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Factors Limiting Native Species Establishment On Former Agricultural Lands

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FACTORS LIMITING NATIVE SPECIES ESTABLISHMENT ON FORMER AGRICULTURAL LANDS

by

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ABSTRACT

Restoration of abandoned, nonnative species-dominated agricultural lands provides opportunities for conserving declining shrubland and grassland ecosystems. Land-use legacies, such as elevated soil fertility and pH from agricultural amendments, often persist for years and can favor nonnative species at the expense of native species. Understanding the factors that limit native species establishment on abandoned agricultural lands can provide important insights for restoration and conservation of native species on human-modified lands. I conducted two field experiments on abandoned agricultural lands: a former pasture on Martha's Vineyard, MA and a former citrus grove at Merritt Island National Wildlife Refuge (MINWR) in Titusville, FL. In these experiments I tested how soil chemical properties affect native and nonnative species abundance and how different methods of removing nonnative, invasive species affect native and nonnative species abundance. In the first experiment, specifically I tested how restoration treatments affect competition between existing nonnative agricultural plant species and native plant species that are targets for sandplain grassland restoration on Martha's Vineyard, MA. At MINWR, I examined how lowering soil fertility with carbon additions and lowering soil pH by applying sulfur affects nonnative species richness and cover (in two former citrus groves that were historically scrub/ scrubby flatwoods. Overall, I found that biotic factors, such as competition with nonnative species, play a stronger role in limiting native species establishment than soil chemical properties. Likewise, control of nonnative, invasive species is most effective with mechanical treatments to physically reduce cover, rather than altering soil chemical properties.

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CHAPTER ONE: LITERATURE REVIEW

Introduction

The conversion of natural lands to agriculture is one of the most important and widespread human endeavors. Agriculture is the most significant cause of loss of natural habitats worldwide (Wilcove et al. 1998, Tilman et al. 2001) and more than 40% of the Earth's surface is now used for livestock and crop production (Mooney 2010). At the same time that agricultural practices have intensified in duration and extent, agricultural lands are also being abandoned due to loss of productivity and economic and social changes (MacDonald et al. 2000). For example, the area of abandoned croplands increased since 1950, caused in part by migration from rural to urban areas (Ramankutty and Foley 1999). This abandonment of former agricultural land now creates opportunities to restore natural vegetation for a variety of purposes, including biodiversity protection and provision of a variety of ecosystem services.

There are many challenges to restoring native species and natural vegetation on former agricultural lands. Abandoned agricultural land often leaves legacies that are both biotic (influence on vegetation composition) (Cramer et al. 2008) and abiotic (influence on soil properties) (McLauchlan 2006) and that can persist for decades to centuries (Tilman et al. 2001, Dupouey et al. 2002). Establishment of native species on former agricultural land is often limited by both the biotic and abiotic legacies of the former land use (Walker et al. 2004, Cramer et al. 2008). Understanding how to overcome these land use legacies is an important goal for restoration ecology and has important conservation implications (Motzkin et al. 1999).

Biotic land use legacies include alteration of species composition in a number of ways. Clearing land for agricultural use directly removes existing vegetation, but also depletes native seedbanks and reduces local sources of propagules from the surrounding landscape (Bakker and Berendse 1999). Agricultural practices typically involve the introduction of nonnative species that dominate the vegetation and stock the seedbanks with seeds of nonnative species (Mack et al. 2000). Nonnative species are in many cases invasive species that are competitive dominants over native species (Tilman et al. 1996), which can therefore inhibit reestablishment of natives after the cessation of agriculture.

Abiotic legacies such as alterations of soil chemical and physical properties by agriculture over many years can also influence modern vegetation patterns (Motzkin et al. 1999). Nutrient enrichment can persist for decades after cessation of fertilization, which in turn can favor fast growing, early successional, non-native invasive species (Von Holle and Motzkin 2007). Additionally, nonnative species themselves can alter soil nutrient dynamics creating positive feedbacks for their persistence (Ehrenfeld 2003).

Several researchers have conducted experimental restorations of former agricultural lands that have been highly modified and have become invaded by nonnative species. In many cases, restorations focus on reducing biotic or abiotic barriers to native plant establishment. In this paper, I review the primary literature on restoration studies of former agricultural lands that aim to reduce biotic or abiotic land-use legacies to promote the establishment of native species. I focus on restorations that have been conducted in grassland and shrubland systems that are currently dominated by nonnative species as a result of previous agriculture. The objectives of this paper are to: (1) synthesize the current state of knowledge on the effects of agricultural land-use legacies on restoration efforts, (2) review the potential management approaches to overcoming and counteracting these legacies, and (3) provide recommendations for increasing the success of future restorations.

Overcoming biotic factors to native plant establishment

Competition with non-native invasive species

Biotic factors, such as competition with nonnative species and recruitment limitation, are among the most important factors limiting native species establishment in abandoned agricultural systems (Bakker and Berendse, 1999, Foster, 1999, Walker et al. 2007). Abandoned agricultural lands quickly become dominated by early successional, fast growing species which are a potential barrier for the establishment of native species because they provide few open sites for natives to occupy (D'Antonio and Vitousek 1992, Corbin et al. 2004). Priority effects (i.e., effects that result from earlier establishment of nonnative species) can impede native species establishment and growth (Grman and Suding 2010). Nonnative species with persistent seed banks have been shown to germinate earlier and grow faster in abandoned wheat fields in Western Australia (Standish et al. 2007). In a greenhouse experiment using species of California grasslands, Grman and Suding (2010) found that priority effects from nonnatives reduced establishment of natives. They also found, however, that when natives arrived before nonnatives, nonnative growth was suppressed by 85%, indicating that removing nonnatives will provide natives with a competitive advantage (Grman and Suding 2010).

In addition to priority effects, biotic constraints such as litter accumulation, decreased light penetration from standing biomass (Foster 1999, Bakker et al. 2003, Buisson et al. 2006, Buisson et al. 2008, Standish et al. 2007; Wilson et al. 2008), and depletion of soil moisture (Eliason and Allen 1997) by nonnative species can cause decreased germination and seedling establishment of native species. Competition with invasive grasses on heathlands that were intensively managed for agriculture in the U.K., for example, is a key constraint to the reestablishment of *Calluna vulgaris*, which is the dominant native shrub of *Calluna* heathlands, because of its intolerance of shade (Dunsford et al. 1998, Lawson et al. 2004, Walker et al. 2007).

Because nonnative and invasive species often impose biotic constraints on native species establishment, removal of aboveground biomass is often effective and necessary for increasing native cover and richness (Corbin et al. 2004). Many methods to reduce nonnative species are also used to promote the establishment of natives (Table 1.1). Herbicide, for example, is widely used to control invasive species during restoration, and it is often effective in reducing nonnative cover which in turn promotes native cover (Bakker et al. 2003). In my review, three of five studies that used herbicide as a treatment to decrease nonnatives and increase natives were successful at both. For example, in a restoration of old fields in Saskatchewan, Canada, Wilson and Gerry (1995) found that killing nonnatives with herbicide was necessary to increase native prairie species establishment and plots that were sprayed had twenty times more native germinants than plots that were not sprayed with herbicide.

In other cases, however, herbicide does not provide a long-term benefit to native species establishment. After four years of annual herbicide applications, the nonnative grass, *Agropyron cristatum,* decreased in cover but persisted in herbicide-treated plots in a similar Saskatchewan grassland restoration study (Bakker et al. 2003, Wilson and Partel 2003). In this case, herbicide did not reduce the seed bank or root mass of nonnatives (Bakker et al. 2003). In a prairie restoration in Grasslands National Park (Canada), herbicide provided no benefits to native species establishment (Wilson et al. 2008).

Grazing, or alternatively mowing with subsequent biomass removal, is another technique that can reduce nonnative species abundance and increase native diversity by reducing competitive dominants (Collins et al. 1998). These methods not only reduce above ground biomass, they also reduce seed rain and limit dispersal of nonnative species (Maron and Jefferies 2001). In a grazing experiment in a tallgrass prairie in Kansas, grazing by native bison nearly doubled species richness (Collins et al. 1998). Similarly, in a coastal grassland in California mowing significantly increased species diversity, specifically of annual forbs (Maron and Jefferies 2001). These results were only seen the first year and were likely due to altering the litter layer which improved conditions for germination (Maron and Jefferies 2001).

Topsoil removal is another method that can reduce nonnative vegetation and provide open sites for native species establishment because it reduces both above- and belowground competition (Buisson et al. 2006, Kardol et al. 2008), as well as the soil seedbank (Buisson et al. 2006, Buisson et al. 2008, Hölzel and Otte 2003, Kiehl et al. 2006). All of the studies I reviewed that tested topsoil removal successfully decreased nonnatives and increased native species (Table 1.1). In a restoration of heathlands in the UK, topsoil removal with the addition of heathland cuttings significantly increased heathland species establishment and diversity (Allison and Ausden 2004). Allison and Ausden (2004) concluded that the reduction in available P, decreased moisture retention, and removal of the non-heathland seedbank reduced competitors that would have limited heathland species establishment. When combined with hay that was harvested from intact reference sites, topsoil removal has been a very effective method to restore native species assemblages in wet fens (Patzelt et al. 2001), calcareous grasslands (Kiehl and Pfadenhauer 2007), and floodplain grasslands (Hölzel and Otte 2003) on former cultivated fields in Germany.

Likewise, tilling is a simpler and often effective method that provides open sites for establishment (Wilson and Gerry 1995; Pywell et al., 2011). In a prairie restoration study on old fields invaded by the nonnative grasses *Agropyron cristatum* and *Bromus inermis*, native establishment was significantly higher on tilled plots than untilled plots suggesting that neighbor-free sites are required for establishment (Wilson and Gerry 1995).

Because topsoil removal and tilling open new sites for establishment, these methods can also provide favorable conditions for non-target species establishment (Bakker and Berendse 1999). In a coastal sandplain grassland restoration on Martha’s Vineyard, MA, Neill et al., (unpublished data) observed emergence of four nonnative species that were not present in the vegetation prior to tilling, indicating that species that persisted in the seedbank germinated when tilling created suitable conditions. Additionally, these methods, specifically topsoil removal, can be cost and labor intensive, and the feasibility of using these methods on a landscape scale restoration should be considered.

Recruitment limitation

Areas converted to row-crop agriculture and many pasture lands contain minimal remnants of native plant communities, such as species composition and soil seedbanks (Bakker and Berendse 1999). Even after removal of nonnative, invasive species, seed dispersal and recruitment limitation often limit the regeneration of native species (Pywell et al. 2002, Seabloom et al. 2003a, Seabloom et al. 2003b, Standish et al. 2007). Several decades of agriculture can impoverish the native seed bank and fragmentation of the landscape can limit dispersal even when native propagules are available (Bakker and Berendse 1999).

In a restoration of an abandoned agricultural field to tall grass prairie in Kansas, seed dispersal was the primary limitation to recovery of native species-rich grasslands, rather than presence of invasive grasses (Foster et al. 2007). Similarly, Kardol et al. (2008) found that seeding alone had a greater effect on increasing grassland native species richness than topsoil removal and carbon addition to reduce soil fertility on a formerly cultivated field in The Netherlands. Indeed, seed addition alone can promote the establishment of native species when added to dense stands of existing non-native vegetation (Seabloom et al. 2003a, Seabloom et al. 2003b).

Several methods to reintroduce native propagules have been used when restoring abandoned agricultural fields, and in my review, every study that added a source of native propagules, such as seeding, transplanting, or hay transfer, had a significant increase in native species establishment (Table 1.1). Broadcasting seed has been more effective in increasing native species diversity and cover than drilling seeds in prairie restorations (Bakker et al. 2003, Wilson et al. 2008). Hay transfer has also been an effective method to increase native species (Allison and Ausden 2004, Kiehl et al. 2006). This method has several benefits over direct seeding in that it reintroduces representative species of the native community, it provides "safe sites" for seedling establishment by regulating soil microclimates, and it is cheaper and less laborious than harvesting and cleaning seeds of individual species. Hay addition increased native richness by 69-86% in a flood meadow restoration near Frankfurt, Germany (Hölzel and Otte 2003, Kiehl et al. 2006).

Transplanting seedlings has also been an effective method of reintroducing native species in restorations of abandoned agricultural lands (Buisson et al. 2006, Buisson et al. 2008). Buisson et al. (2006) reported 89% survival after three months of transplanting the native perennial grass, *Danthonia californica,* in plots in which topsoil was removed and 73% survival in plots in which topsoil was left intact in a coastal prairie restoration in California. After 1.5 years, the survival in the topsoil removal was 39% and in intact topsoil plots it was 12% indicating that topsoil removal significantly increased survival of transplants, likely by reducing competitors. Similarly, in a restoration of oak-saw palmetto scrub in a former citrus grove, (Schmalzer et al. 2002) reported survival of transplanted oaks to be 56% eight months after planting. While transplants often demonstrate high establishment success, transplanting seedlings is more costly and time intensive than seeding (Buisson et al. 2008).

Regardless of the method of reintroducing native species, selecting certain species for restoration can constrain invasions by increasing biotic resistance. Restoring native species within the same functional group as invaders can confer resistance to further invasion and lead to successful establishment of native species (Bakker and Wilson 2004, Hooper and Dukes 2010).

For example, the concept of limiting similarity (MacArthur and Levins 1967) predicts that invasive species will be less likely to establish when native species with similar traits are present or when there are no open niches to invade (Funk et al. 2008). Evidence of biotic resistance by similar functional groups has been shown by Bakker and Wilson (2004) with a reduction in the spread of a nonnative, C3 grass, *Agropyron cristatum*, by one third in a prairie in Saskatchewan by using native species within the same functional group as the restoration target. Likewise, Hooper and Dukes (2010) found strong biotic resistance to invasion by species within the same functional groups in a serpentine grassland in California. Symstad (2000) on the other hand, found that resistance to invasion by functionally similar natives was only weakly supported in old fields comprised of prairie species in Minnesota. Further testing of this concept in large-scale restorations is necessary.

Overcoming abiotic constraints to native species establishment

Soil fertility

Abiotic agricultural land-use legacies, such as modified soils, are among the factors that increase invasibility by nonnative species (Davis et al. 2000, Walker et al. 2004). The fluctuating resource hypothesis states that invasions are facilitated by increased available resources caused by disturbance or low resource uptake by the native plant community (Davis et al. 2000). Soils in former agricultural lands typically have increased fertility, and specifically increased levels of plant available nitrogen and phosphorus, caused by repeated applications of fertilizers (Pywell et al. 1994, Kulmatiski et al. 2006). Tillage and uniform additions of fertilizers reduce heterogeneity of soil nutrients and this decreased heterogeneity has also been shown to decrease native species diversity (Pywell et al. 1994, Baer et al. 2005). Nonnative species are often stronger competitors than natives for available resources in high-nutrient environments (Daehler 2003, Davis et al. 2000), whereas native species are typically stronger competitors than nonnatives in low-nutrient environments (Wedin and Tilman 1990), indicating that reducing available resources would favor natives. Funk and Vitousek (2007) however, found that nonnatives from three different habitats in Hawaii were also able to compete under low-nutrient conditions due to increased resource use efficiency, suggesting that there are several factors that influence competitive interactions in modified soils.

Several methods to reduce soil fertility have been tested experimentally in restorations, and some methods are more effective than others (Table 1.2). Mowing with subsequent biomass removal is one method that was demonstrated to reduce soil N and to increase native species diversity in a Kansas tallgrass prairie (Collins et al. 1998). Maron and Jefferies (2001), however, did not see a significant reduction in the total soil N pool or an increase in native species after 5 years of annual mowing in a California grassland. Although results have not been consistent, mowing is a low tech, cost-effective method to reduce biomass of nonnative species and should be considered when appropriate.

Another method of restoring agricultural fields that has been widely used is to apply soil amendments aimed at restoring historic soil properties. As agricultural lands often have increased extractable inorganic N, adding carbon in the form of sucrose, sawdust, woodchips, and/or mulch has been suggested as a method to immobilize extractable N rendering it unavailable for plant use (Morgan 1994). Several studies have shown that inorganic N levels have decreased in response to carbon additions (Zink and Allen 1998, Morghan and Seastedt 1999, Blumenthal et al. 2003, Averett et al. 2004, Eschen et al. 2007; Kardol et al. 2008), although some of the effects were short-lived (Morghan and Seastedt 1999).

The source of carbon will influence the effects on soil chemical properties and plant responses. In five of six studies, carbon addition had a significant effect on decreasing soil fertility; however, only two out of those six studies were successful in both controlling nonnative species and promoting natives (Table 1.2). Sucrose addition, for example, is rapidly consumed by soil microbes, whereas mulch, sawdust and woodchip additions decompose slower and may have longer-lasting effects. In a C-addition experiment on formerly cultivated grasslands in the UK and Switzerland, nitrate rapidly decreased with a sawdust plus sucrose addition and remained lower than in plots that received sawdust plus woodchip additions (Eschen et al. 2007). Corbin and D'Antonio (2004), however, found that sawdust reduced N-mineralization rates but did not decrease available nitrate in California grasslands.

Carbon additions have had mixed results on increasing native species establishment and on decreasing abundance of nonnative species in empirical studies (Table 1.2). For example, none of the studies that I reviewed that used sawdust additions increased natives species (Table 1.2). Sawdust additions alone have had little or no effect in increasing biomass of native species in a mixed-grass prairie in Canada or grasslands in California (Wilson and Gerry 1995; Corbin and D'Antonio 2004, respectively). Sucrose plus sawdust additions, on the other hand, have had a stronger effect on vegetation responses. Blumenthal et al. (2003) found that sawdust plus sucrose additions decreased nonnative species growth and increased native prairie species on former agricultural fields in Minnesota. Likewise, adding sucrose plus sawdust significantly reduced persistent grasses and increased desirable forbs and legumes during restoration of abandoned agricultural fields in the UK and Switzerland (Eschen et al. 2007).

Mulch additions are another source of carbon to add to soils to immobilize nitrogen (Wilson and Gerry 1995, Bakker et al. 2003, Wilson et al. 2008) and have the potential benefit of maintaining soil moisture while promoting seedling establishment. Wilson et al. (2008) added a mulch of shredded grass and straw to an old field in Sasketchewan, Canada to reduce soil nutrients, but it had no effects on seedling establishment or survivorship. Overall, the varying success of these treatments is likely due to the different sources and application rates of carbon. Additionally, species may have varying responses to carbon additions (Eschen et al. 2006); therefore, tailoring amendments to control or promote certain species may be required.

Removing the top layer of soil is another effective method to reduce soil fertility (Buisson et al. 2006; Walker et al. 2007), and in all seven of the studies I reviewed that employed topsoil removal to decrease fertility, it was successful (Table 1.2). Topsoil removal reduces soil organic matter, removes soil biota, and alters the water holding capacity of soil (Kardol et al. 2008) which may affect establishment of nonnative or ruderal species that would be competing with natives (Allison and Ausden 2004). Topsoil removal has been used to successfully reduce soil nutrients for restoration of wet fens (Patzelt et al. 2001), calcareous grasslands (Kiehl et al. 2006, Kiehl and Pfadenhauer 2007), heathlands (Allison and Ausden 2004), and floodplain grasslands (Hölzel and Otte 2003) on formerly arable fields in Europe.

Topsoil removal, however, can cause changes in soil structure that could also have negative effects on native establishment. For example, topsoil removal decreased success of native *Calluna* establishment during restoration of acid grassland in the U.K. by removing the organic matter and reducing water retention capacity, leaving only mineral soils (Allison and Ausden 2004, Walker et al. 2007). Likewise, topsoil removal slightly decreased the success of late-successional native species on sandy soils in The Netherlands (Kardol et al. 2009). In some restorations, topsoil removal has increased soil pH, leaving native species adapted to acid soils with a disadvantage (Allison and Ausden 2004, Diaz et al. 2008, Walker et al. 2007). Reducing soil fertility via topsoil removal, overall, has been very effective. However, because it is relatively expensive, can negatively impact establishing native species, and can provide new open sites for colonizing competitors, site conditions must be considered carefully before topsoil removal should be used as a management option.

Soil pH

On soils that are naturally acidic, a common agricultural practice is to apply liming agents to raise the soil pH to provide more suitable conditions for crops and pasture species. Plants vary in their tolerance to soil pH, however, many nonnative or weedy species thrive between a pH of 5 and 7 (Grime et al. 1988), whereas many native shrubland and grassland species are adapted to acidic soils with a pH near 4 (Owen and Marrs, 2000, Neill et al. 2007). Elevated pH on formerly cultivated fields in the U.K., for example, promotes ruderal species abundance and inhibits reestablishment of native heathland species such as *Calluna vulgaris* (Owen and Marrs 2000, Lawson et al. 2004, Walker et al. 2007).

Reduction of pH has been most commonly used for heathland restoration on formerly cultivated fields in the U.K. and elsewhere across northern Europe (Table 1.2). Elemental sulfur is applied to soils as a means of lowering pH; microbial oxidation converts the sulfur to sulfuric acid thereby decreasing the pH. Five out of seven studies that I reviewed in which elemental sulfur was added had significant increases in native species establishment (Table 1.2). Elemental sulfur applied to former fields in the U.K. for the restoration of heathlands reduced nonnative and ruderal species and promoted establishment of heath species such as *Calluna vulgaris* (Owen et al. 1999, Owen and Marrs, 2000, Lawson et al. 2004, Diaz et al. 2008).

Other techniques to reduce soil pH include addition of bracken litter and *Pinus* chippings (Owen et al. 1999, Allison and Ausden 2004). These methods have had limited success in promoting native species establishment. Owen and Marrs (2001), however**,** found that a combination of elemental sulfur and bracken litter reduced pH and abundance of weeds more so than when each was applied separately. Dunsford et al. (1998) used acidic peat to reduce soil pH for the restoration of *C. vulgaris* heathlands, which significantly reduced soil pH and increased germination and abundance of *C. vulgaris*. While peat decreased many weedy species, a few that were tolerant to acid conditions remained, and required further management such as mowing or herbicide to successfully restore the heathland.

While addition of elemental sulfur has had the most success out of all restoration treatments in reducing soil pH, decreasing cover of weeds, and increasing native species establishment (Lawson et al. 2004, Walker et al. 2007), high rates of S addition can be toxic to establishing seedlings (Walker et al. 2007). Further, Lawson et al. (2004) and Walker et al. (2007) observed an increase in extractable P with pH reduction which increased weed establishment and decreased *Calluna* establishment in British heathlands. Overall, application rates of S addition are site specific and must be considered based on soil type, cover of ruderal weeds, and species that are targets for restoration (Owen and Marrs 2000).

Thesis

Numerous factors are known to inhibit native species from establishing on highly disturbed and modified lands such as abandoned agricultural fields. Abandoned agricultural lands quickly become dominated by early successional, fast growing exotic species (Corbin et al. 2004, Von Holle and Motzkin 2007), or species that were intentionally introduced for agricultural purposes (such as nonnative forage species) persist and spread, ultimately inhibiting native species establishment. Also, agricultural land-use legacies, such as elevated fertility and pH, and lack of native propagules, can persist for decades after abandonment and control modern vegetation patterns (Motzkin et al. 1999). Thus, establishment of native species on former agricultural land is often limited by both biotic and abiotic land-use legacies (Walker et al. 2004, Cramer et al. 2008). For my thesis, I was interested in further understanding the factors that limit native species establishment on abandoned agricultural lands. Specifically, I tested mechanisms that inhibit native species establishment on highly invaded, modified grassland and shrubland habitats.

Coastal grassland and shrubland habitats are among the most threatened ecosystems worldwide, due to loss to development and conversion to agricultural systems (Hoekstra et al. 2005). These ecosystems are a high priority for conservation and restoration as they support large numbers of rare plant and animal species. For example, coastal sandplain grasslands of the northeastern United States and scrub habitat of Florida are ecoregions that are vulnerable to the threat of elimination (Hoekstra et al. 2005), yet provide critical habitat for several endemic species (Woolfenden and Fitzpatrick 1984, Vickery and Dunwiddie 1997). In the face of increasing habitat loss and global climate change, it is critical that we learn to effectively manage these biodiversity hotspots (Myers et al. 2000). Restoring native species-rich ecosystems on highly modified lands is critical to protect the species they contain, therefore, minimizing the threat of species extinctions (Ricketts et al. 2005).

As discussed above, methods to mitigate land use legacies, specifically reducing nonnative species abundance, soil fertility, and pH to promote the establishment of native species have been tested numerous times in highly invaded, abandoned agricultural fields. However, most of the literature on restorations occurs in temperate or Mediterranean grassland systems that have had relatively low-intensity agriculture such as used for grazing and cereal crops. For the first part of my thesis, I tested techniques to reduce nonnative competitors and decrease soil fertility and soil pH in a subtropical, shrub-dominated system that has been highly modified by citrus agriculture. These methods have not been tested in the subtropics, and specifically in abandoned citrus groves that are highly invaded with aggressive nonnative species. Specifically, I examined how methods to remove nonnative biomass, reduce soil fertility with sawdust addition and reduce soil pH with sulfur additions would decrease the existing nonnatives and promote native species establishment in abandoned citrus groves.

Furthermore, understanding how native species compete with established nonnative species in a restoration context provides important insights into the controls of native species establishment on human modified lands. For the second part of my thesis, I conducted a field experiment on a former pasture dominated by nonnative plants on Martha's Vineyard, MA to determine how manipulating soil chemical properties affects competitive interactions between native species that are targets for sandplain grassland restoration and the existing nonnative species. I compared native target species responses when grown with and without nonnative neighbors within treatments aimed at 1) reducing soil fertility with sawdust additions, 2) reducing soil pH with sulfur additions, and 3) increasing nitrogen to understand how elevated N affects native establishment within a matrix of nonnatves. Understanding these factors will provide important insights to restoring and conserving declining ecosystems on highly modified lands.

Tables

Table 1.1. Degree of success of biotic treatments for reducing nonnative species and increasing native species. + indicates success, 0 indicates no effect.

Study	**Habitat type**	**Methods**	**Degree of success (nonnative reduction)**	**Degree of success (increase in natives)**
Wilson and Gerry 1995	Formerly cultivated field to prairie, Saskatchewan Canada	Herbicide and tilling	+ tilling + herbicide	+ tilling + herbicide
Maron and Jefferies 2001	Coastal CA grassland	Mowing	NA	+
Patzelt et al. 2001	Formerly cultivated field to wet fens, Germany	Topsoil removal, hay transfer	+	+
Pywell et al . 2002	Formerly cultivated field to grasslands, UK	Shallow tilling, deep tilling, seed addition sowing with nurse crop	0 shallow tilling + deep tilling	+ seed addition 0 nurse crop
Schmalzer et al. 2002	Former citrus grove to oak-saw palmetto scrub, FL	Herbicide, transplanting natives	+	+
Bakker et al. 2003	Formerly cultivated field to prairie, Saskatchewan Canada	Herbicide, broadcasting and drilling seed	0	+ broadcasting 0 drilling
Holzel and Otte 2003	Formerly cultivated field to floodplain grasslands, Germany	Topsoil removal, hay transfer	+	+
Wilson and Partel 2003	Formerly cultivated field to prairie, Saskatchewan Canada	Herbicide, broadcasting seed	+ short term	+ herbicide + seed addition
Buisson et al. 2008	Coastal prairie, CA	Topsoil removal, transplanting natives	+	+
Buisson et al. 2006	Coastal prairie, CA	Topsoil removal, transplanting natives	+	+

Study	Habitat type	Methods	Degree of success (nonnative reduction)	Degree of success (increase in natives)
Foster et al. 2007	Tallgrass prairie, Kansas	Disturbance (mowing and raking) and sowing native seeds	NA	0 disturbance + sowing
Allison and Ausden 2004	Formerly cultivated field to heathlands, UK	Topsoil removal, hay transfer	+	+
Kiehl and Pfadenhauer 2007	Formerly cultivated field to calcareous grasslands, Germany	Topsoil removal, hay transfer	+	+
Kardol et al. 2008	Formerly cultivated field, The Netherlands	Topsoil removal, seeding	0	+
Wilson et al. 2008	Formerly cultivated field to prairie, Saskatchewan Canada	Herbicide, broadcasting and drilling seed, hay transfer	+ herbicide	0 herbicide + broadcasting + drilling 0 hay transfer
Bouressa et al. 2010	Pasture/prairie WI	Grazing, burning, grazing+burning	NA	0 grazing + burning 0 grazing+burning

Table 1.2. Degree of success of abiotic treatments for altering soils and vegetation. + indicates success, 0 indicates no effect.

Study	Habitat type and location	Method	Degree of success (effects on soil)	Degree of success (increase in natives)
Soil fertility reduction				
Wilson and Gerry 1995	Old field to mixed-grass prairie, Saskatchewan	Sawdust sprinkled on surface 0.4 kg/m2	+	0
Patzelt et al. 2001	Ex-arable fields to wet fens, Germany	Topsoil removal of 20, 40, and 60 cm	+	+
Blumenthal et al. 2003	Old agricultural field to tallgrass prairie, MN	Sucrose + sawdust various quantities tilled to 20cm	+	+
Corbin and D'Antonio 2003	Pasture to grasslands, CA	Sawdust 1.2 kg/m2 raked into ground	+	0
Holzel and Otte 2003	Ex-arable fields to floodplain grasslands, Germany	Topsoil removal of 30 and 50cm	+	+
Allison and Ausden 2004	Ex-arable fields to heathlands, UK	Topsoil removal of 25cm	+	+
Averett et al. 2004	Formerly cultivated to tallgrass prairie, OH	Sawdust 6 kg/m2 tilled into ground, broadcast seed	+	0
Eschen et al. 2007	Ex-arable fields to grassland, Switzerland and UK	Sawdust+sucrose and sawdust+woodchips at 1.1 and 0.95 kg C/m2 respectively	+	+
Kiehl and Pfadenhauer 2007	Ex-arable fields to calcareous grasslands, Germany	Topsoil removal of 40cm	+	+
Walker et al. 2007	Ex-arable fields to heathlands, UK	Topsoil removal of 45cm	+	+
Diaz et al. 2008	Ex-arable fields/ pasture to heathland, UK	Topsoil removal 20cm	+	+
Kardol et al. 2008	Ex-arable field to grassland,	Topsoil removal of 40-50cm	+	+

Study	Habitat type and location	Method	Degree of success (effects on soil)	Degree of success (increase in natives)
pH reduction				
Dunsford 1998	Ex-arable fields to heathlands, UK	Acidic peat (50% and 75% by volume) tilled into ground	+	+
Owen et al. 1999	Ex-arable fields to heathlands, UK	Elemental sulfur at 0, 1, 2, 4, 8, 10, 12 t/ha tilled into ground	+	0
		Bracken litter, tilled into ground at 0, 2, 4, 8cm depth	+	0
		Pine chippings, tilled into ground at 0, 2, 4, 8cm depths	0 lower additions + higher additions	0
Owen and Marrs 2000	Ex-arable fields to heathlands, UK	Elemental sulfur at 0, 1, 2, 4, 8, 10, 12 t/ha tilled into ground	+	+
Owen and Marrs 2001	Ex-arable fields to heathlands, UK	Elemental sulfur 0, 0.5, 1, 2, 4, and 8 t/h raked on soil surface	+	0
		Bracken litter, tilled into ground at 0, 2, 4, 10cm depths	+	+
		Various quantities of elemental sulfur + bracken litter	+	+
Allison and Ausden 2004	Ex-arable fields to heathlands, UK	Topsoil removal + bracken litter 2cm on surface and tilled	+	+
		Topsoil removal + *Pinus* chipping 2cm on surface and tilled	0	0 pH + topsoil removal
Lawson et al. 2004	Ex-arable fields to heathlands, UK	Elemental sulfur 0.36 kg/m2	+	+
Walker et al. 2007	Ex-arable fields to heathlands, UK	Elemental sulfur, 3 and 6 t/ha tilled into ground	+	+

CHAPTER TWO: BIOTIC CONSTRAINTS OUTWEIGH ABIOTIC FACTORS DURING NATIVE SPECIES ESTABLISHMENT IN FORMER AGRICULTURAL FIELDS

Introduction

Many factors can inhibit native species from successfully establishing on lands that have been highly disturbed and modified over long time periods by human agricultural activities. In some cases, native species establishment on abandoned agricultural lands is inhibited by the rapid growth of early successional nonnative species or by the persistence of nonnative species that were intentionally introduced as forage (Corbin and D'Antonio 2004c, Von Holle and Motzkin 2007). In others, legacies of previous agricultural land use such as elevated fertility or pH or the lack of propagules of native species can persist for decades after abandonment and shift modern vegetation patterns toward nonnative species (Motzkin et al. 1999). Understanding the controls of native species establishment on abandoned agricultural land is important because former agricultural lands represent a large potential land area for restoration or establishment of native species.

The constraints on native species establishment on former agricultural land can be both biotic and abiotic. There are many examples of biotic effects. For example, conversion to row-crop agriculture or pastures alters species composition and native species recruitment by depleting native seedbanks, reducing local sources of propagules, and fragmenting the landscape beyond the limit of seed dispersal (Bakker and Berendse 1999, Standish et al. 2007, Cramer et al.

2008). Even when remnant intact native communities occur near former agricultural fields, native species often do not reestablish because existing nonnative species provide few open sites for native species to establish (Standish et al. 2007). This biotic resistance is often a barrier for the establishment of native species because nonnative species are often stronger competitors under the conditions of elevated resources caused by agriculture and the long-term presence of nonnative species (D'Antonio and Vitousek 1992, Tilman et al. 1996, Corbin and D'Antonio 2004b, Ehrenfeld 2003). Additionally, biotic constraints such as litter accumulation, decreased light penetration from standing biomass (Foster 1999, Bakker et al. 2003, Wilson et al. 2004, Buisson et al. 2006, Standish et al. 2007, Buisson et al. 2008), and depletion of soil moisture (Eliason and Allen 1997) by nonnative species can cause decreased germination and seedling establishment of native species. Biotic resistance has been widely tested by investigating invasions by nonnatives into established native vegetation (Von Holle and Simberloff 2005, Maron and Marler 2008), however, fewer studies have investigated the establishment of native species into existing nonnative communities (Eliason and Allen 1997, Foster 1999, Seabloom et al. 2003b).

Abiotic legacies of land use also promote the persistence of nonnative species on abandoned agricultural lands (Kulmatiski et al. 2006, Von Holle and Motzkin 2007). Applications of soil amendments, such as fertilizers and lime to provide favorable conditions for crop and pasture species, can persist for decades after agricultural abandonment (Tilman et al. 2001, Neill et al. 2007). Tillage and additions of fertilizers increase nutrient supply and reduce heterogeneity of soil nutrients (Pywell et al. 1994, Baer et al. 2005) as well as the organic soil horizon (Neill et al. 2007). These effects are important because increased plant-available nitrogen provides nonnative species with a competitive advantage over native species, particularly in grasslands and shrublands (Daehler 2003, Corbin and D'Antonio 2004b). In addition, plants vary in their tolerance to soil pH, and pH can therefore influence composition and structure of vegetation communities. Many nonnative or weedy species thrive between pH of 5 and 7 (Grime et al. 1988), whereas many native shrubland and grassland species, for example, are adapted to acidic soils with a pH near 4 (Owen and Marrs 2000, Neill et al. 2007).

Grasslands and shrublands are threatened globally by losses to agriculture, residential development and encroachment of woody vegetation (Archer et al. 1994, Hoekstra et al. 2005). In the northeastern US, coastal sandplain grasslands occur from Long Island, NY to Cape Cod and the Islands of Massachusetts (Motzkin et al. 2002). These grasslands serve as important habitats for rare plant and animal species (Swain et al. 2001) but have been declining in area since the early 20th century because of the elimination of grazing and fire and the rapid expansion of residential development (Motzkin and Foster 2002). Sandplain grasslands are now regional targets for conservation and restoration (Foster and Motzkin 2003).

The abundance of native plant species of coastal sandplain grasslands is greatest on sandy soils with low nutrient concentrations and low water-holding capacity. This differs from conditions in lands modified by crop agriculture. Neill et al. (2007) showed that the soils in areas of the Martha’s Vineyard, MA sandplain where agriculture recently occurred have a higher pH, absence of an organic soil horizon, higher concentrations of extractable calcium and magnesium, more extractable nitrogen in the form of nitrate, and a higher organic matter than soils of sandplain grasslands and shrublands on soils that were never tilled. These soil conditions, specifically high nitrogen and elevated pH, appear favor non-native pasture species in competition with native sandplain grassland species because native species are adapted to low-fertility, acidic soils (Neill et al. 2007).

Restoring abandoned agricultural land by removing nonnative species and decreasing soil fertility has been tested widely in grassland and shrubland ecosystems (Wilson and Gerry 1995, Blumenthal et al. 2003, Corbin and D'Antonio 2004a, Eschen et al. 2007) and pH (Dunsford et al. 1998, Owen et al. 1999, Owen and Marrs 2000, Owen and Marrs 2001, Lawson et al. 2004, Diaz et al. 2008). Some of these treatments, such as addition of carbon, have led to mixed results (Wilson and Gerry 1995, Blumenthal et al. 2003, Corbin and D'Antonio 2004a, Eschen et al. 2007). Others, like additions of elemental sulfur and acidic plant materials to reduce soil pH have been tested in restorations of acid grasslands and heathlands in northern Europe (Owen and Marrs 2000, Owen and Marrs 2001, Lawson et al. 2004, Allison and Ausden 2004, Diaz et al. 2008), but have had limited use in restorations in the U.S. Much of this work has been done to understand how agricultural alterations affect native and nonnative species diversity and abundance (Baer et al. 2002, Walker et al. 2004, Gross et al. 2005, Elmore et al. 2006, Kulmatiski et al. 2006, Neill et al. 2007, Foster et al. 2007); however, less work has been done to understand how native species interact with existing nonnative species within these restoration treatments.

We conducted a field competition study to test the relative importance of biotic and abiotic mechanisms that affect the establishment of native sandplain grassland plant species during attempts to establish sandplain grasslands in areas of former pasture. Specifically, we tested: (1) the biotic effects of competition with existing nonnative vegetation on the germination and growth of three native plant species, and (2) the abiotic controls of soil conditions (pH and nitrogen supply) on native species germination and growth. We predicted that: (1) reducing nonnative competitors by clipping all vegetation around target species for restoration would increase the native establishment, (2) decreasing soil nitrogen with carbon (sawdust) additions and lowering soil pH with elemental sulfur additions would provide native species with a competitive advantage and increase native species establishment, and (3) raising soil nitrogen supply with nitrogen additions would have the opposite effect.

Methods

Study site and species

The experiment was located at the East Field of Herring Creek Farm (HCF) (41°21' N, 70°31' W) on Martha's Vineyard, Edgartown, MA (Figure 2.1). Herring Creek Farm is agricultural grassland that is currently maintained as a hay field. It is located on the glacial outwash plain on the southeast side of Martha's Vineyard and is adjacent to extant high-quality sandplain grassland at Katama Airfield. Mean annual temperatures range from 10-12 °C and mean annual precipitation ranges from 104-122 cm. Soils are deep, excessively drained Typic Udipsamments of the Carver and Katama Soil series with 0-3% slopes (Fletcher & Roffinoli 1986). HCF was used as pasture and occasionally cropland since the early 1900s and has been hayed pasture since about 1980. Soils have a well-defined Ap horizon indicating previous tillage (Neill et al. 2007). Soils at HCF have mean pH of 5.5, bulk density of 1.14 g/cm^3, and mean inorganic N of 4.1 μgN/g dry soil, whereas intact sandplain grasslands on Martha's Vineyard have a mean pH of 4.2, mean bulk density of 0.7 g/ cm^3, and mean extractable inorganic N of 1.1 μgN/g dry soil (Neill et al. 2007).

In 2007, we initiated an experiment at HCF to restore the former pasture to coastal sandplain grassland. Despite the location of HCF adjacent to sandplain grasslands there has been almost no recruitment of native species. At the beginning of the restoration experiment in June 2007, HCF was dominated by a mix of nonnative pasture species, the most abundant of which were sweet vernal grass (*Anthoxanthum odorata*), orchard grass (*Dactylis glomerata*), velvet grass (*Holcus lanatus*), narrow-leaved plantain (*Plantago lanceolata*), and queen-anne's lace (*Daucus carota*).

To test how native species establishment is affected by the existing non-native vegetation, we selected three native species that are targets for establishment in sandplain grassland restoration: little bluestem grass (*Schizachyrium scoparium),* butterflyweed *(Asclepias tuberosa)*, and downy goldenrod (*Solidago puberula)*. These species are typical of sandplain grasslands and have local populations near HCF from which seeds could be collected, but they occur only as scattered individuals at HCF. *S. scoparium* is a C4 perennial bunchgrass that grows on dry soils in prairies, old fields, and open woods, and it is a dominant grass species of coastal sandplain grasslands. *A. tuberosa* is a common perennial forb of sandplain grasslands that typically occurs on sandy soils in prairies and upland woods. *S. puberula* is another perennial forb that typically grows on sandy or acid soils. All species descriptions followed Gleason and Cronquist (1991). Seeds of these species were collected from natural populations within 16 km of HCF in September and October of 2008 and stored until seeding in late October.

Experimental design

We set up our competition experiment within abiotic manipulations of soils that were established as part of a larger experimental restoration experiment. The restoration experiment contained 5 × 5m plots (hereafter referred to as restoration plots) located in five replicate randomized blocks (Figure 2.1). We selected ten abiotic treatments from the larger restoration study that tested various methods of manipulating soils properties to provide more favorable conditions for native species. All restoration plots were tilled in June and August 2008 prior to application of treatments. A homogenized mix of field-collected native seed from Martha's Vineyard was added to the central 3x3 m portion of each plot in November 2008. The abiotic treatments were applied to the entire 5x5 m plot and included three levels of carbon addition (1x, 2x and 3x) in the form of sawdust to reduce soil fertility (85, 165, 210 g /m^2, added once); three levels of sulfur addition to reduce the soil pH (90, 180, 270 g S/m^2, added once); three levels of nitrogen addition in the form of urea to test competitive responses to increasing nitrogen (1.5, 3.0, 4.5 g N/m^2/yr, added annually), a control that was tilled but received no soil amendments, and an unmanipulated control that received no amendments and was not tilled. Additionally, we used unseeded control plots from the larger restoration study as a reference for our competition plots. The amendments were applied in October 2008 and were subsequently tilled into the ground. Nitrogen was added again in November 2009 by surface broadcasting in November 2009. Nitrogen additions were selected to double, triple and quadruple the average rate of atmospheric N deposition for the coastal Massachusetts region (Bowen and Valiela 2001).

Competition experiment

Within the restoration plots, we established 20 × 20 cm competition subplots that were randomly located in area outside the central 3 × 3m of the restoration plots (Figure 2.1). We used the buffer area for the competition study to ensure that our plots received the abiotic restoration treatments but were not affected by seeding treatments or data collection within the larger restoration study. Within the area outside the central 3 x 3 m of the plot there was adequate space between competition subplots established within adjacent restoration plots. The competition study was a split-plot design with the restoration treatment as the whole 5 × 5m plot level, and the competition treatment as the split-plot. Competition subplots were either clipped, in which all existing vegetation was removed, or unclipped in which vegetation was left intact. We established three replicate competition subplots for each target species within the restoration treatment plots to ensure that we would have adequate germination and seedling establishment. This design yielded a total of 18 competition subplots per restoration treatment with five replicates for a total of 990 subplots.

In November 2008, forty seeds of each species were broadcast onto the soil surface within the competition plots. We distributed the seeds as evenly as possible and covered them with a thin layer of soil. Seeding occurred within two weeks of tilling.

In the clipped plots, we cut the matrix of aboveground vegetation at ground level and removed it, leaving seedlings of target species intact. There was no initial clipping because seeds were planted into recently-tilled soil. Clipping in 2009 occurred every other week from 24 June to 9 August and again on 23 September. During 2010 plots were clipped and seedlings were counted one time per month in June and July. We did not clip any seedlings that we could not identify until they were large enough to identify at the species level.

Soil sampling

To monitor responses of soil chemical and physical properties to treatments, we collected soil samples during early July of 2009 and 2010. Two subsamples were collected from random sampling points within each 5 × 5 m restoration plot using a 10 cm-deep by 5 cm-diameter steel corer. The two subsamples were combined into one plastic zip-lock bag and immediately placed in a cooler. In the lab, the two subsamples were homogenized by hand mixing. Soil pH was determined by mixing a subsample of air-dried soil with deionized water in a 1:1 weight ratio (10 g soil: 10 mL DI water) and then read on an Orion Research Model 611 digital pH meter (Orion Research Inc., Jacksonville, FL). Extractable NO_3^- and $NH_4^\pm$ were analyzed at the Marine Biological Laboratory, Woods Hole, MA, by extracting approximately 10 g soil with a 1N KCl. Nitrate in the extracts was analyzed by Cd reduction on a Lachat 8000 Series Flow Injection Analyzer (Lachat Instruments, Loveland, CO). Ammonium in the extracts was analyzed using the phenol-hypochlorite method and read on a Cary 50 spectrophotometer (Agilent Technologies, Santa Clara, CA).

Data collection on recruitment

In 2009 we counted seedlings in each plot every other week from 24 June to 9 August and again on 23 September. In 2010 we counted seedlings one time per month in June and July. From 11 to 19 August 2010, we counted individuals of the target species and harvested biomass from each competition plot. In the unclipped plots, we cut all individuals of the seeded species at ground level and placed them into one paper bag. We also harvested all the biomass of other species, which was also clipped at ground level and placed into another paper bag. At the time of harvesting biomass, we recorded the number of individuals of the target species with flowering structures as well as number of individuals with signs of herbivory. Harvested biomass was dried at 60°C for 48 hours and weighed.

Statistical analysis

Because soil samples were collected from the center of the restoration plots, we analyzed them using a one-way ANOVA, with treatment as the main effect. Nitrate data were log transformed prior to analysis in order to meet the assumptions of ANOVA. We conducted Tukey's HSD test when we obtained significant results to determine pairwise differences among treatments.

To analyze vegetation response we analyzed each species separately and separated the analyses by experiment: N-reduction, pH-reduction, N-addition. We analyzed total plot biomass in which we summed the biomass from each subplot. We also analyzed biomass per individual in which the total plot biomass was divided by the number of individuals that were counted while harvesting biomass. All analyses for vegetation responses were conducted with MIXED procedure in SAS (SAS/STAT® 9.22 User's Guide). Treatment and clipping were the main effects, and any significant results were followed by a Tukey test.

Results

Soil response to treatments

Sawdust additions had no significant effects on plant available nitrogen (Table 2.1). Sulfur additions had no significant effect on soil extractable $NH_4^{\pm}$ concentrations (Table 2.1). Sulfur additions decreased soil extractable NO_3^- concentrations. Nitrate in the sulfur 3x treatment was significantly lower than the multi-till control (p=0.024), nitrogen 2x (p=0.009), and nitrogen 3x (p=0.009), indicating that reducing soil pH with sulfur additions had a stronger effect on available nitrogen than carbon additions. Sulfur additions had significant effects on soil pH, with the largest reduction to a pH of 3.67 in the sulfur 3x treatment. Soil pH was significantly lower in sulfur addition plots than all other treatments (Table 2.1). Each level of sulfur addition significantly lowered soil pH (Table 2.1).

Nitrogen reduction

Asclepias and *Solidago*

Sawdust addition treatments and clipping did not significantly affect total plot biomass (Table 2.2) or biomass per seedling (Table 2.3) of *Asclepias* or *Solidago*.

Schizachyrium

Plot biomass and biomass per individual (Table 2.2 and Table 2.3, respectively) for *Schizachyrium* was significantly affected by soil treatments and clipping within these treatments. Clipping significantly increased both total biomass and biomass per seedling in each N-reduction treatment (Figure 2.1a and Figure 2.1b, respectively). Within the N-reduction treatments, the tilled control, sawdust 2x, and sawdust 3x had significantly higher total biomass than the control (Figure 2.1a); however, after adjustments for multiple comparisons, there were no significant differences in biomass per seedling among N-reduction treatments (Figure 2.1b).

Nitrogen addition

Asclepias

Addition of nitrogen did not affect total *Asclepias* biomass (Table 2.2) or biomass per seedling (Table 2.3). Clipping also did not affect total biomass of *Asclepias* within the N-addition treatments (Table 2.2); however, it significantly increased the amount of biomass per seedling for *Asclepias* for each N-addition treatment (Table 2.3, Figure 2.2).

Solidago

Total plot biomass of *Solidago* was significantly affected by the N-addition treatments but not clipping (Table 2.2). Nitrogen at the highest level increased the biomass of *Solidago* compared to the control (Figure 2.3a). Biomass per seedling of *Solidago* was significantly affected by clipping and the N-addition treatments, and had a significant clipping×treatment interaction (Table 2.3). Clipping significantly increased biomass per individual in each N-addition treatment (Figure 2.3b). Additionally, the tilled control, nitrogen 2x, and nitrogen 3x treatments had significantly higher biomass per individual than the control (Figure 2.3b). For the significant interaction, we looked at differences among treatments within the clipped and the unclipped plots separately. Similar to the significant treatment effect, within the clipped plots, biomass per seedling of *Solidago* was higher in the tilled control, nitrogen 2x, and nitrogen 3x than in the control, but there were no differences among treatments in the unclipped plots.

Schizachyrium

For *Schizachyrium*, total plot biomass and biomass per seedling were significantly affected by clipping (Table 2.2 and Table 2.3, respectively); both were higher in clipped plots than unclipped plots in each N-addition treatment (Figure 2.4). Total plot biomass of *Schizachyrium* was also significantly affected by each N-addition treatment and the clipping×treatment interaction (Table 2.2). Among the N-addition treatments, the tilled control, nitrogen 1x, and nitrogen 2x had significantly higher biomass than the control (Figure 2.4a). Within the unclipped plots, total plot biomass of *Schizachyrium* was higher in the tilled control, nitrogen 2x, and nitrogen 3x than in the control, which accounts for the interaction between clipping and soil treatments; there were no differences among treatments within the clipped plots. Biomass per seedling of *Schizachyrium* also had a significant clipping×treatment interaction (Table 2.3). Within the unclipped plots, biomass per seedling was higher in the tilled control, and nitrogen 2x than in the control (Figure 2.4b).

pH reduction

Asclepias

Addition of sulfur to reduce soil pH did not have any effects on *Asclepias* biomass (Table 2.2) or biomass per seedling (Table 2.3).

Solidago

Biomass of *Solidago* was significantly affected by sulfur addition treatments, but not by clipping (Table 2.2). Adding sulfur at the highest level (3x) produced significantly more total plot biomass of *Solidago* than the control (Figure 2.5a). Biomass per seedling of *Solidago* was also significantly affected by the pH-reduction treatments, as well as by clipping (Table 2.3). Clipping aboveground competitors significantly increased biomass per seedling in each pH-reduction treatment (Figure 2.5b), and sulfur 3x produced significantly more biomass per seedling than the control (Figure 2.5b).

Schizachyrium

For *Schizachyrium*, biomass and biomass per seedling were significantly affected by clipping, soil treatment, and there was a clipping×treatment interaction (Table 2.2 and Table 2.3, respectively). Clipping significantly increased biomass and biomass per seedling in each pH-reduction treatment (Figure 2.6). Additionally, all pH-reduction treatments had significantly higher biomass than the control (Figure 2.6a). Within the unclipped plots, biomass of *Schizachyrium* was higher in all treatments compared to the control, but there were no differnces among treatments within the clipped plots. Biomass per seedling of *Schizachyrium* was higher in the sulfur 2x and sulfur 3x than the control (Figure 2.6b). Within the unclipped plots, biomass per seedling was significantly higher in sulfur 2x and sulfur 3x than the control plots (Figure 2.6b), which accounts for the significant interaction between clipping and pH reduction.

Discussion

We used three native species that are targets for restoration of coastal sandplain grasslands to test the predictions that removing nonnative competitors would increase native establishment, and decreasing plant available nitrogen and soil pH would provide natives with a competitive advantage, while increasing levels of nitrogen would inhibit native growth. For the purpose of this experiment, we consider all individuals that were harvested at the end of the second growing season to have been established. The results of our study supported our first prediction in that clipping increased biomass or biomass per individual for all species within at least one set of treatments. Our second prediction was partially supported as additions of sawdust to decrease soil fertility increased biomass in one of three species, and reducing pH with additions of sulfur increased native establishment in two of our three species. Our final prediction that additions of nitrogen would decrease establishment of native species was not supported, as two of the three species produced more biomass in the nitrogen addition treatments. Overall, our results suggest that biotic factors more strongly regulated native species establishment than abiotic factors.

Clipping the nonnative vegetation surrounding our target species had a stronger effect on increasing biomass per individual than on increasing total biomass of the target natives. Clipping the surrounding matrix of nonnatives increased biomass per individual for both *Solidago puberula* and *Schizachyrium scoparium*, and it increased total biomass for *S. scoparium*, indicating that growth and establishment of these native species is limited by aboveground competition. Removing the nonnative matrix around our target native species allows individuals to grow more, so while there may be fewer individuals, they are bigger. This is important for increasing establishment because fewer individuals can reach reproductive maturity faster. For restoration, we do want an increased number of individuals of our target species, but reproducing is more important. These results could also be explained by the fact that overall, *S. scoparium* had higher biomass than *S. puberula* or *Asclepias tuberosa*.

Nitrogen reduction

The sawdust additions had little effect on altering plant available N and native species establishment. While many studies have observed decreases in inorganic N levels in response to carbon additions (Zink and Allen 1998, Morghan and Seastedt 1999, Blumenthal et al. 2003, Averett et al. 2004, Eschen et al. 2007, Kardol et al. 2008), in our study, sawdust addition had no significant effects on plant available N. Total biomass and biomass per individual of *S. scoparium* was higher in the sawdust addition treatments compared to the control; however, this increase in biomass did not significantly differ from the tilled control, indicating that tilling alone may be driving the increase in biomass. Sawdust additions provided no measurable benefits to growth of the other native species which is similar to results found by Wilson and Gerry (1995) and Corbin and D'Antonio (2004a).

It is likely that we did not observe an effect of sawdust addition due to the large stock of organic matter in the former pasture that supplies mineralized N over time. Eschen et al. (2007) suggest that the age of existing vegetation can affect whether or not C additions alter N supply and influence vegetation because strong mycorrhizal associations may be better at providing plants with N in well-established vegetation. Hence, the fact that HCF has been maintained with pasture grasses for several decades may also have reduced the effect of sawdust additions. In either case, reducing soil N may require large amounts of repeated carbon additions that are not economically feasible. There is some evidence that sucrose plus sawdust additions have had better success on establishing natives than sawdust alone (Blumenthal et al. 2003, Eschen et al. 2007), because sucrose provides C that is more available to microorganisms, and can therefore, have more rapid and stronger effects on reducing plant available N (Blumenthal et al. 2003, Eschen et al. 2007).

Nitrogen addition

Nitrogen addition had no effects on soil NH_4^+; however, N-addition plots had elevated NO_3^- compared to all treatments except the tilled control. Within the N-addition treatments, removing competitors increased biomass per individual of *A. tuberosa*, which was the only instance where we saw a significant clipping effect for this species. Therefore, removing competitors and adding N allows each individual to add more biomass.

Adding N at the highest level increased the total biomass for *S. puberula* compared to the control, indicating that elevated soil N benefits this species. Additionally, biomass per individual was also higher in the nitrogen 2x and nitrogen 3x treatments compared to the control, but these responses did not differ from the tilled control, indicating, again, that tilling alone may have a stronger effect on the establishment of natives than altering the soils.

For *S. scoparium*, adding N in low and moderate levels increased biomass; however biomass at the highest N-addition level did not differ from the control indicating that high levels of N suppress growth. This is in accord with other N-addition experiments which find a threshold in species response, where native species performance declines after nitrogen saturation has been reached (Suding and Hobbs 2009). Likewise, even within the unclipped plots, N additions increased biomass compared to the control indicating that even when competitors remain, low levels of N addition benefit the growth of this species. Again, however, the N-addition plots did not differ from the tilled control, indicating that the disturbance caused by tilling increased the growth of this species. Seabloom et al. (2003a), however, found in a California grassland restoration that establishing natives were competitively superior to exotic annuals and found that in response to N-additions native perennials reduced the soil N more than the exotics annuals.

pH reduction

Sulfur additions at all levels had the strongest effects on native species establishment than sawdust and N-additions. Sulfur addition significantly reduced soil pH, which has also been observed in restorations of heathlands in the U.K. (Owen et al. 1999, Patzelt et al. 2001, Walker et al. 2007). In addition, sulfur addition at the highest level decreased nitrate concentrations to undetectable levels, indicating that reduction in soil pH strongly decreased nitrate concentrations (Ste-Marie and Paré 1999). Sulfur additions increased total biomass and biomass per seedling for both *S. puberula* and *S. scoparium*, but not *A. tuberosa*. For *S. scoparium,* even within the unclipped plots, biomass and biomass per seedling increased with decreasing pH, indicating that even when competitors remain lower, pH promotes the growth of this species. Similar results have been observed in ex-arable fields in the U.K. for the restoration of heathlands in which elemental sulfur has promoted establishment of heath species such as *Calluna vulgaris* (Owen et al. 1999, Owen and Marrs 2000, Lawson et al. 2004, Diaz et al. 2008). These results support our prediction that soil pH promotes establishment of these target species. On the other hand, sulfur additions did not benefit *A. tuberosa* indicating that pH-reduction had different effects on the species. This suggests that it is important to understand how soil treatments for restoration will affect different target native species.

Conclusions

While we did observe a number of significant treatment effects as compared to the unmanipulated control, none of the soil treatment effects differed significantly from the tilled control. All treatments except the unmanipulated control were tilled twice prior to the application of treatments and seeding. *S. scoparium* and *S. puberula* total biomass and biomass per individual was reduced in the unmanipulated control compared to all treatments, suggesting that tilling created open microsites that promoted germination and growth of these native species, which has been demonstrated in other locations (D'Antonio and Vitousek 1992, Wilson and Gerry 1995, Corbin et al. 2004, Corbin and D'Antonio 2004a). Tilling removes the litter layer which may be an important factor that limits germination because of reduced light penetration (Eliason and Allen 1997, Foster 1999). In a similar study, plant litter significantly decreased establishment of *S. scoparium* (Foster 1999). Because there were no significant differences between the tilled control, which received no soil amendments, and all other treatments, soil conditions were suitable for germination of *S. scoparium* and *S. puberula* when litter was removed. *Asclepias tuberosa*, on the other hand, was not affected by the soil treatments, and a litter layer may have facilitated establishment of *A. tuberosa* by regulating soil moisture and preventing desiccation. Similarly, Suding and Goldberg (1999) found that at higher productivity sites, vegetation and litter facilitated seedling emergence and growth.

Because clipping and tilling had stronger effects on increasing biomass of the target natives than the soil amendment treatments, we conclude that biotic land-use legacies are a stronger barrier than abiotic legacies for native species establishment in abandoned agricultural lands. However, although biomass of plants in the soil amendment plots did not significantly differ from the tilled control, there were a number of trends for target species response to soil amendment treatments. Specifically, biomass of *S.puberula* and *S. scoparium* was higher in sulfur addition treatments than the tilled control. This effect might have become stronger, and potentially and significant, over a longer timeframe; thus, soil amendments should be considered, in addition to nonnative removal, as a restoration method.

Implications

These results provide several important insights into the drivers of native plant establishment in nonnative-dominated abandoned agricultural fields and have practical implications for native species restoration in these ecosystems that are common targets for native species restoration. First, our finding that both clipping and soil treatments had different effects on different target species indicate that target species composition and species response to treatments must be considered prior to deciding on restoration methods. Second, the biotic controls on growth and establishment were much stronger than abiotic controls. Removing nonnative biomass surrounding the target natives significantly increased biomass of all native species in at least one set of soil treatments. In addition, opening microsites for establishment by tilling had a stronger effect on establishment than all of the abiotic soil treatments. The clear implication for restoration of native species into old agricultural fields is that eliminating the existing nonnative vegetation is critical and more important for successful short-term native species establishment than attempts to undo the changes to pH and higher N supply that are the soil chemical legacy of past agricultural activity. Third, while many studies have shown that reducing soil fertility is necessary to reduce nonnative abundance and increase native abundance (Blumenthal et al. 2003, Eschen et al. 2007), our results supported findings that lowering soil pH was more important for increasing establishment of native species in acid grasslands (Dunsford et al. 1998, Owen et al. 1999, Owen and Marrs 2000, Owen and Marrs 2001, Lawson et al. 2004, Diaz et al. 2008). Additions of sulfur deserve more attention as a restoration tool where establishment of acid-tolerant native plants is the management goal, though potentially of secondary importance to the control of nonnative vegetation during native plant establishment.

Tables

Table 2.1. Average (± s.e) soil chemical parameters by treatment in July 2010. Different letters represent significant differences per parameter based on Tukey's HSD.

Treatment	**NH4**	**NO3**	**pH**
Control	3.01 ± 0.66 a	0.06 ± 0.01 ab	6.45 ± 0.10 a
Control - MT	3.91 ± 0.57 a	**0.25 ± 0.10 a**	6.31 ± 0.16 a
Nitrogen 1x	3.15 ± 0.43 a	0.17 ± 0.07 ab	6.41 ± 0.06 a
Nitrogen 2x	4.16 ± 0.69 a	**0.26 ± 0.07 a**	6.25 ± 0.08 a
Nitrogen 3x	3.34 ± 0.58 a	**0.28 ± 0.10 a**	6.29 ± 0.15 a
Sawdust 1x	3.25 ± 0.40 a	0.07 ± 0.02 ab	6.27 ± 0.06 a
Sawdust 2x	3.39 ± 0.50 a	0.18 ± 0.11 ab	6.30 ± 0.13 a
Sawdust 3x	3.19 ± 0.28 a	0.18 ± 0.06 ab	6.51 ± 0.09 a
Sulfur 1x	2.47 ± 0.39 a	0.08 ± 0.04 ab	**5.33 ± 0.18 b**
Sulfur 2x	2.02 ± 0.42 a	0.03 ± 0.02 ab	**4.64 ± 0.20 c**
Sulfur 3x	2.17 ± 0.37 a	**0 ± 0 b**	**3.67 ± 0.18 d**

Table 2.2. Results for total biomass, by species. ‘N-reduction’ indicates carbon addition treatments in the form of sawdust, N-addition indicates nitrogen addition in the form of urea, and pH-reduction indicates sulfur addition. ‘Clipping’ refers to the surrounding vegetation removal treatment. Bold values indicate significant effects.

Source	N-reduction		N-addition		pH-reduction	
	F-value	**p-value**	**F-value**	**p-value**	**F-value**	**p-value**
Asclepias						
Treatment	$F_{4,16}$= 0.51	0.7322	F4,16=0.56	0.6918	F4,16=1.25	0.3313
Clipping	F1,4= 0.95	0.3845	F1,4= 2.4	0.196	F1,4= 0.48	0.5251
Treatment x Clipping	F4,16=0.58	0.6818	F4,16=1.86	0.1668	F4,16=1.43	0.2695
Schizachyrium						
Treatment	**F4,16=8.59**	**0.0007**	**F4,16=4.44**	**0.0133**	**F4,16=12.53**	**<.0001**
Clipping	**F1,4= 17.57**	**0.0138**	**F1,4= 9.34**	**0.0378**	**F1,4= 15.42**	**0.0172**
Treatment x Clipping	F4,16=2.18	0.1171	**F4,16=3.7**	**0.0257**	**F4,16=5.34**	**0.0063**
Solidago						
Treatment	F4,16=2.47	0.0865	**F4,16=3.49**	**0.0312**	**F4,16=4.58**	**0.0118**
Clipping	F1,4= 0.24	0.6508	F1,4= 1.43	0.2978	F1,4= 3.67	0.128
Treatment x Clipping	F4,16=0.89	0.4902	F4,16=2.51	0.0832	F4,16=0.87	0.5049

Table 2.3. Results for biomass per individual, by species. Bold values indicate significant effects.

Source	N-reduction		N-addition		pH-reduction	
	F-value	**p-value**	**F-value**	**p-value**	**F-value**	**p-value**
Asclepias						
Treatment	$F_{4,16}= 0.59$	0.6772	$F_{4,16}= 0.43$	0.7832	$F_{4,16}= 1.38$	0.2863
Clipping	$F_{1,4}= 2.14$	0.217	**$F_{1,4}=12.42$**	**0.0244**	$F_{1,4}=5.11$	0.0867
Treatment x Clipping	$F_{4,16}= 0.78$	0.5544	$F_{4,16}= 2.03$	0.1386	$F_{4,16}= 1.38$	0.2857
Schizachyrium						
Treatment	**$F_{4,16}= 3.6$**	**0.0283**	$F_{4,16}= 2.05$	0.1356	**$F_{4,16}= 4.56$**	**0.012**
Clipping	**$F_{1,4}=33.08$**	**0.0045**	**$F_{1,4}=20.46$**	**0.0106**	**$F_{1,4}=26.79$**	**0.0066**
Treatment x Clipping	$F_{4,16}= 2.91$	0.0551	**$F_{4,16}= 4.71$**	**0.0105**	**$F_{4,16}= 4.21$**	**0.0162**
Solidago						
Treatment	$F_{4,16}= 2.2$	0.1153	**$F_{4,16}= 6.93$**	**0.002**	**$F_{4,16}= 5.11$**	**0.0076**
Clipping	$F_{1,4}=0.66$	0.4632	**$F_{1,4}=4.74$**	**0.0952**	**$F_{1,4}=5.62$**	**0.0768**
Treatment x Clipping	$F_{4,16}= 0.75$	0.5736	**$F_{4,16}= 4.85$**	**0.0094**	$F_{4,16}= 1$	0.4373

Figures

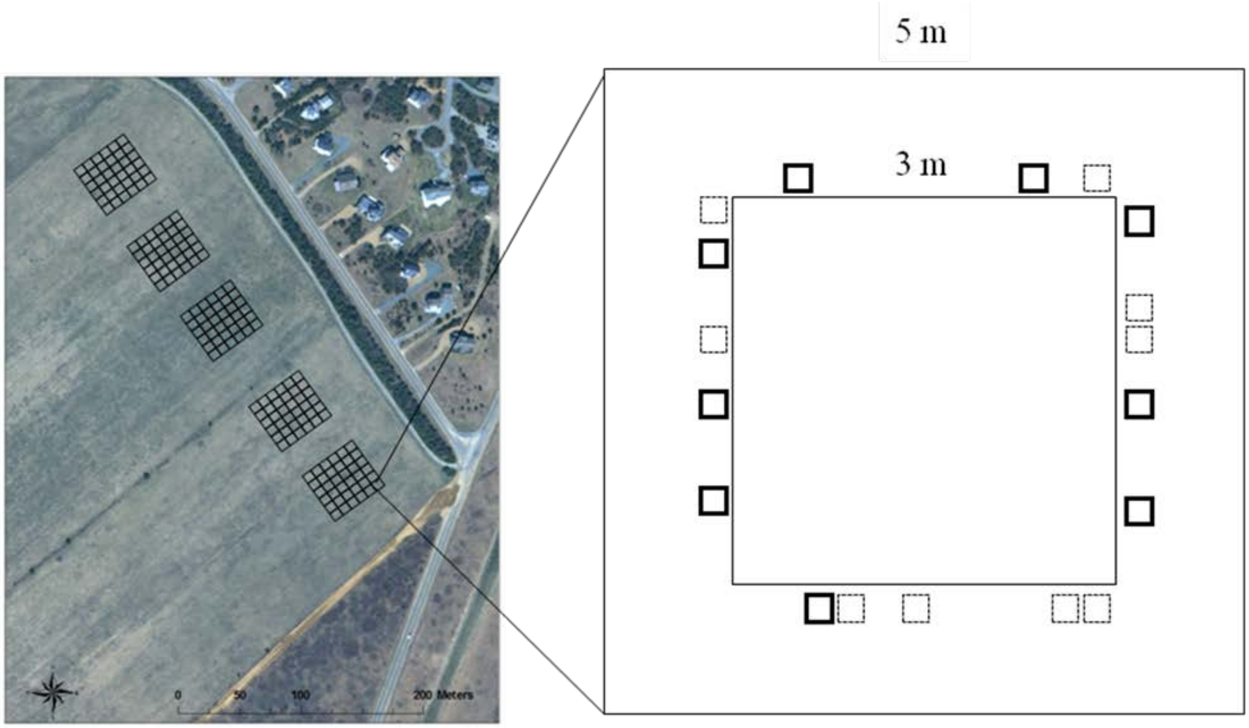

Figure 2.1. Layout of the experimental design at Herring Creek Farm. The restoration experiment was a randomized block design with 5 replicate blocks. The competition study occurred in eleven of the restoration treatments. Within each 5 × 5 m restoration plot we randomly placed 18 20 × 20 cm competition plots in the buffer area outside of the 3 × 3 m plot where data for the restoration was collected. Three replicate competition plots were randomly assigned to one of three native species and were randomly selected to be clipped (dashed) or unclipped (bold).

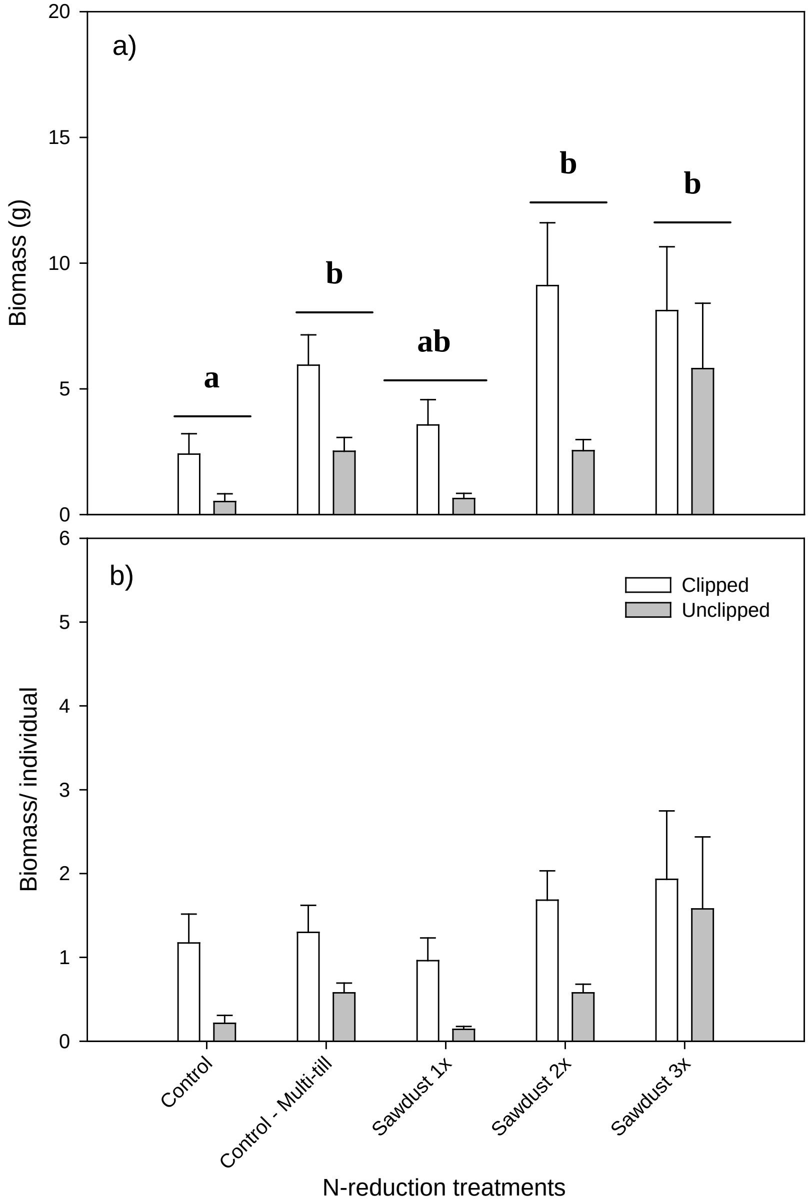

Figure 2.2. Response of a) biomass and b) biomass/ individual for *Schizachyrium scoparium* in the N-reduction (sawdust) treatments. Different letters indicate significant differences among treatments. In both a) and b) clipped plots had significantly higher biomass and biomass per individual than unclipped plots.

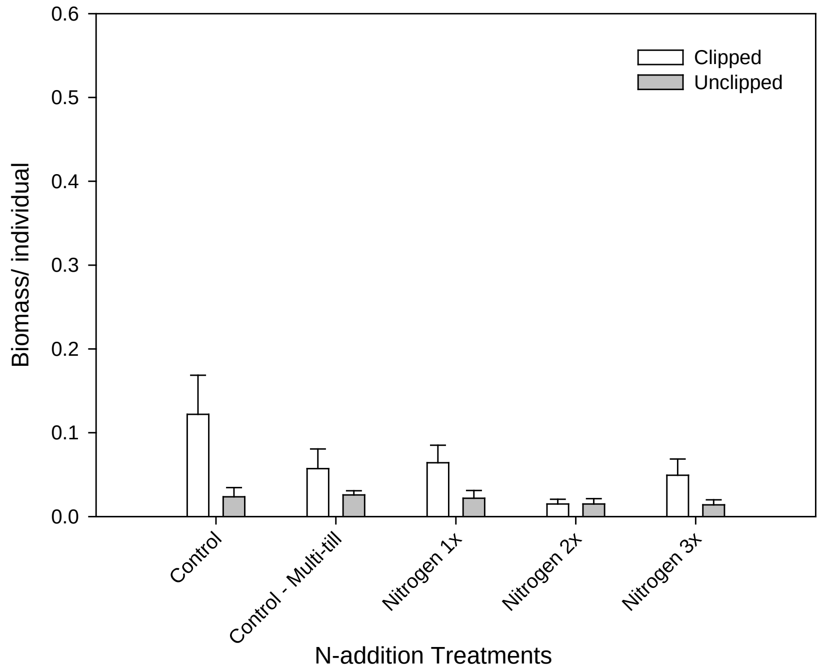

Figure 2.3. Biomass per individual for *Asclepias tuberosa* within N-addition treatments. Overall, clipped plots had significantly higher biomass/individual than unclipped plots.

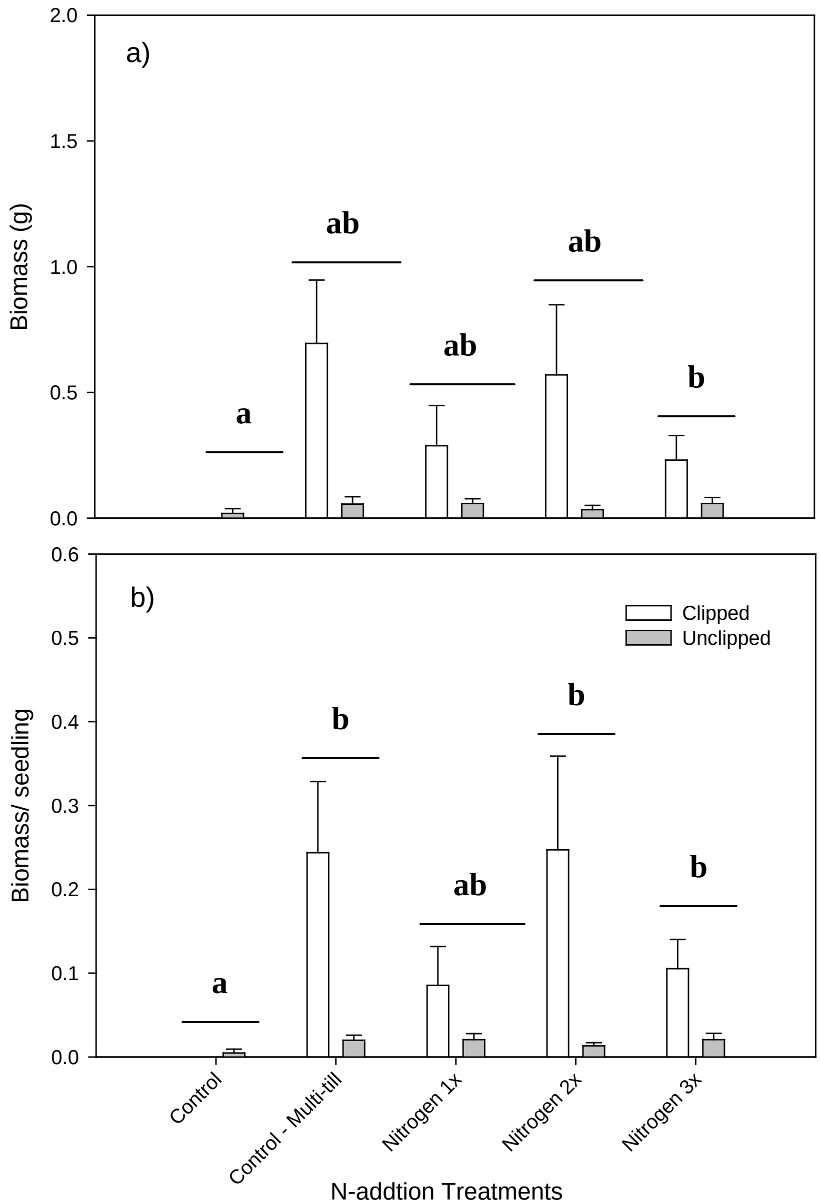

Figure 2.4. Response of a) biomass and b) biomass/ individual for *Solidago puberula* in the N-addition treatments. Different letters indicate significant differences among treatments. In b) clipped plots had significantly higher biomass and biomass per individual than unclipped plots.

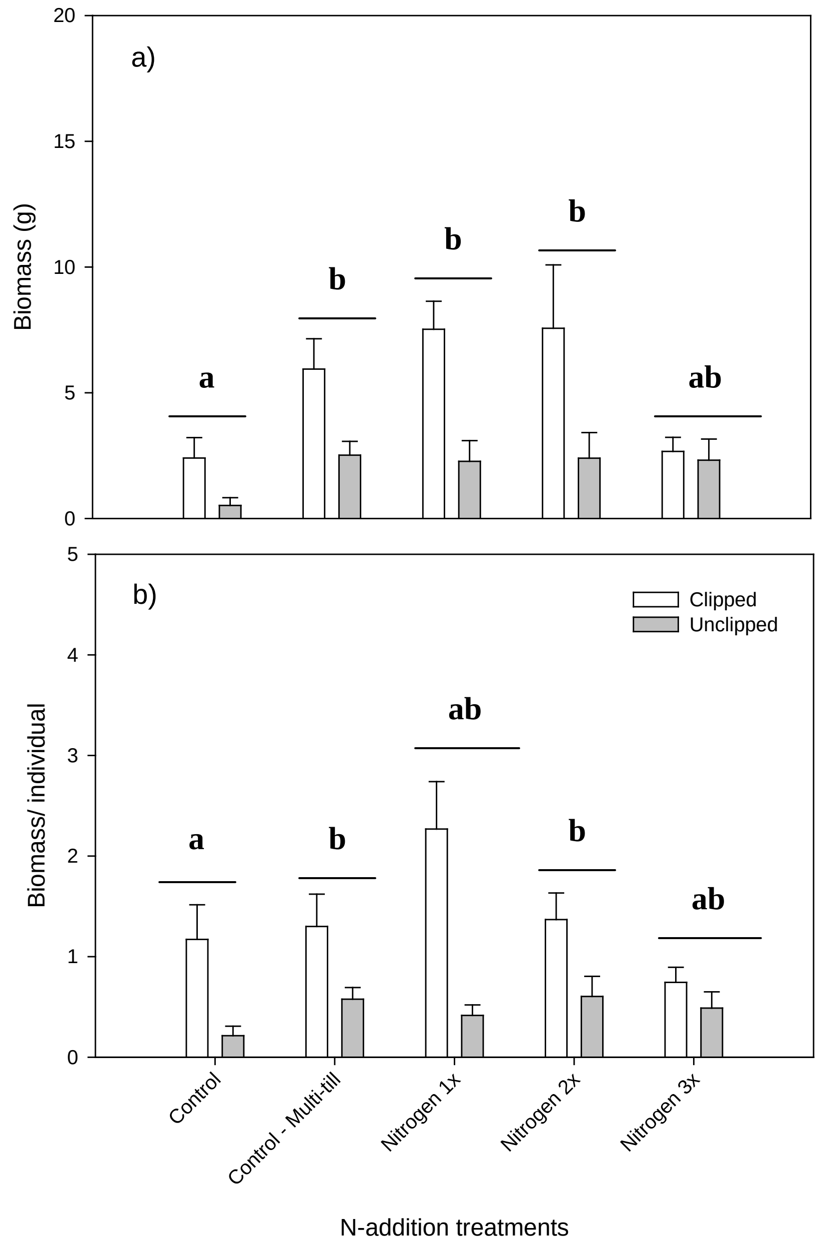

Figure 2.5. Response of a) biomass and b) biomass/ individual for *Schizachyrium scoparium* in the N-addition treatments. Different letters indicate significant differences among treatments. In both a) and b) clipped plots had significantly higher biomass and biomass per, respectively, individual than unclipped plots.

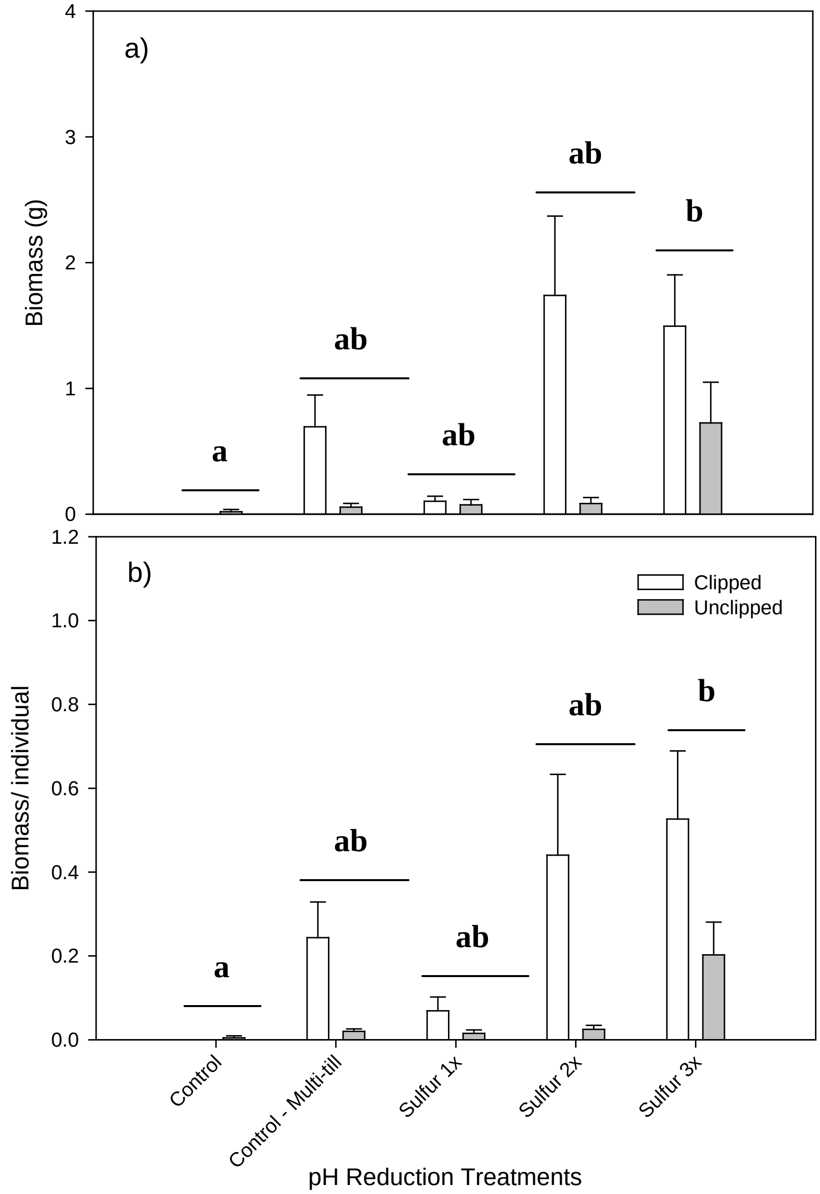

Figure 2.6. Response of a) biomass and b) biomass/ individual for *Solidago puberula* in the pH-reduction treatments (sulfur addition). Different letters indicate significant differences among treatments. In b) clipped plots had significantly higher biomass and biomass per individual than unclipped plots.

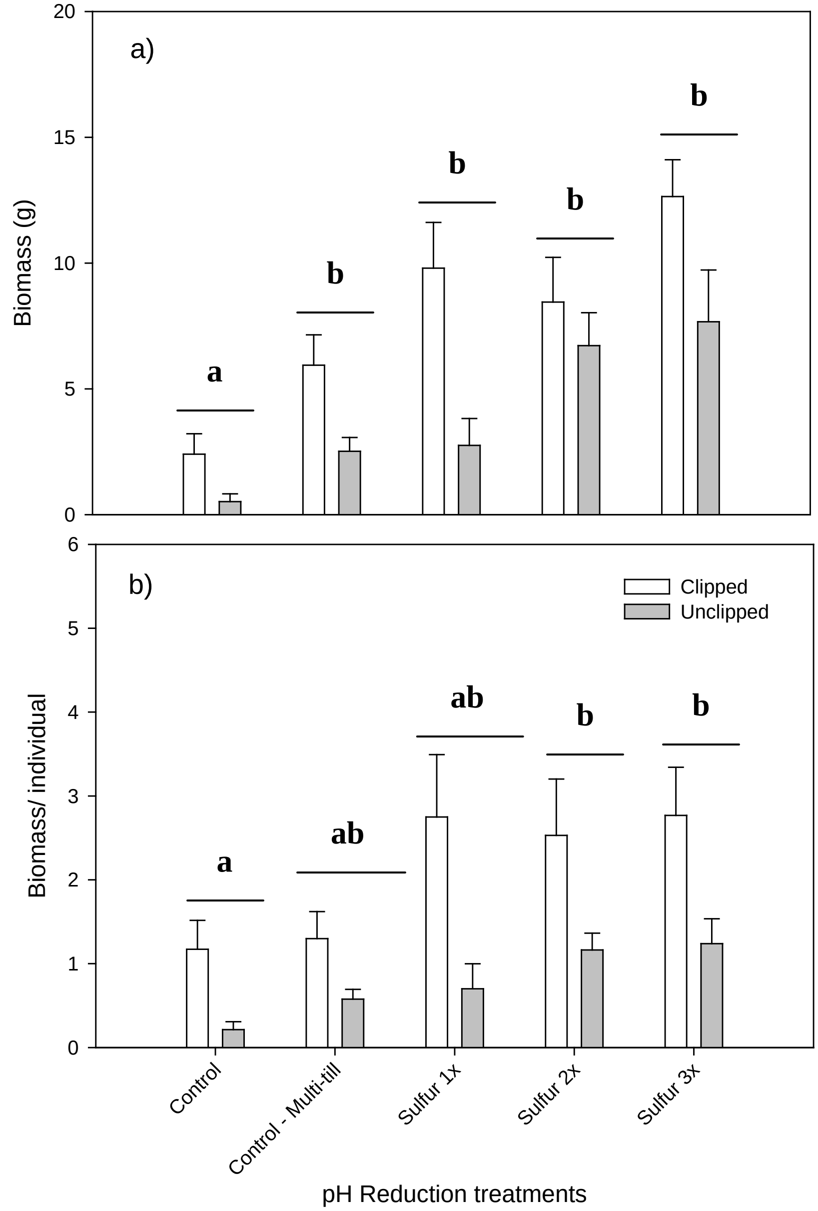

Figure 2.7. Response of a) biomass and b) biomass/ individual for *Schizachyrium scoparium* in the pH-reduction treatments (sulfur additions). Different letters indicate significant differences among treatments. In both a) and b) clipped plots had significantly higher biomass and biomass per, respectively, individual than unclipped plots.

CHAPTER THREE: RESTORING ABANDONED CITRUS GROVES: REDUCING BIOTIC AND ABIOTIC BARRIERS TO NATIVE PLANT ESTABLISHMENT

Introduction

Land-use history is one of the most important factors controlling modern vegetation patterns (Foster et al. 2003). Agricultural land use is known to leave legacies that can persist for decades to even centuries after agriculture ceases (Dupouey et al. 2002, Foster et al. 2003). These land-use legacies, such as alterations to natural disturbance regimes (Motzkin et al. 1999), lack of native species recruitment due to clearing native vegetation for agriculture, and highly modified soils from agricultural amendments (Bakker & Berendse 1999) can promote invasions by non-native species on abandoned agricultural lands and limit native species reestablishment. Even when abandoned agricultural lands are surrounded by intact native communities there is often little native species recruitment (Standish et al. 2007) and invasive non-natives often quickly colonize and become dominant. Understanding how to overcome legacies that promote invasions will have important implications for restoration of vast areas of abandoned agricultural land.

In Florida, citrus agriculture has been abandoned across the state since the 1980s due to diseases such as canker (Gottwalt et al. 2001) and citrus greening (Halbert and Manjunath 2001), freezing events (Schmalzer et al. 2002), and socioeconomic changes (Myers et al. 1990). When groves are abandoned and left to fallow, they rapidly become invaded by non-native species and there is little native recruitment even when intact communities are present nearby (Schmalzer et al. 2002). Many citrus groves were historically scrub or sandhill habitat prior to conversion to citrus. These habitats are now threatened by further loss to development and agriculture, and alterations of natural fire regimes. Florida scrub, for example, is a biodiversity hotspot comprised of pyrogenic native plant communities that provide critical habitat for several endemic species (Myers et al. 1990, Myers et al. 2000). Remaining scrub is a high priority for conservation, and abandoned citrus groves in this region provide opportunities for restoration of this habitat.

Management of invasive species on abandoned agricultural lands, such as abandoned citrus groves, is often aimed at eradication via chemical or mechanical methods (DiTomaso 2000) and often only targets individual invaders (Hobbs and Humphries 1995). Such efforts are often costly, ineffective, and may have non-target effects on native species (Zavaleta et al. 2001). Restoration to native species communities may be an effective method to provide long-term control of invasive species, in addition to providing habitat for native species, including threatened and endangered species. Removal of invasive species is merely the first step in the restoration of an ecosystem after agricultural abandonment. Additional edaphic restoration to counteract or reverse the effects of agriculture on soil properties may be required to successfully remove invasive species and restore native plant communities (Blumenthal et al. 2003).

Methods to reduce soil fertility and soil pH have been tested using a variety of treatments in highly invaded, abandoned agricultural fields (Owen et al. 1999, Blumenthal et al. 2003, Eschen et al. 2007). Carbon additions, for example, have been used widely to promote nitrogen immobilization, reducing soil nitrogen fertility, which is expected to decrease non-native species and promote native species (Blumenthal et al. 2003, Corbin & D'Antonio 2004). Similarly, additions of elemental sulfur to soils have been used to decrease soil pH on lands that would have naturally low pH, but currently have elevated pH because of amendments with lime when the soil was in agriculture (Owen et al. 1999, Lawson et al. 2004). Reducing elevated soil pH has successfully increased the competitiveness of native species that are adapted to low pH (Owen et al. 1999, Lawson et al. 2004). Most of the literature on restoration of soil chemical properties occurs in temperate or Mediterranean grassland systems that have had relatively low-intensity agriculture such as grazing and cereal crops (Wilson and Gerry 1995, Blumenthal et al. 2003, Corbin and D'Antonio 2004, Eschen et al. 2007, Kardol et al. 2008). These methods have not been tested in the subtropics, and specifically in abandoned citrus groves which have highly modified soil conditions resulting from tilling and intensive nutrient and pesticide additions.

We conducted a field restoration experiment in highly invaded former citrus groves. We tested how soil fertility and pH reduction combined with different methods to reduce non-native species affected native and non-native species abundance. Specifically, our objectives for this experiment were to: (1) determine how different methods to reduce non-native species would affect non-native and native species abundance, and (2) determine if decreasing soil pH and plant-available N would decrease non-native species abundance and increase native species abundance.

Methods

Study site

We conducted our study in two abandoned citrus groves at Merritt Island National Wildlife Refuge (MINWR). MINWR is a 57,000 ha barrier island complex in east-central Brevard County, Florida (latitude 28°43', longitude 80°45). Elevation at MINWR ranges from sea level to 3 m on inland ridges. These ridges consist of oak-saw palmetto scrub vegetation, where soils are acid, low in nutrients and excessively well-drained (Schmalzer and Hinkle 1992). Annual precipitation averages 131 cm and ranges from 5.6 cm (January) to 20.22 cm (September) with high inter-annual variability. Mean maximum daily temperatures are 22.3°C for January and 33.3°C for July, and mean minimum daily temperatures are 9.6°C for January and 21.8°C in July (Schmalzer and Hinkle 1992).

Citrus agriculture was established at MINWR between 1958 and 1965 (Schmalzer et al. 2002), and was abandoned beginning in 1987 after a series of freezes. Citrus groves in this region were heavily fertilized, limed, sprayed with pesticides, and planted with non-native grasses such as *Paspalum notatum* (bahiagrass) as ground cover between rows of trees to prevent erosion (F. Adrian 2010, Merritt Island National Wildlife Refuge, Titusville, FL, personal communication).

The two groves are separated by 3.3 km and will be referred to hereafter as the "north site" and the "south site". Soils at the north site are of the Paola Fine Sand and the Candler Fine Sand series with 0-5% slopes. Soil pH at this site is 5.91±0.30 and total extractable-N is

3.03±1.51 ugN/ g dry soil. The citrus trees were not removed after abandonment, and still remain in the ground. The grove has been invaded by the non-native grasses *Panicum maximum* (guineagrass), *Rhynchelytrum repens* (natalgrass), and *Paspalum notatum*. There are also several ruderal native species such as *Sabal palmetto* (cabbage palm), *Smilax auriculata* (greenbriar), and *Physalis walterii* (ground cherry). Since abandonment, the north site has been sprayed with herbicide and burned several times to control invasive grasses. Several gopher tortoise burrows occurred throughout the north site, and a substantial amount of soil disturbance was caused by heavy machinery. We did not place experimental plots where soil disturbance was evident.

Soils at the south site were from the Cocoa Sand series with 0-5% slopes. Soil pH in this grove is 6.94±0.10 and total extractable-N is 3.40±0.49 ugN/ g dry soil. Citrus trees in the south site were cleared and burned in 2006, and since then management of the grove has included annual herbiciding, prescribed fires, and disking to control weedy, invasive species. Vegetation at the south site is dominated by non-native grasses *Cynodon dactylon* (bermudagrass), *P. maximum* and *R. repens*, and ruderal natives such as *Ambrosia aretmisiifolia* (ragweed), *Galactia elliotii* (Elliot's milk pea), and *P. walteri*.

Experimental design

We established a split-plot experiment to test the most effective methods for decreasing non-native species and increasing natives by: 1) physically removing non-natives, and 2) manipulating soil chemical properties. We randomly placed six replicate 20 x 20-m blocks within each grove, and each block was separated by at least 20-m. Within each block, we established sixteen 5 x 5-m plots, for a total of 192 plots. Because *Sus scrofa* (feral pigs) are a pest species at MINWR and have caused damage during previous restoration attempts (Schmlazer et al. 2002), we installed fences around three randomly selected blocks in each grove to test how pigs affected our restoration treatments. Fences were trenched six inches into the ground and were four feet high. Unfenced plots were also trenched to provide similar disturbance around the blocks associated with building the fences.

Prior to applications of treatments, we mowed all blocks at the south site and raked out the vegetation. At the north site we removed all herbaceous vegetation, orange trees, and small to medium cabbage palms (greater than 15-cm dbh) from plots using a chainsaw and loppers or shears. Larger cabbage palms that we were unable to remove with a chainsaw were left in the plots and we clipped off all branches to minimize shading. There were no trees greater than 30-cm dbh in any of the plots.

Treatments

In each of the 16, 5 x 5-m plots in each block, we randomly assigned one of 16 treatments for a full factorial design. We employed one of four biomass removal (hereafter referred to as **biotic**) treatments to every plot: 1) black plastic to kill aboveground vegetation, 2) tilling to kill above and belowground vegetation, 3) topsoil removal to kill above and belowground vegetation and to remove the soil seed bank, and 4) control (no manipulations). These treatments were combined with one of four soil manipulation (hereafter referred to as **abiotic**) treatments: 1) addition of carbon (sawdust) to reduce soil fertility, 2) addition of elemental sulfur to reduce soil pH, 3) addition of sulfur+carbon, 4) no manipulation. Due to a timing conflict of the black plastic applications with the other treatments, these results were not included in the analyses and will not be discussed further.

To determine the amount of carbon to add, we calculated the amount of labile C in the plots and determined that adding 56 g/m^2 of carbon would decrease the available N to target levels. Sawdust was obtained from a local landscape supplier (Sunrise Landscape Supply Inc., Orlando, FL) and was comprised of local pine. The target soil pH for our restoration treatments was based on native scrub reference sites located near the groves that have an average pH of 4.84±0.20, which were comprised of the same soil series as the respective groves. To determine the amount of sulfur to add to reach the target soil pH, we used a soil amendment reference (Clemson University, 2009). We applied 92 g/m^2 and 180 g/m^2 of sulfur to the north and south sites, respectively.

Treatments at the south site were applied from 3 May to 8 May, 2009. In the tilling and topsoil removal treatments, soil was tilled with a tractor and removed with a front loader, respectively. Soil amendments were applied to the plots after the tilling/topsoil removal. The amendments were hand sprinkled evenly across each plot then raked into the soil. Treatments at the north site were performed from 18 to 21 June 2009 using the same methods.

Soil sampling

We sampled soils in both groves on September 2009 (4 months post-treatment) and April 2010 (1 year post-treatment) to record soil response to treatments. We collected 10-cm deep soil samples from a randomly placed diagonal within the inner 3 x 3-m quadrat in each plot. Each sample was homogenized by sifting through a 2-mm mesh sieve. One subsample of soil (10-11g) was extracted with 50-mL of 2M KCl for determination of extractable NH_4^+ and NO_3^-. Extracts for NH_4^+ were analyzed using the phenol-hypochlorite method on a Cary 50 Spectrophotometer (Foster City, CA, U.S.A.). The extracts for NO_3^- were analyzed by cadmium reduction on a Lachat 8000 Series Flow Injection Analyzer (Loveland, CO, U.S.A.). For analysis we summed the NO_3^- and NH_4^+ concentrations for total extractable N. Soil pH was tested in a 1:1 ratio of soil to DI water at Brookside Laboratories, Knoxville, OH.

Vegetation surveys

Within each 5 x 5-m plot, we surveyed the vegetation in the inner 3 x 3-m quadrat. This provided a buffer between the treatments to reduce edge effects. All plots were surveyed for species composition and abundance in late April 2009 prior to application of treatments. We surveyed all plots again in September 2009 (4 months post-treatment) and April 2010 (1 year post-treatment). All species were identified and placed into one of nine cover classes: R=1 individual, 1=<1%, 2=1-3%, 3=3-5%, 4=6-15%, 5=16-25%, 6=26-50%, 7=51-75%, 8=>75%.

For statistical analyses, these cover classes were converted to the midpoint of each class. Every plant species was classified by origin (native or non-native), functional group (graminoids, forbs, or shrubs), and habitat type (ruderal or scrub) based on Wunderlin (1998).

Statistical Methods

Due to strong initial site differences, we analyzed north and south sites separately. For each site, we analyzed soils, species cover, and species richness at 4 months and 1 year post-treatment to determine short and long-term effects of our restoration treatments. In the north site, one of the fences was stolen and pigs entered the block; therefore, these plots were eliminated from the analysis. We analyzed species cover data and soil responses using the MIXED procedure in SAS (SAS/STAT® 9.22 User's Guide). This method of computing degrees of freedom and model fitting matches the ANOVA results for a balanced split-plot design with the main plot consisting of a one-way factorial design (fencing) and the subplot consisting of a two-way factorial design (biotic and abiotic). All data were transformed as necessary prior to analysis to meet assumptions of normally distributed residuals and homogeneity of variance.

Because species richness was count data and could be considered Poisson distributed, we analyzed those responses using the GLIMMIX procedure in SAS (SAS/STAT® 9.22 User's Guide). This procedure allows for the analysis of mixed models for non-normal data. When we obtained significant results, differences among treatments were determined with Least Square Means and Bonferroni corrections were made when appropriate.

Results

Soils

In the north site, 4 months post-treatment, there was a significant biotic treatment effect on soil pH (Table 3.1); pH was significantly lower in the topsoil removal than in the control plots (Figure 3.1). This biotic effect on pH remained 1 year post-treatment.

There were significant abiotic treatment effects in the north site 4 months post-treatment (Table 3.1). Adding sulfur+carbon significantly lowered pH relative to control and carbon addition (Figure 3.2A); this effect remained 1 year post-treatment (Table 3.1, Figure 3.2B). Additionally, 1 year post-treatment sulfur addition had significantly lower pH than control and carbon addition (Figure 3.2B).

In the south site 4 months post-treatment, there was a significant abiotic main effect, biotic×abiotic interaction, and a significant three-way interaction (Table 3.1). For the abiotic effect, the pH in the sulfur and sulfur+carbon treatments was significantly lower than the control and carbon treatments (Figure 3.3). In the south site 1 year post-treatment the significant abiotic treatments effects remained (Table 3.1).

Given the significance of the fencing×biotic×abiotic interaction, a separate analysis was run for fenced and unfenced plots. For fenced plots there was a significant abiotic main effect ($F_{3,22} = 9.45$, $p = 0.0003$). Control and carbon additions had significantly higher pH than sulfur and sulfur+carbon additions (Figure 3.4A). For unfenced plots there was a significant abiotic main effect and a significant biotic×abiotic interaction ($F_{3,22} = 7.12$, $p = 0.0016$ and $F_{6,22} = 3.38$, $p = 0.0162$, respectively). For the abiotic main effect the control had significantly higher pH than the sulfur and the sulfur+carbon treatments (Figure 3.4B). For the significant biotic×abiotic interaction, there were a number of significant effects; however, there does not appear to be any biological significance of these interactions.

There were no effects on soil N in the north site 4 months or 1 year post-treatment. In the south site, there was a significant biotic treatment effect on soil N ($F_{2,8}$=36.58, p<0.0001): topsoil removal significantly reduced soil N compared to the control and the tilled treatments (Figure 3.5). However, these effects were no longer seen 1 year post-treatment. There were no significant effects of abiotic treatments on soil N in the south site.

Vegetation

Species cover

There was a significant biotic treatments effect on non-native species cover 4 months post-treatment in both the north and south sites (Table 3.2). In the north site, tilling and topsoil removal significantly reduced non-native abundance compared to the control (Figure 3.6A). In the south site, topsoil removal had significantly lower non-native cover than both tilling and the control (Figure 3.6B). There were no significant differences in non-native cover 1 year post-treatment. There was no effect of biotic treatments on native cover, and abiotic treatments did not affect native or non-native species cover in either site.

For native species cover there was a significant biotic×abiotic interaction and a significant three-way interaction in the north site 1 year post-treatment (Table 3.3). Among fenced plots there were no effects for biotic or abiotic treatments; however, among unfenced plots there was a significant biotic×abiotic interaction ($F_{6,12} = 8.67$, $p = 0.0009$). In unfenced, topsoil removal plots with carbon addition, native species cover was significantly higher than all other treatments (Figure 3.7).

Species richness

There was no difference in non-native species richness among any of the treatments 4 months or 1 year post-treatment at either site. There was a significant fencing×biotic treatment effect for native richness (all of which are ruderal species) in the south site 4 months post-treatment (Table 3.4). In the fenced plots, the control had significantly lower native species richness than the topsoil removal (Figure 3.8A); however, in the unfenced plots, the control had significantly higher native species richness than the tilling and topsoil removal treatments (Figure 3.8B). These differences disappeared after 1 year.

Discussion

We tested methods that have been widely used in habitat restorations to reduce non-native species and promote native species richness and cover in abandoned citrus groves. Although the abiotic treatments of sulfur and carbon additions did significantly alter soil pH, this did not translate into significant effects on non-native or native species cover or richness. Tilling and topsoil removal decreased non-native species cover but not richness on a short-term scale, but did not affect native species richness or cover. Fencing alone had no significant effects due to the very low disturbance caused by feral pigs during the one year time frame of our experiments; however, there were several significant interactions with fencing most of which are likely a result of the location of the blocks within each site.

Abiotic treatments

Sulfur addition, both alone and when combined with carbon, significantly decreased soil pH in both groves for at least 1 year post-application, indicating that this treatment provides long-term alterations of soil pH. Sulfur additions have been highly successful in reducing non-native species cover and increasing native species on lands that are naturally acidic (Owen et al. 1999, Lawson et al. 2004). Although we reduced soil pH with our sulfur addition treatments, it did not affect native or non-native species cover or richness in the groves. Perhaps we did not apply enough sulfur to affect the vegetation, or the dominant species, such as *Panicum maximum* and *Cynodon dactylon*, may have a delayed response to decreased pH. Therefore, we may see a decrease in non-native cover in response to lower soil pH on a longer-term basis, and believe this treatment should be considered when restoring abandoned citrus groves.

Although we significantly altered soil pH, we did not affect plant available nitrogen. Carbon additions did not reduce soil fertility in our plots; however, similar results were found in prairie sites in Colorado (Morghan and Seastedt 1999). The quantity of sawdust in our experiment may have been too low and did not reach a threshold level (Blumenthal et al. 2003) to reduce plant available N. Likewise, tilling the sawdust into the ground may have provided a stronger effect, as it would have incorporated the sawdust into the soil making it more available for microorganisms, rather than only occurring on the soil surface.

Carbon addition combined with topsoil removal significantly increased native species richness in the north site unfenced plots 1 year post-treatment, however had no other effects on the vegetation. It is likely that this effect was detected in the unfenced plots but not the fenced plots as a result of losing one of the fenced replicates, leading to reduced power. However, the reason we did not see this effect in the south site as well is unclear, but perhaps may be due to site differences. Overall, carbon additions, specifically sawdust, have had mixed results in altering plant species abundance (Blumenthal et al. 2003, Corbin & D'Antonio 2004). It is likely that repeated applications or providing a longer timeframe for the sawdust to decompose and be consumed by microbes would have had a greater effect on both the soils and plants in both abandoned groves.

Biotic treatments

Our biotic treatments had a much larger effect on reducing non-native cover than altering the soils. Topsoil removal significantly reduced non-native species cover in both sites. Mechanical removal of non-natives, such as tilling and topsoil removal have successfully reduced non-native cover in a number of other studies (Wilson & Gerry 1995, Allison & Ausden 2004, Buisson et al. 2008). In our study, tilling significantly decreased non-native cover in the north site but not the south site, indicating that initial site conditions, such as present species and amount of cover, will lead to different outcomes of restoration treatments. The effects of our treatments on non-native abundance were short-lived as there were no significant differences in non-native cover 1 year after the treatments were applied. This suggests that reducing non-native species cover in this system will take time and repeated control efforts to deplete the non-native seed bank.

Native species richness was significantly higher in the topsoil removal plots than the controls in the fenced blocks in the south site; however, in the unfenced blocks, native species richness was significantly lower in the topsoil removal compared to the control, suggesting that fencing affected native species recruitment. Since there was no significant main fencing effect, and very little rooting by feral pigs, we cannot attribute this difference to animal disturbance. Rather, two of the three unfenced plots were located only 20-m apart and this may have misrepresented differences in species composition and richness across this grove.

While we used topsoil removal as a method to decrease non-native species and open sites for native establishment, it also had effects on the abiotic conditions in the groves. Topsoil removal significantly affected the fertility and pH of the soils. In the south site, topsoil removal significantly decreased total extractable-N 4 months post-treatment, but this effect did not remain 1 year post-treatment. Removing the top layer of soil has also effectively reduced soil fertility in California grasslands (Buisson et al. 2008) and heathlands in the U.K. (Walker et al. 2007). Topsoil removal reduces soil organic matter, removes soil biota, and alters the water holding capacity of soil (Kardol et al. 2008) in addition to removing above and belowground vegetation and the non-native seed bank (Buisson et al. 2008). These could be important factors in our system given the success of topsoil removal as a biotic treatment.

Tables

Table 3.1. Results of mixed model effects for soil pH 4 months and 1 year post-treatment in the north site and south site. Bold indicates significant effects.

	4 months		1 year	
Effect	***F-value***	***Pr>F***	***F-value***	***Pr>F***
North site				
Fenced	0.86	0.4215	1.40	0.3225
Biotic	**5.86**	**0.0388**	**10.28**	**0.0115**
Fenced x Biotic	2.29	0.1820	3.13	0.1170
Abiotic	**4.28**	**0.0389**	**9.78**	**0.0034**
Fenced x Biotic	0.42	0.7417	1.25	0.3490
Biotic x Abiotic	1.51	0.2325	1.20	0.3515
Fenced x Biotic x Abiotic	0.94	0.4916	1.85	0.1456
South site				
Fenced	0.32	0.6034	0.01	0.9181
Biotic	4.08	0.0600	2.80	0.1201
Fenced x Biotic	0.59	0.5785	0.38	0.6970
Abiotic	**12.14**	**0.0006**	**22.10**	**0.0001**
Fenced x Biotic	0.49	0.6940	1.04	0.4115
Biotic x Abiotic	**3.28**	**0.0168**	1.75	0.1516
Fenced x Biotic x Abiotic	**3.11**	**0.0212**	1.34	0.2778

Table 3.2. Results of mixed model effects for nonnative species cover 4 months post treatment for the north and south site. Bold indicates significant effects.

	North site		South site	
Effect	***F-value***	***Pr>F***	***F-value***	***Pr>F***
Fenced	2.48	0.2136	1.40	0.3020
Biotic	**12.04**	**0.0079**	**9.36**	**0.0080**
Fenced x Biotic	0.70	0.5315	0.26	0.7778
Abiotic	0.14	0.9360	0.61	0.6236
Fenced x Biotic	0.11	0.9507	2.03	0.1637
Biotic x Abiotic	0.68	0.6671	0.78	0.5950
Fenced x Biotic x Abiotic	0.96	0.4803	0.63	0.7056

Table 3.3. Results of mixed model effects for native species cover in the north site 1 year post-treatment. Bold values indicate significant differences.

Effect	***F-value***	***Pr>F***
Fenced	1.38	0.3246
Biotic	0.44	0.6627
Fenced x Biotic	2.16	0.1970
Abiotic	3.20	0.0767
Fenced x Biotic	1.36	0.3169
Biotic x Abiotic	**3.26**	**0.0237**
Fenced x Biotic x Abiotic	**7.53**	**0.0004**

Table 3.4. Results of mixed model effects for native species richness 4 months post-treatment for the south site. Bold values indicate significance.

Effect	***F-value***	***Pr>F***
Fenced	1.92	0.2386
Biotic	0.00	0.9973
Fenced x Biotic	**6.18**	**0.0239**
Abiotic	0.12	0.9491
Fenced x Biotic	0.72	0.5589
Biotic x Abiotic	0.15	0.9873
Fenced x Biotic x Abiotic	0.30	0.9333

<u>Figures</u>

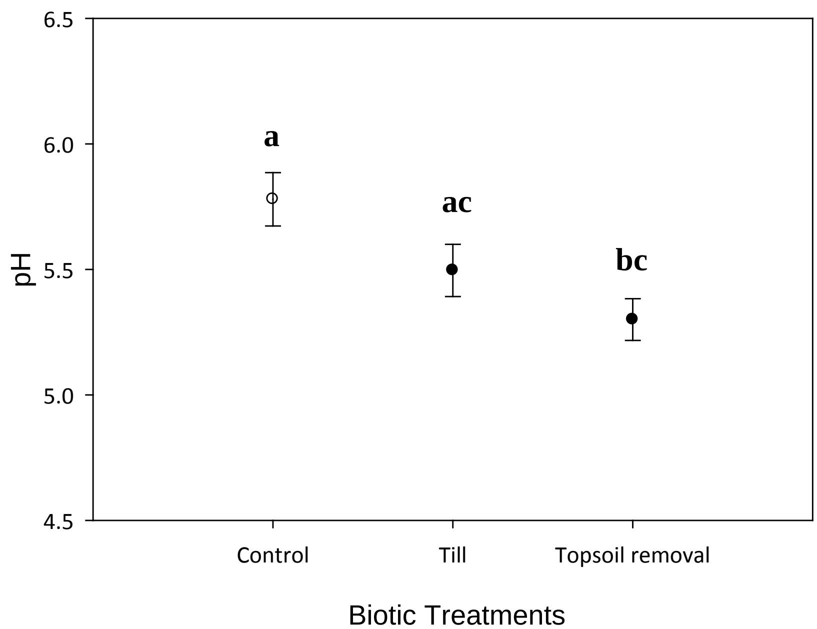

Figure 3.1. Mean pH ± se in the north site biotic treatments 4 months post treatment. Different letters indicate significant differences.

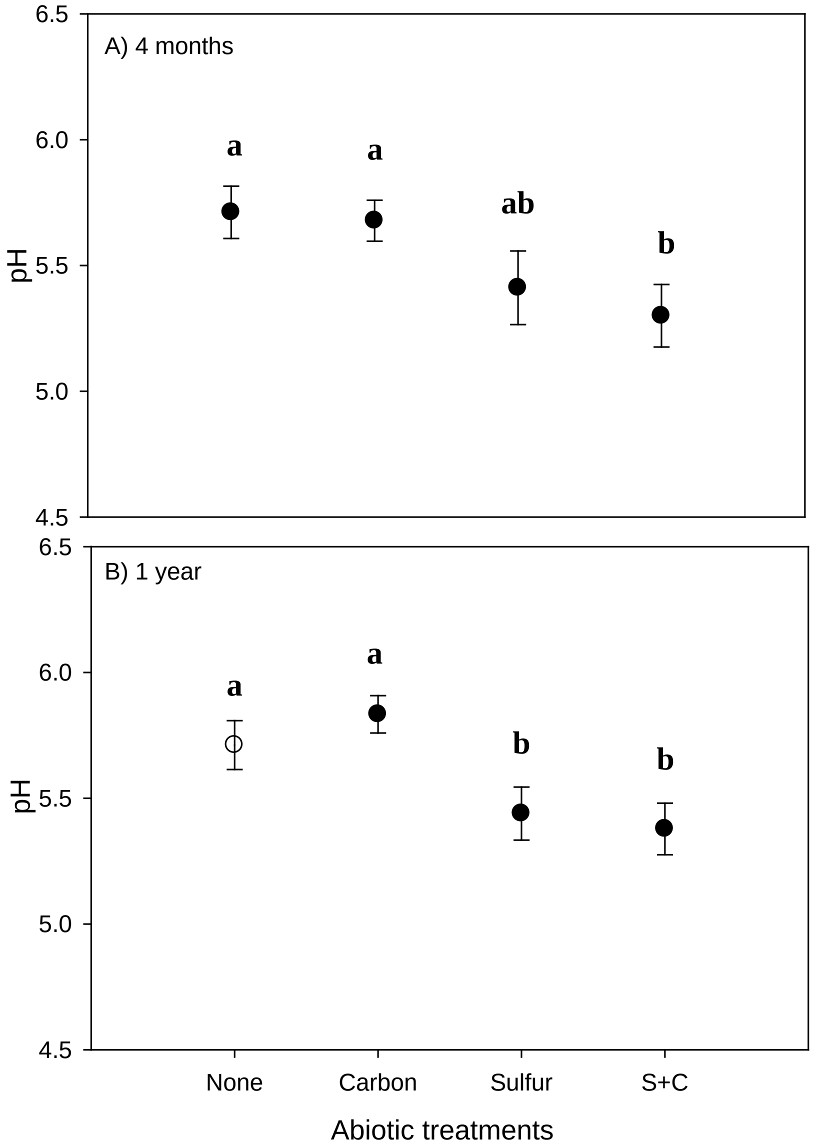

Figure 3.2. Mean pH ± se in the north site abiotic treatments A) 4 months and B) 1 year post-treatment. Different letters indicate significant differences.

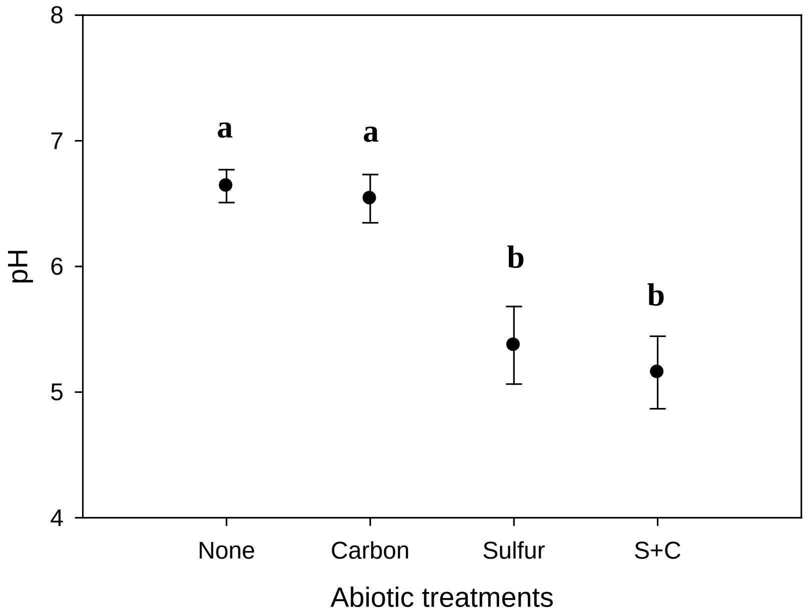

Figure 3.3. Mean pH ± se in the south site abiotic treatments 4 months post-treatment. Different letters indicate significant differences.

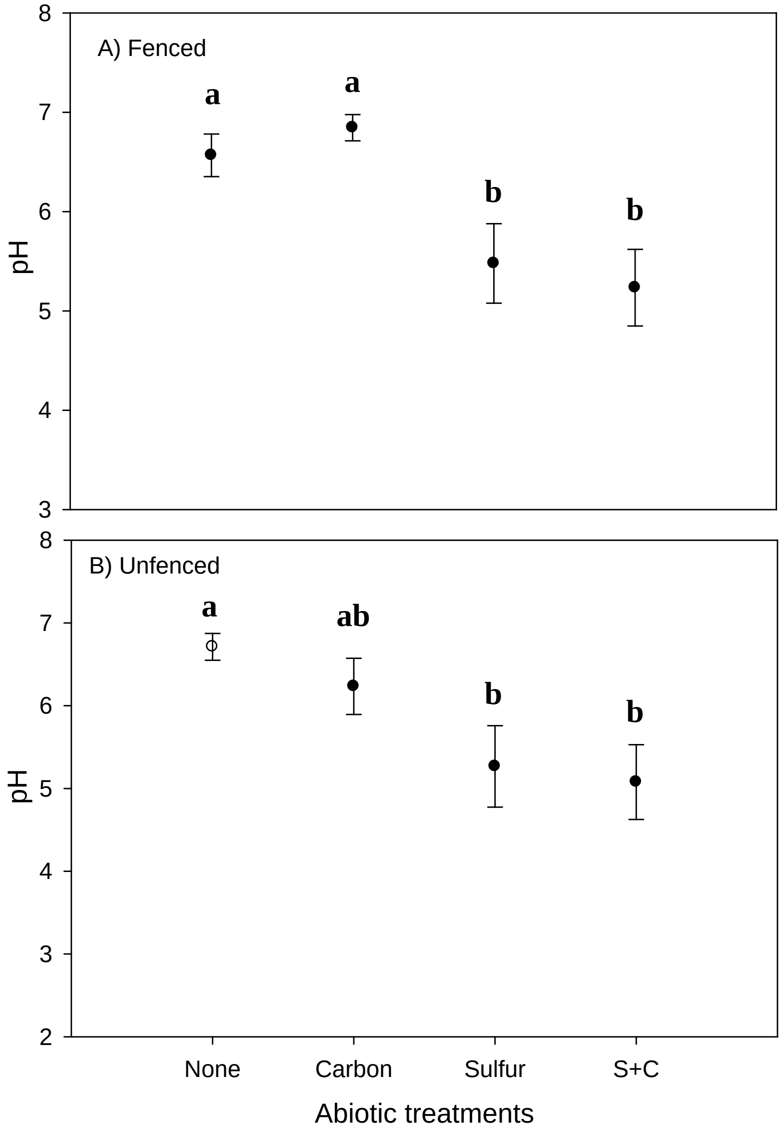

Figure 3.4. Mean pH ± se in the south site abiotic treatments 4 months post-treatment for A) fenced blocks and B) unfenced blocks. Different letters indicate significant differences.

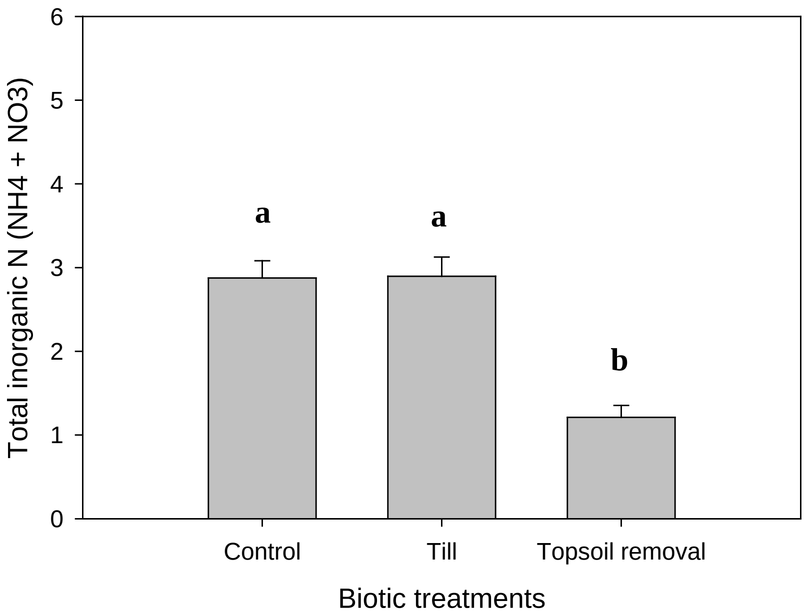

Figure 3.5. Mean total inorganic N + se in the south site 4 months post-treatment for the biotic treatments. Different letters indicate significant differences.

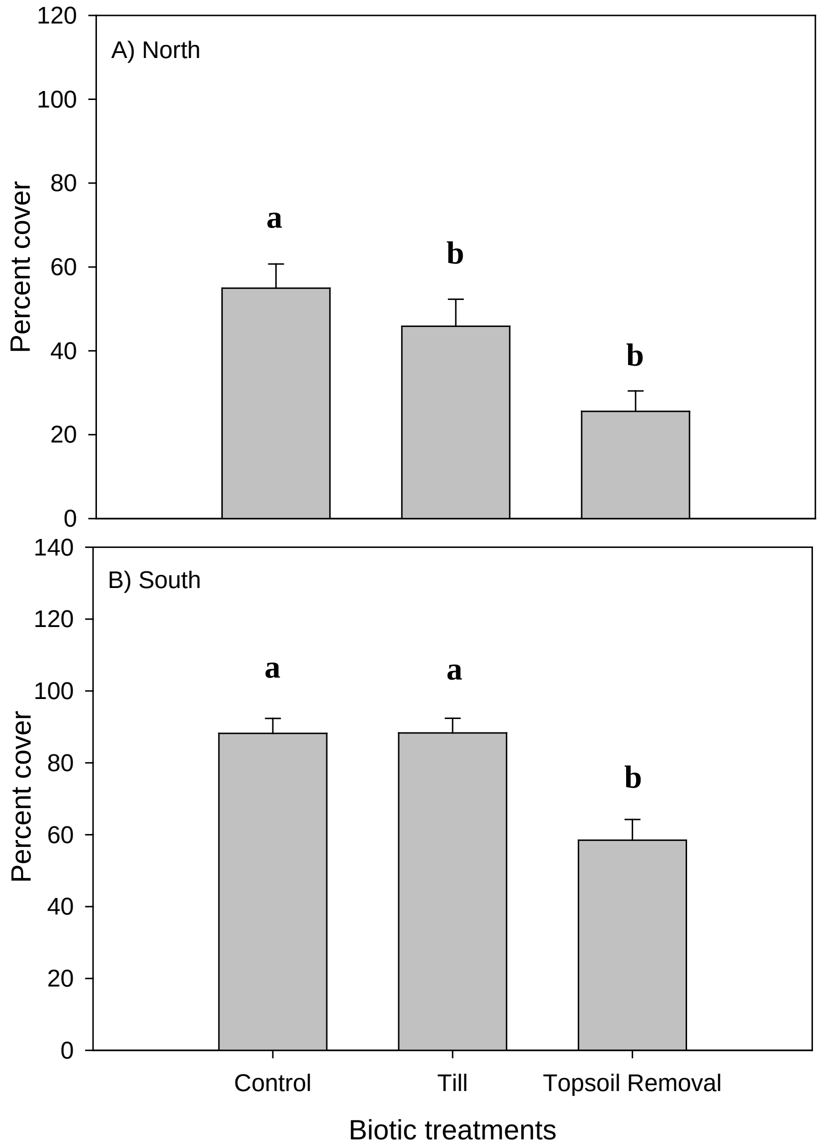

Figure 3.6. Mean nonnative species cover + se 4 months post-treatment for A) north site and B) south site. Different letters indicate significant differences among biotic treatments.

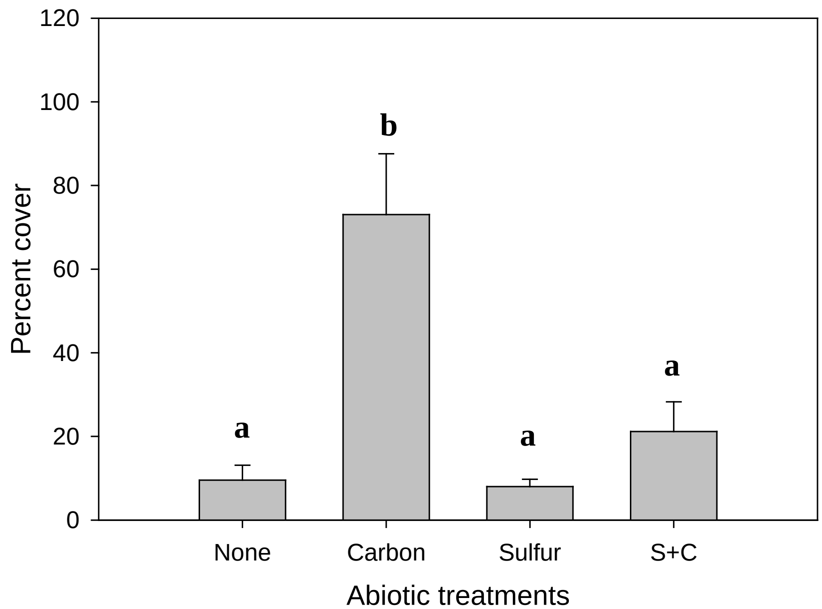

Figure 3.7. Mean native species cover + se for unfenced topsoil removal plots in the north site 1 year post treatment. Different letters indicate significant differences.

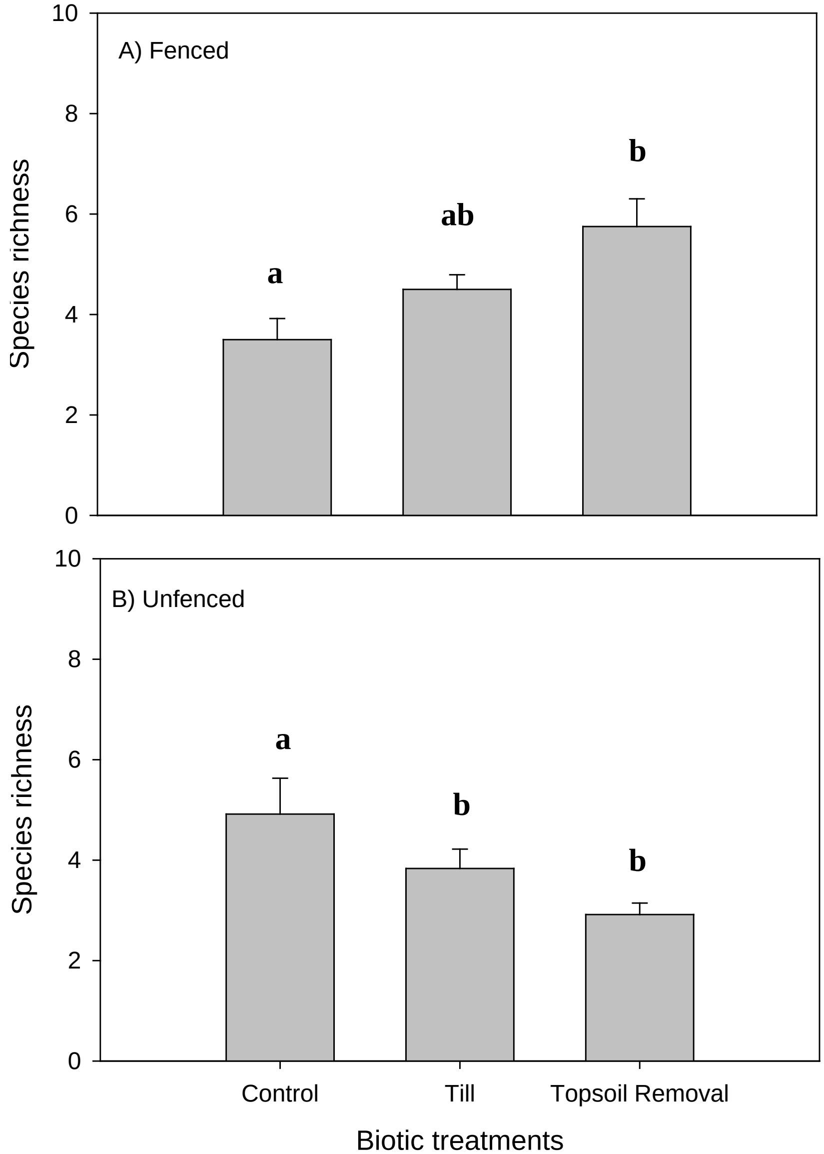

Figure 3.8. Mean native species richness + se for A) fenced and B) unfenced blocks at the south site 1 year post treatment. Different letters indicate significant differences.

CHAPTER FOUR: GENERAL DISCUSSION

Restoration of abandoned agricultural lands provides opportunities for expanding native vegetation which will protect biodiversity and provide a range of ecosystem services. When performing a restoration, land managers must address both biotic and abiotic land-use legacies and their barriers to native species establishment (Cramer et al. 2008). Because agriculture imposes myriad vegetation and soil modifications and leaves persistent land use legacies, it is unlikely that any one management tool will successfully restore former agricultural fields that are highly invaded (Corbin et al. 2004).

Overcoming biotic barriers, such as competition with nonnative species and native recruitment limitations, can have important consequences for restoration but may be more difficult, and in some cases more important, to address than abiotic factors (Norton 2009) due to the persistence of aggressive, nonnative species under varying abiotic conditions (Von Holle et al. 2003). Nonnative invasive species can thrive under a variety of soils conditions and act as barriers to native species reestablishment on abandoned agricultural fields.

Reducing competition and reintroducing native propagules may be all that is necessary for reestablishing natives without overcoming abiotic legacies. At HCF tilling increased establishment of our target species more than our soil amendments. Indeed, in some systems, recruitment limitation is often a key factor preventing native species establishment, and seeding alone can increase native species richness (Standish et al. 2007). Further, it is possible to restore native species that will constrain invasions. Choosing species that have similar traits has been shown to effectively restore a community that confers resistance to invasive species (Bakker and Berendse 1999, Bakker and Wilson 2004, Pokorny et al. 2005).

There are several methods to restore agricultural soils, and some methods are more effective than others. Altering soil fertility, overall, has had limited success in decreasing nonnatives and increasing natives. Additions of sawdust, as we saw, produced almost no increases in native species similar to results found across a variety of ecosystems. Sucrose additions have been more successful in other restorations; however only provide short term decreases in fertility. Repeated applications may be necessary, but are not cost effective; as such, sucrose may not be method to meet long-term restoration goals. On the other hand, topsoil removal effectively and quickly reduces fertility, in addition to removing nonnative competitors as well as the nonnative seedbank.

Finally, altering soil pH where liming agents have been applied for agriculture may be a necessary step in increasing native species adapted to acidic soils (Walker et al. 2004). Specifically, additions of elemental sulfur have been highly effective in reducing soil pH and increasing native establishment. Altering soil pH is an effective method to increase native species establishment on naturally acidic soils, however, effects of this treatment on systems that naturally have higher pH is unknown and may not be appropriate.

Based on my review of the literature and thesis research, native species reestablishment on abandoned agricultural lands appears to be more limited by biotic factors than abiotic factors. However, restoration methods that address both biotic and abiotic land-use legacies, such as the addition of propagules combined with topsoil removal or tilling with sulfur additions, will likely be the most successful in decreasing the presence of nonnative competitors and increasing native species recovery.

It is important to consider that many restoration treatments that address biotic and abiotic land-use legacies often only have short term effects on increasing natives and decreasing nonnatives. Most studies, such as this one, publish results on restoration after a few years of treatments, with little long-term monitoring; therefore, success of restoration treatments must also be considered on a temporal scale. For example, in a heathland restoration in the U.K., Pywell et al. (2011) observed short term success of several restoration treatments; however, 17 years after the treatments were implemented, there were very few differences between pre- and post-restoration plots. Restoration of openland habitats that are invaded may require ongoing management and intervention even after natives have established (Norton 2009). In my study, we may have found different vegetation responses to soil changes over a longer timeframe, but the results, overall, provide a clear picture of how the restoration treatments I employed affect native and nonnative species on a short-term scale in these highly degraded openland systems.

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