27.8±6.9
Caesar's weed abundance (%)	1.9±1.2	<	8.0±0.1*

Table 2.2: Mean (±SE) maximum fireline temperatures (MaxT) and flame residence times (RT) from a January 2016 prescribed burn at DMA and 16 prescribed burns in northern Florida.

Time Since Previous Fire (years)	*Source*	*Collection height*	*MaxT (^oC)*	*RT (seconds)*	*# of Thermocouples*
2	This study	1 m	464 ±134	4 ±2	3
2	This study	-2 cm	105 ±20	0	3
3-5	Cronan et al. 2015	5 cm	423 ±15	28 ±2	172

Results

Effect of Prescribed Burning and Soil Disturbance on Caesar's weed

Burning or tilling removed all Caesar's weed from the treatment plots allowing for post treatment recovery of all plots to begin with no Caesar's weed present; however, pretreatment Caesar's weed abundance was higher in Unit 18 prior to treatments ($F_{1, 38}$ = 5.82, p = 0.021; Table 2.1), and was therefore included as a covariate for assessment of post-treatment invasion. In the 3-month period prior to the second prescribed burn, the factorial comparison showed no significant effect of burning ($F_{1, 35}$ = 0.18, p = 0.677; Figure 2.2), tilling ($F_{1, 35}$ = 0.38, p = 0.542; Figure 2.2), or the combination of the two treatments ($F_{1, 35}$ = 0.43, p = 0.518; Figure 2.2) on Caesar's weed abundance (0.65±0.39%; n=40). There was also no significant effect on the frequency of plots with Caesar's weed three months after burning (p = 0.245), tilling (p = 0.275), or the combination of the two treatments (p = 0.307; Figure 2.3). Similarly, after 16 months the burned Unit 3 plots showed no significant effect of mechanical tilling on Caesar's weed abundance ($F_{1, 17}$ = 0.00, p = 0.955) or stem count (Chi-Square = 0.24, p = 0.628: Figure 2.4).

Effect of feral swine on the soil seed bank

There was no block effect on the abundance of seeds created by site ($F_{2, 22}$ = 0.08, p = 0.927) or the combination of site and soil condition (disturbed and undisturbed) ($F_{2, 22}$ = 1.37, p = 0.276). The total number of seeds (Chi-Square = 3.87, p = 0.049) and seed species richness (Chi-Square = 5.84, p = 0.016) were reduced in feral swine disturbed soils (Table 2.3). While disturbed soils showed no difference in the abundance of Caesar's weed seeds (Chi-Square = 0.30, p = 0.590), they had a greater ratio of Caesar's weed seed-to-total seed abundance compared to undisturbed soils (Chi-Square = 29.44, $p < 0.0001$). Additionally, Caesar's weed seeds in swine disturbed soils were predominantly husked (89%) whereas all seeds in undisturbed plots were intact (i.e., not husked) ($p = 0.009$). Caesar's weed seedlings only emerged from disturbed samples, although the comparison was not statistically significant ($p = 0.491$).

Seed rain had greater total seed abundance (Chi-Square = 5.85, $p = 0.016$; Table 2.3) and seed species richness (Chi-Square = 5.86, $p = 0.016$) in swine disturbed soils, but there was no difference in Caesar's weed seed abundance (Chi-Square = 2.07, $p = 0.150$) or ratio of Caesar's weed-to-total seed abundance ($p = 0.784$) between disturbed and undisturbed soils.

Effect of seed heating on Caesar's weed germination

The baseline (unheated; ambient temperature) germination rate was low (2%, n=100; Table 2.4). Low-intensity (200 ^{o}C), short-interval (10 sec) seed heating significantly increased Caesar's weed seed germination to 36% (Chi-Square = 19.87, $p < 0.001$; Table 2.4), but any additional heating intensity or duration had no effect on germination compared to the control (Table 2.4). However, low baseline germination limited the ability to statistically detect whether the low observed germination was due to heat-related mortality.

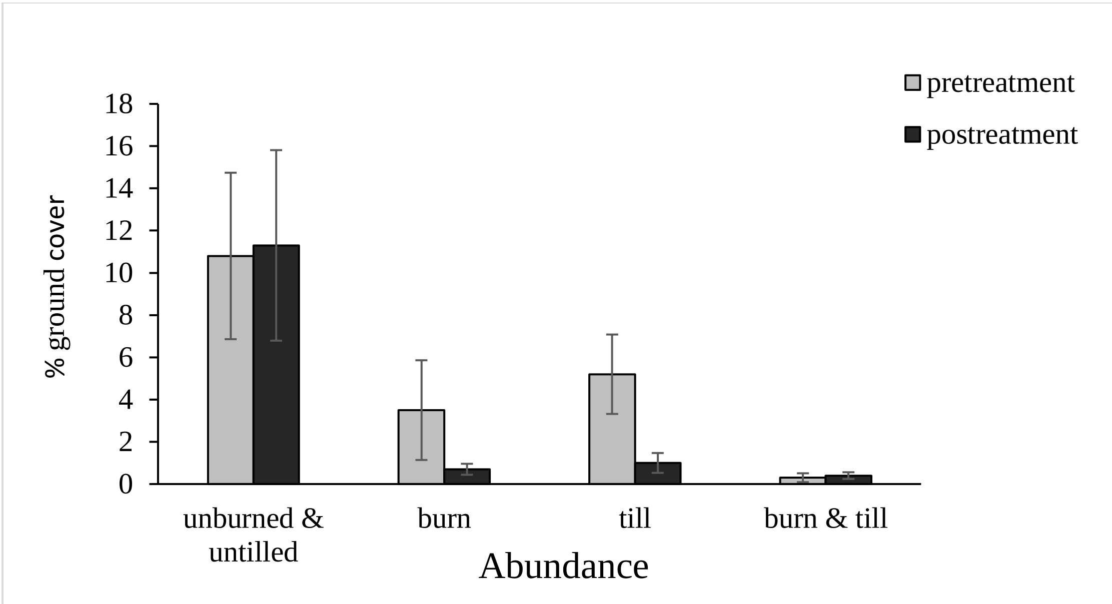

Figure 2.2: Abundance of Caesar's weed (Mean ±SE) in plots prior to and three months post treatments.

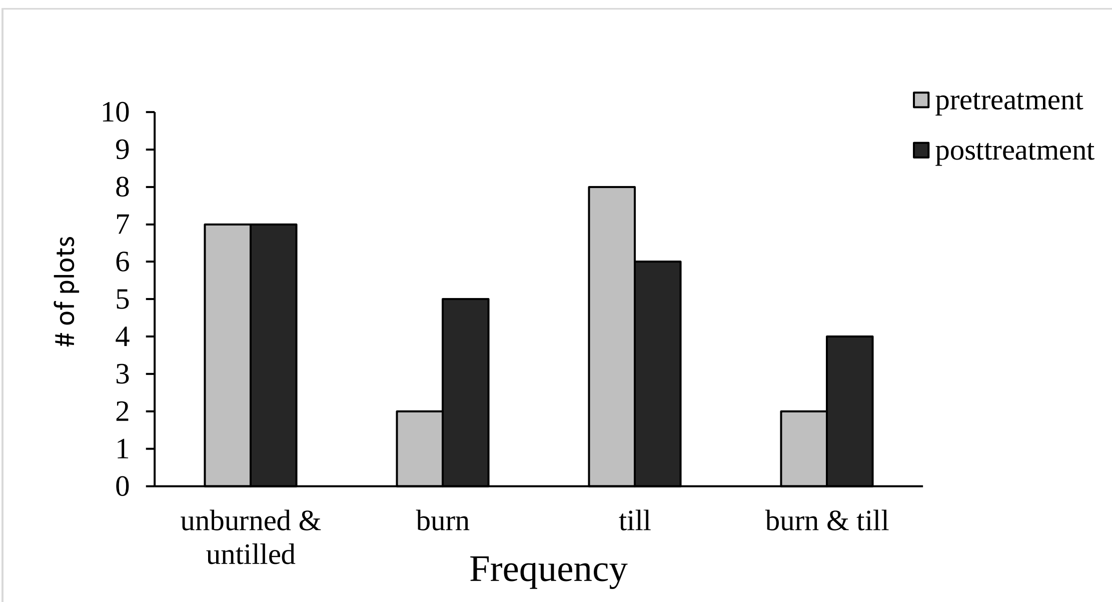

Figure 2.3: Number of plots with Caesar's weed present prior to and three months post treatment.

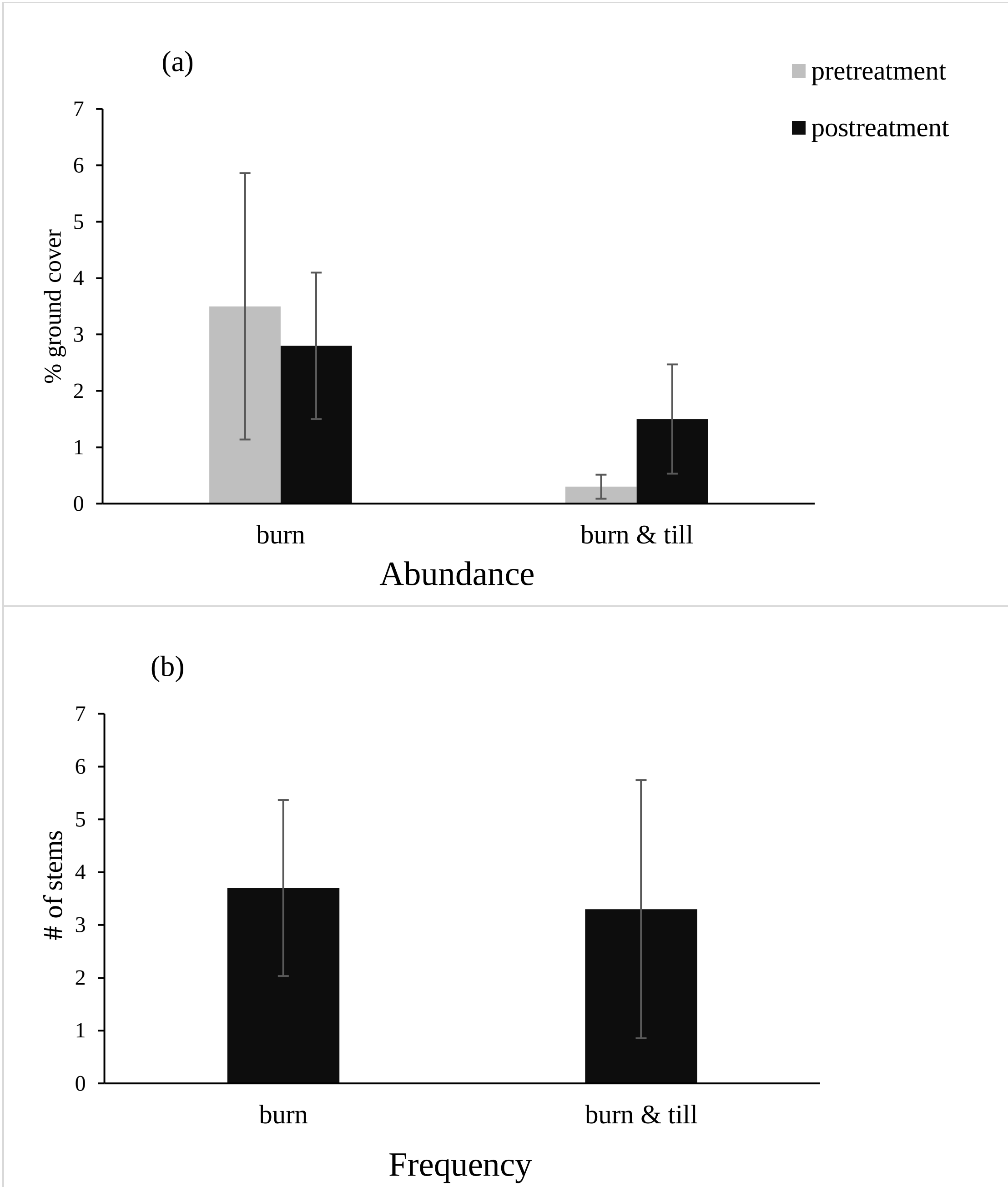

Figure 2.4: Abundance (a) and plot stem frequency (b) of Caesar's weed (Mean ±SE) 16 months following prescribed burning in mechanically tilled and untilled soils.

Table 2.3: Abundance of seeds, seed species richness, and greenhouse emergence of Caesar’s weed (Mean ±SE) collected from soil seed banks and seed traps within feral swine disturbed and undisturbed soils. Emergence of Caesar’s weed seeds was not tested for seeds collected in seed trap samples. Significantly different comparisons indicated with an asterisk.

	Soil seed bank (n= 15)			*Seed trap (n= 15)*		
	Feral swine disturbed		Undisturbed	Feral swine disturbed		Undisturbed
Total seed abundance	4.40±1.66	<	9.60±3.66*	0.93±0.25	>	0.20±0.11*
Seed species richness	1.40±0.24	<	2.40±0.31*	0.87±0.22	>	0.20±0.11*
Caesar’s weed abundance	1.21±1.00		0.21±0.15	0.13±0.09		0
Husked Caesar’s weed abundance	1.07±0.92		0	0		0
Emerged Caesar’s weed	0.29±0.22		0	n/a		n/a

Table 2.4: Germination rates of Caesar's weed seeds after their assigned heating treatment. Treatments with germination significantly different than seeds not exposed to a heating treatment indicated with an asterisk.

Temperature (°C)	*Exposure time (seconds)*	*% germination*
25 (ambient temperature)	0	2
200	10	36*
	20	2
	30	1
	40	0
	50	1
	60	0
250	10	7
	20	0
	30	0
	40	3
	50	2
	60	1
300	10	6
	20	0
	30	0
	40	0
	50	0
	60	0
350	10	8
	20	0
	30	0
	40	0
	50	0
	60	0
400	10	0
	20	0
	30	0
	40	0
	50	0
	60	0

Discussion

Management of exotic invasive plants can be costly and difficult, particularly for species like Caesar's weed that may be facilitated by invasive feral swine or even by traditional land management practices like prescribed burning and mechanically tilled fire breaks. Contrary to our initial hypothesis, mechanical tilling and prescribed fire did not increase Caesar's weed presence. However, while mature plants were initially removed there was also no lasting decrease in Caesar's weed presence indicating these are not effective methods for eradicating Caesar's weed from an area. A considerably larger abundance of Caesar's weed and subsequently an assumed greater amount of seeds in unit 18 may have influenced the lack of increase found between the burned and unburned treatments. Due to unit 18 plots comprising the 'unburned' treatment being subsequently burned by a prescribed fire on April 26, 2016, the assessment of fire effects on Caesar's weed abundance was only allowed three months of recovery time and the lack of recovery time may have been a major factor in not seeing an increase in Caesar's weed presence. My plots may not correlate with observations of increased Caesar's weed in tilled fire break because fire breaks can be repeatedly tilled and kept bare for multiple prescribed burns over many years increasing Caesar's weed seeds chance of being scarified and allowing these rapidly sprouting plants a higher chance of becoming established in open soil.

Mechanical soil disturbances such as tilling firebreaks or roadside mowing could create the potential for seed dormancy to be broken by damaging or removing the seed coat. However, germination of Caesar's weed is greatest at the soil surface and is greatly reduced below 2cm depth (Awan et al. 2009) so with the typical depth of mechanically tilled soils being considerably deeper than 5cm seeds may be buried too deep to emerge. While my plots exposed to a single winter prescribed fire showed no statistical increase, repeated exposures to dormant season prescribed fire over several years has been shown to significantly increase shrub presence in pine flatwoods compared to growing season prescribed fire (Drewa et al. 2005).

Feral swine rooting and wallowing appears to increase the potential for Caesar's weed to become established in an area by lowering seed bank competition and enhancing the chance of Caesar's weed seeds being husked, which has been shown to increase the germination rate of Caesar's weed seeds (Wang et al. 2009). Feral swine conducting widespread, rigorous soil disturbing activities satisfies major requirements for Caesar's weed to invade an area. As in this study, foraging swine have been shown to reduce seed bank densities (Siemann et al. 2009) reducing seed bank competition for post-disturbance recruitment. It is unlikely that feral swine actively forage for Caesar's weed considering an individual fruit weighs <100 mg and feral swine have been shown to target seeds > 250 mg (Siemann et al. 2009). Dormancy due to a hard seed coat is common in plants from the Malvaceae family and husking and scarification have been shown to increase the germination rate of Caesar's weed seeds to 10% and 42%, respectively, compared to a germination rate of 2% for unmanipulated seeds (Wang et al. 2009). In addition to potentially serving as vectors for dispersal, feral swine can increase the chance of Caesar's weed invasion success through seed scarification (husking) of Caesar's weed seeds and lowering total seed bank seed abundance resulting in increased relative abundance of Caesar's weed seeds in disturbed soils, suggesting feral swine soil disturbances may be more beneficial for Caesar's weed than other soil disturbances (e.g., tilling).

Seed heating may also serve as a mechanism for seed coat scarification that promotes germination. Flame exposure can cause contraction and expansion of hard seed coats, especially in wet and hot environments, thus breaking physically induced dormancy and increasing seed germination (Auld et al. 1991, Tieu et al. 2001). and the patchy, low intensity ground fires characteristic of pine flatwoods (Abrahamson and Hartnett 1990, Wilcox and Giuliano 2010) may be creating scenarios beneficial to Caesar's weed seeds. In our study, soil heating was minimal (Table 2.2), leaving Caesar's weed seeds in the soil seed bank relatively protected from intense heat capable of killing seeds during the prescribed burn. Mechanical soil disturbances reduce fuel load and fireline intensity, which can increase the extent of habitat that experience lower heating intensities capable of increasing Caesar's weed seed germination. Mechanical soil disturbances can also bury seeds and protect them from intense heat, although negative effect of deep burial of seeds (Awan et al. 2009) may outweigh the potential for the positive effect of husk removal (Wang et al. 2009).

Dormant season versus growing season fire has been shown to have no effect on the intensity of prescribed burns in Florida pine flatwoods (Cronan et al. 2015), so seasonality of burning is unlikely to affect fire-related seed mortality of Caesar's weed. However, seasonality of prescribed burns has been shown to have significant effects on the abundance of invasive species in other landscapes (Emery et al. 2005) and encroaching shrubs in Florida pine flatwoods (Drewa et al. 2002). Pine flatwoods dormant season prescribed burns have been shown to increase shrub invasion especially when conducted multiple times, compared to growing season prescribed burns that neither increased nor decreased shrub presence (Drewa et al. 2002). Individual Caesar's weed plants in an area flower and fruit asynchronously throughout the year (Francis 2004), reducing the effectiveness of planning prescribed burns during periods of Caesar's weed vulnerability (i.e., prior to flowering). However, growing season burns have been shown to reduce the duration of multiple forb and shrub species flowering times (Platt et al. 1988) and could have similar effects on Caesar's weed.

While the application of prescribed fire appears to be effective at initially killing Caesar's weed plants in burned areas it does not appear to be sufficient in controlling Caesar's weed in pine flatwoods due to seedlings rapidly sprouting. Caesar's weed ability to grow several meters in height can protect canopy-held seeds from more intense heating near a burning litter/duff layer, while the ability for Caesar's weed seeds to be dispersed by feral swine and lay dormant lowers the effectiveness of removing mature plants from an area with hopes of long-term eradication, due to lingering seeds that are protected from intense heat in the soil seed bank. This calls for a commitment to possibly repeated treatments to rid an area of seeds and prevent new ones from being developed. Due to a variety of attributes, Caesar's weed will require specific mixed-management strategies for the complete removal of this invasive species. A variety of herbicides (e.g., 2,4-D ester, Glyphosate) have been shown to be extremely effective at removing Caesar's weed post-emergence during multiple growth stages (Awan et al. 2014). Eradication efforts will require the removal of mature plants followed by rapid (e.g., <6 months) retreatment to remove seedlings before they flower and set seed. The characteristics of Caesar's weed seeds create a need to address rapidly increasing populations of feral swine. Without managing feral swine in an area Caesar's weed seeds, with an increased chance of establishment, will most likely continuously be redistributed throughout an area. As feral swine populations change so should the regulations on feral swine hunting. Hunting regulations could be a key factor is addressing growing feral swine populations and indirectly reduce Caesar's weed presence. With pine flatwoods being exposed to the combination of dormant season prescribed burns, human soil disturbances, and increasing feral swine populations, specialized management techniques appear to be called for to control Caesar's weed.

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