8-2009

Effects of vegetation structure on fire behavior and wiregrass seedling establishment in xeric sandhills

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EFFECTS OF VEGETATION STRUCTURE ON FIRE BEHAVIOR AND WIREGRASS SEEDLING ESTABLISHMENT IN XERIC SANDHILLS

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Masters of Science
Forest Resources

by
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August 2009

Accepted by:
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ABSTRACT

The xeric sandhills on Carolina Sandhills National Wildlife Refuge have a monospecific overstory of longleaf pine and an understory dominated by turkey oak and wiregrass. The understory vegetation is spatially heterogeneous within stands, with small patches dominated by either turkey oak or wiregrass, or lacking understory vegetation. I described the fuel complexes created by the variable vegetation structure, in terms of their chemical and physical properties, and used prescribed fire to test for differences in fire behavior among the vegetation types. In addition, I compared the effects of the vegetation structure and below-ground competition on the establishment of wiregrass.

Turkey oak-dominated sites had the highest potential fuel weights, and contained high-energy fuels. The duration of burn above 60 °C and the heat output were longest on these sites. Longleaf pine-dominated sites contained energy-rich fuels but low potential fuel weights; they also had a long duration of burn above 60 °C, but lower heat output than turkey oak-dominated sites. Wiregrass-dominated sites had low potential fuel weights, the lowest fuel energy content, and a well-aerated fuel bed. These sites had the shortest duration of burn above 60 °C and the lowest heat output. Rate of spread and peak fire temperature were highly variable, and did not vary with understory vegetation.

The effect of vegetation structure on wiregrass seedling establishment was only significant directly following planting, which coincided with the driest portion of the growing season. Early in the study, seedlings had the lowest survival rates, and seed the lowest numbers of germinants in the turkey oak-dominated sites. Understory vegetation

structure was only marginally linked to measures of above-ground light resources, with longleaf pine-dominated sites having the least available sunlight in the understory, but the most available light at ground level. Below-ground competition limited seedling survival and growth, and establishment from seed during the entire season, and across all vegetation types. Below-ground competition reduced soil moisture, a limiting resource in the xeric sandhills.

Management goals to reduce turkey oak cover will change the fuel structure and fire behavior, but may not be sufficient to increase wiregrass cover in the long term. Where turkey oak is already restricted to the understory through frequent burning, negative effects on wiregrass seedling establishment may only exist during drought conditions or the earliest stages of seedling establishment. At other times, competition from pines and other understory vegetation is comparable to that produced where turkey oak is present.

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CHAPTER 1.

INTRODUCTION AND LITERATURE REVIEW

Longleaf pine (*Pinus palustris* Mill.) woodlands and savannas once covered vast

areas of the Southeastern U.S. (37 million hectares) (Frost 1993). According to early

descriptions, these ecosystems are characterized by a scattered pine overstory and a low

herbaceous groundlayer (Platt 1999). The longleaf pine ecosystem ranges from near sea-

level on the coastal plain to higher elevation forests in northern Alabama and Georgia,

and from mesic, seasonally-wet depressions to well-drained xeric sandhills. The

associated plant communities also vary greatly over this area (Peet 2006, Sorrie and

Weakley 2006). The dependence of the longleaf pine community on fire as a disturbance

factor is well known (Frost 1993, Platt 1999, Sorrie and Weakley 2006), and it is

considered a fire-climax community, with fire maintaining a relatively open canopy.

Frequent fire disturbance reduces hardwood cover and encourages regeneration of

longleaf pine, wiregrass (*Aristida* spp.), and several forbs (Streng et al. 1993, Glitzenstein

et al. 1995, Brockway and Lewis 1997, Reinhart and Menges 2004).

Intact longleaf pine savannas have a diverse groundcover, dominated by perennial

grasses and containing many forb species, several of which are endemic, rare or

endangered (Walker and Peet 1983, Harcombe et al. 1993, Peet and Allard 1993, Sorrie

and Weakley 2001). The land mass making up the coastal plain was formed during the

early Tertiary, 50 mya; though it is not as old as some neighboring regions, it has been

available for plant colonization for nearly the entire period. It served as a refuge for plant

life during periods of glaciation, and only parts have been covered by ocean inundations (Sorrie and Weakley 2006). Because of this long and uninterrupted period of colonization and speciation, high rates of endemism occur in the region. Over 1600 species are only known from within the range of longleaf pine, a 26.7 % endemism rate (Sorrie and Weakley 2001, Sorrie and Weakley 2006). Species richness is also notable. Peet and Allard (1993) noted sites with over 40 species per square meter, a similar value to that found in a tropical rainforest, but almost all were at ground-level, in the herbaceous layer.

The flora of the longleaf pine ecosystem is also of conservation value for fauna. Significant primary productivity takes place in the ground layer in savannas, encouraging a diverse herbivore fauna, including arthropods which provide a food source for larger insectivorous species. The gopher tortoise (*Gopherus polyphemus*) is a longleaf pine specialist, and a keystone species whose burrows are utilized by over 300 other species of vertebrates and invertebrates. Where present, the gopher tortoise is an important grazer in the ecosystem, eating a variety of grasses and forbs, thus requiring healthy groundlayer vegetation (Means 2006). Species richness is high for reptiles and amphibians, and specific taxa include the federally threatened and endemic eastern indigo snake (*Drymarchon corais*) and flatwoods salamander (*Ambystoma cingulatum*) (Means 2006). The federally protected red-cockaded woodpecker (*Picoides borealis*) requires mature pine stands for nesting, and prefers a forest structure free of midstory hardwoods for foraging and nesting (Walters et al. 2002). Therefore, red-cockaded woodpecker habitat should be managed to encourage herbaceous species cover and reduce midstory hardwoods (U.S. Fish and Wildlife Service 2003). Though not as notably diverse as the

flora, the fauna also includes many endemic species, and maintaining the historic plant community and forest structure is crucial for their conservation.

A combination of land use changes, including timber harvesting, intensive land management and fire suppression, over the past two centuries reduced the range of longleaf pine to less than 1.2 million hectares (Outcalt and Sheffield 1996). Of the current distribution, only part of this area (0.5-0.8 million ha) has an intact understory (Noss 1989). Where fire has been suppressed for several decades, even in tracts of old-growth longleaf pine, there is sparse herbaceous cover, low species diversity, and increased hardwood cover (Gilliam et al. 1993, Glitzenstein et al. 2003). The high plant species diversity, especially of endemics, coupled with the loss and degredation of land and changes in ecosystem processes, increase the conservation value of remaining longleaf pine habitat. Several fauna species depend on intact groundlayer vegetation, and groundcover species (especially bunchgrasses) help create the fuel bed required to carry the frequent, low-intensity fires (Clewell 1989), which maintain this fire-climax system. Understanding how interruptions and alterations in this cycle affect its ability to maintain itself is necessary for restoration and management.

Platt and others (2001) suggest that vegetation change caused by fire exclusion can alter the fire regime and subsequent response of the vegetation in longleaf pine savannas. In Florida sandhill communities there is a segregation of the sandhill vegetation (a savanna with a longleaf pine overstory and a grass and forb understory) and the scrub vegetation (a woody shrub layer with a variable pine overstory and a sparse grass and forb layer) (Menges and Hawkes 1998). Studies have suggested that historic

fire regimes maintained both vegetation communities, with the sandhill burning more frequently and less intensely than the scrub, but fire suppression in the past century has enabled the scrub species to invade the sandhill community (Laessle 1958). Scattered turkey oak (*Quercus laevis* Walt.) is always present in the longleaf pine sandhill community, however, in areas where turkey oak stems become dense there is little to no herbaceous layer (Rebertus et al. 1989b). There is concern that turkey oak stem cover has increased as a result of fire suppression in the xeric sandhills of the Carolinas, creating turkey oak barrens (Menges and Hawkes 1998, Christensen 1981), similar to the invasion of the sandhill communities by scrub vegetation in the Florida sandhills. In addition, several studies have shown that when fire is reintroduced, there will be a segregation of turkey oak and longleaf pine in sandhill communities, creating patches of turkey oak that are able to persist. Once established, these turkey oak patches can withstand frequent fire through resprouting, creating a different set of fire conditions than found where fuels are dominated by pine needle litter (Rebertus et al.1989a and 1989b, Williamson and Black 1981).

At the Carolina Sandhills National Wildlife Refuge (CSNWR) there is significant patchiness in vegetation at a small scale. Some patches of turkey oak are no more than five meters in diameter, much smaller than that of a turkey oak barren. It is unknown whether such patches are capable of affecting the intensity and behavior of prescribed burns, or creating a unique set of environmental conditions that could affect the establishment of desirable vegetation (such as longleaf pine or wiregrass seedlings).

The soils in the xeric sandhills are well-drained, resource-limited sands with a low nutrient retention capacity, and extremely low N-mineralization rates (Morton 1995, Mitchell et al. 1999). These environmental stresses create a discontinuous layer of groundcover vegetation, with the presence of plants significantly altering their immediate soil conditions, through increased soil microorganism populations, C-mineralization, and moisture content (Mulligan and Kirkman 2002a, West and Donovan 2004). Annual net primary productivity is positively correlated to soil moisture for both herbaceous and woody species (Mitchell et al. 1999). Species richness also increases along a soil-moisture gradient (Kirkman et al. 2001).

The CSNWR upland longleaf pine savannas are found on excessively drained Alpin sands (Morton 1995). Annual net primary productivity and species diversity are low in comparison to other longleaf pine savannas. Longleaf pine, wiregrass, and turkey oak are the dominant species, but where past soil disturbance and fire suppression have impacted the ecosystem, especially the understory vegetation, wiregrass is slow to reestablish (Clewell 1989). Wiregrass depends on fire for seed production, only producing significant quantities of viable seed following growing-season burns (Abrahamson 1984, Clewell 1989). Natural reestablishment on sites without wiregrass populations is infrequent (Clewell 1989), and wiregrass seeds have short dormancy (Coffey and Kirkman 2006). Wiregrass disperses seed over short distances, with seedling recruits no more than 6 m from the parent plant (Mulligan et al. 2002). Reintroduction is required to attain wiregrass plant densities capable of reproducing the historic fuel structure and fire regime (Outcalt et al. 1999). Significant work has been done on how to

best reestablish a wiregrass groundlayer through direct seeding or planting seedlings, especially in newly-restored longleaf pine stands (Hattenbach et al. 1998, Outcalt et al. 1999, Cox et al. 2004, Walker and Silletti 2006), and other studies have focused on factors such as seedling recruitment and competition, which may influence natural regeneration of wiregrass (Harrington et al. 2003, Mulligan et al. 2002, Mulligan and Kirkman 2002a, Mulligan and Kirkman 2002b).

In areas where wiregrass is found in low densities, it is unknown what limits wiregrass establishment in the unoccupied areas. Environmental (soil and light) and biological factors (neighboring species, competition) may all function together to determine wiregrass species distribution on a small scale. Mulligan and Kirkman (2002a) found no evidence that wiregrass seedling survival was facilitated by neighboring wiregrass plants, and Mulligan and Kirkman (2002b) found decreased seedling survivorship in close proximity to adult plants. Outcalt and others (1999) found that seedling survival was higher in areas with a pine needle groundlayer than in areas with a blueberry (*Vaccinium spp.*) groundlayer. In other studies not specific to wiregrass, but in longleaf pine systems, Pecot and others (2007) found a positive response of herbaceous vegetation growth to light levels, but no response to below-ground competition in a mature stand; and Harrington and others (2003) found a positive response of herbaceous species cover to reduced above- and below-ground competition in a young plantation. Harrington and Edwards (1999) determined that, in a young plantation, light is a more limiting factor than soil moisture on herbaceous vegetation, and Mulligan and others

(2002) found that thinning the overstory leads to increased wiregrass seed production and seedling recruitment.

These studies suggest that, regardless of stand age, light is the most influential factor in determining where wiregrass grows, reestablishment to neighboring areas is slow due to dispersal limitations, and below-ground competition is only sometimes relevant. Plants may need to reach natural densities of 5 plants per square meter before the structure and function of wiregrass in the ecosystem can be restored (Noss 1989, Clewell 1989).

The presence of turkey oak in high densities creates a different situation for reestablishing wiregrass in, when compared with sites where the understory vegetation is absent or primarily herbaceous. Below-ground root competition is increased (for turkey oak and wiregrass most fine root biomass is in the top 10 cm of soil (Saterson and Vitousek 1984, Donovan and Pappert 1998)), and above-ground turkey oak creates a different type of litter layer (Williamson and Black 1981), as well as another canopy layer limiting light at the ground-level.

The reduction in wiregrass cover and increase in turkey oak cover on CSNWR has several implications for land management and conservation. Prescribed fire is a key land management tool used on the refuge, to reduce fuels, to maintain an open mid-story, and to encourage regeneration of longleaf pine, wiregrass and other herbaceous species (U.S. Fish and Wildlife Service 2009). In an intact longleaf pine ecosystem these goals may all be attained, but where the plant community structure has changed, as described above, the effects of the vegetation on the fire, the subsequent fire effects on the

vegetation, as well as the regeneration potential of species may differ (Menges and Hawkes 1998). In this thesis, I address these concerns in the next two chapters. In Chapter 2, I describe fuels and fuel complexes based on their chemical and physical properties and species composition, and test whether small-scale variation in fuel complexes affects fire properties. In Chapter 3, I examine the effect of surrounding vegetation and exposure to below-ground competition on wiregrass seedling establishment, survival, and growth.

CHAPTER 2.

CHARACTERIZATION OF WITHIN-STAND VARIATION IN FUEL COMPLEXES

AND FIRE BEHAVIOR ON CAROLINA SANDHILLS NATIONAL WILDLIFE

REFUGE

INTRODUCTION

Fire is an integral part of the longleaf pine (*Pinus palustris* Mill.) ecosystem in the

southeastern U.S., with three-to-five year fire intervals found in areas where fuel

accumulation is sufficient (Christensen 1981, Platt 1999). Fires at such intervals support

the regeneration of longleaf pine and many herbaceous species (Christensen 1981,

Brockway and Lewis 1997). Consequently, land managers throughout the southeast

commonly use fire as a management tool in order to maintain and restore the longleaf

pine ecosystem. On the Carolina Sandhills National Wildlife Refuge (CSNWR),

prescribed burning has been used to reduce fuel loads, maintain an open understory, and

encourage longleaf pine and herbaceous species regeneration.

The CSNWR is dominated by the xeric sandhills ecosystem, an upland longleaf

pine forest characterized by a longleaf pine overstory, turkey oak (*Quercus laevis* Walt.)

in the shrub- and mid-story, and a wiregrass (*Aristida stricta* Michx.) and mixed forb

ground layer. Throughout this ecosystem, plant cover has changed in the past two

centuries due to land and resource use, resulting in decreased pine and grass cover and

increased hardwood cover (Christensen 1981) and, accordingly, new fuel complexes that

may change the way fire behaves within the ecosystem.

Understanding how fuels affect fire behavior and desired fire effects is a necessary component of using prescribed fire (Johnson and Miyanishi 1995). Fire behavior is affected by both the chemical (intrinsic) and physical (extrinsic) properties of fuels (Pyne 1984). The chemical property of a fuel is best described by its energy and mineral (ash) contents, where the energy content affects the amount of heat released and the mineral content affects the ignitability of the fuel. Physical properties include fuel load, morphology, and arrangement, all affecting fire behavior.

Previous studies have shown differences in chemical properties among fuel species within an ecosystem (Dickinson and Kirkpatrick 1985, Dimitrakopoulos and Panov 2001) and among ecosystems (Dickinson and Kirkpatrick 1985, Golley 1961), as well as between native and non-native species (Dibble and others 2007, Lippincott 2000). Some of these studies couple chemical analysis with laboratory or field studies on fire behavior to suggest that intrinsic properties are related to other measures of flammability, such as rate of flame movement. Moreover, there is evidence that the chemical properties of species in fire-prone environments are more likely to encourage fire (Mutch 1970). The dependence of the longleaf pine ecosystem on fire provides an ideal setting for further studies on the properties of fuels and their effects on fire behavior.

Fires may burn heterogeneously on a small-scale for several reasons, including spatial and compositional variability of vegetation or fuels (Thaxton and Platt 2006, Price et al. 2003, Molina and Llinares 2001) and exotic plant invasion (Brooks et al. 2004, Lipincott 2001). The patchy distribution of vegetation in the longleaf pine ecosystem creates numerous fuel complexes on a small or within-stand scale. The variation in fuels

(species, structure, quantity, etc.) has been recognized and the effect of fuel variation on fire has been studied in Southeastern sandhills ecosystems (Thaxton and Platt 2006, Platt et al. 1991, Rebertus et al. 1989b, Williamson and Black 1981). These studies concentrated on the heterogeneity in pine canopy cover and pine fuel loading. Small-scale variation in pine fuels was shown to affect fire intensity and shrub abundance, with areas of increased fuel loading causing higher-temperature burns and increased shrub mortality (Thaxton and Platt 2006). Several studies looked at the effect of distance to nearest pine, pine density, or canopy species on fire temperature and turkey oak mortality (Platt et al. 1991, Rebertus et al. 1989b, Williamson and Black 1981). Fuel arrangement and architecture, such as the positions of oak leaves and longleaf pine needles in the fuel bed, may also affect fire behavior (Rebertus et al. 1989b, Williamson and Black 1981), but differences in fuel arrangement have not been measured in sandhills ecosystems. Even though the small or within-stand variation in fuel complexes has been previously used to study fire behavior and fire effects in the sandhills (Thaxton and Platt 2006, Platt et al. 1991, Rebertus et al. 1989, Williamson and Black 1981), a detailed description of those fuel complexes and their associated effects on fire is still missing.

Thermocouple probes have been used to measure fire parameters in several ecological experiments (Bova and Dickinson 2008, Wally, Menges and Weekely 2006, Kennard et al. 2005, Iverson et al. 2004, Molina and Llinares 2001). Though thermocouples have some limitations (cost, heating lag time, etc.), they are an effective way to collect real-time temperature data linked to locations (Bova and Dickinson 2008, Wally et al. 2006, Kennard et al. 2005). Thermocouple data may be analyzed to create

time-temperature curves, which can be used to determine maximum thermocouple temperature, time of passage of flaming front, duration of burn, and area under the curve (i.e., total heat output above a threshold temperature). A combination of temperature, time, and location data also makes it possible to calculate rate of spread of the burn (Simard et al. 1984, Iverson et al. 2004).

The importance of fire in maintaining the sandhills longleaf pine ecosystem, and the role of fuels in determining fire behavior, necessitate a better understanding of the chemical and physical properties of the dominant fuels in the ecosystem and their effects on fire. The objectives of this study were to: 1) quantify the chemical properties (energy, ash and moisture content) of several common species found in the sandhills, 2) compare the physical fuel properties (potential fuel weight, litter depth, and fuel arrangement) of three fuel complexes found within longleaf pine stands in the sandhills, and 3) study the effect of fuel complexes and fuel properties on several fire parameters (fuel consumption, peak temperature, rate of spread, duration, and area under the time-temperature curve). A better understanding of fuel properties and their effects on fire behavior should improve the use of prescribed fire as a management tool, especially where altered understory species composition has lead to new fuel complexes.

MATERIALS AND METHODS

Study Area

I conducted two experiments, one primarily laboratory-based to describe fuel chemistry, and one field-based to describe fuel complexes and compare fire temperature

and behavior among fuel complexes. The study site for both experiments was CSNWR (34.58N, 80.23W), which is situated on the fall line of the Upper Atlantic Coastal Plain in Chesterfield County, South Carolina. Elevations for this area range from 70 m along Black Creek to 180 m on the highest ridges. Soils are well-drained sands of the Alpin-Candor series (Morton 1995). Mean annual precipitation is 110 cm and mean annual temperature is 15.6 °C. Although several plant communities are found within CSNWR, all study sites were located in the upland longleaf pine-wiregrass community.

Fuel Chemistry

Experimental design and sampling

I used a complete block design with six blocks, and, to account for variability among individuals, I sampled at least ten individuals of each species per block, using composite samples for the laboratory analysis. In November of 2007, I collected plant matter from five species (needle litter from longleaf pine, dead leaves of turkey oak, and leaves of wiregrass, little bluestem (*Schizachyrium scoparium*), and weeping lovegrass (*Eragrostis curvula*)) for chemical analysis. The first four species are common native species and are the dominant fuels in the system; the fifth is an exotic bunchgrass species. Prior to laboratory analysis, I separated live and dead tissue for the three grass species (wiregrass, little bluestem, and weeping lovegrass), and analyzed each separately.

Chemical analysis

To prepare samples for analytical tests, I oven-dried the plant matter at 65 °C for 48 hours and ground it to 60-mesh using a Thomas Scientific® Wiley Mill. For energy content analysis, longleaf pine needle and turkey oak leaf samples were combusted in pellet form. Milled samples were pressed into 0.4 - 0.5 g pellets under 24.1 MPa using a Carver Inc. laboratory press. Grass samples were combusted in powder form, with milled plant material packed in plastic bags prior to combustion. I measured energy content with an IKA® C200 oxygen bomb calorimeter in isoperibol mode, running three subsamples of each species per block. Subsample weights ranged from 0.8 to 1.3 g, depending on the species (weight was determined based on an ideal temperature rise of 2.7 - 3 ℃ for the water surrounding the combustion chamber). I calibrated the calorimeter with certified benzoic acid to determine the heat capacity of the system. Energy content was measured in Jg^{-1}.

Mineral ash analysis was performed by the Agricultural Service Laboratory at Clemson University. Milled plant material was used for the analysis, and ash content was determined by heating samples for two hours at 600 °C in a Thermo Scientific® muffle furnace. Two subsamples (each approximately 1 g) were analyzed for each sample.

Moisture content analysis

Moisture content of milled samples was determined at the time of chemical analysis to correct the energy and ash results for ambient moisture content. Between 1-2

g of milled plant material was placed in a crucible and oven-dried at 65 °C for 48 hours to attain a dry weight.

Field fuel moisture content was also determined, with samples collected from four burn units on CSNWR on the day of prescribed burns in each of those units. Samples of longleaf pine needle litter, turkey oak leaf litter, turkey oak twigs, and wiregrass were collected, immediately placed in ziplock bags, and refrigerated or placed on ice in a cooler within 0-6 hours. Wet weights were taken the following day, and dry weights after oven-drying the samples for 48 hours at 65 ºC.

Statistical analysis

I used two-way analyses of variance in PROC GLM (SAS Institute Inc. 2008) to test for significant differences in measured chemical properties among species, using a block term to account for location effects (and time effects for field-moisture content analysis). I used least squares means tests in PROC GLM to calculate means and pooled estimates of standard error, and to make specific comparisons between species. I used linear contrasts to compare woody versus grass species for energy and ash content. PROC MEANS (SAS Institute Inc. 2008) was used to calculate the means and standard errors presented in tables and figures, in addition, the pooled estimate of the standard error is presented at the bottom of each figure. All levels of significance displayed in figures are based on $\alpha = 0.05$.

Fuel Complexes

Experimental design

I identified three fuel complexes, based on the natural variation of fuel distribution observed in the ecosystem, to describe physical differences in understory fuels, and to compare fire temperature and behavior among fuel complexes. Fuel complexes were identified visually according to the dominant species. The first was dominated by longleaf pine needle litter, with live fuels nearly absent, the second by turkey oak stems and litter, and the third by wiregrass. Longleaf pine needle litter was present in all fuel complexes.

I used a complete block design with seven blocks; four blocks contained one plot of each fuel complex, and three blocks had two plots of each. I selected sites with all three fuel complexes present and in close proximity to each other within each block. I installed 4 m by 4 m plots for each fuel complex, because fuels were relatively uniform at this scale; on a larger scale there would have been significant variation within a fuel treatment plot. All plots were located in areas with a mature longleaf pine canopy over Alpin soils. Finally, all sites were selected to have a similar burn history, with the last prescribed burn conducted in the spring of 2003 or 2004, and scheduled to burn during late winter or early spring of 2008.

Fuel complex descriptions

In February and March of 2008, I sampled all plots to estimate potential fuel weight by measuring all standing vegetation (live and dead) less than 2 m in height and

all ground litter. The fuel components measured for all fuel complexes included turkey oak stems, wiregrass plants, and litter (separated into needle litter, turkey oak litter, and unidentified fractions).

I destructively sampled turkey oak stems outside the study plots to construct height versus weight regressions, which I used to estimate stem weights of all stems within plots. Leaves were not attached to stems at the time of burn, and the regressions estimate the weight of stems without leaves. Separate regression analyses were used for live stems 0-70 cm, live stems >70 cm, dead stems 0-70 cm, and dead stems >70 cm (Figure A-1). I sampled wiregrass plants outside the study plots to develop a relationship between wiregrass plant basal area and weight (Figure A-2). Wiregrass basal area was estimated by taking two perpendicular measurements of plant crown diameter. Basal area and plant weight were estimated for all plants within each plot.

Litter weight was estimated from samples collected adjacent to study plots. Litter samples from a 1 m by 1 m area were used to estimate the litter weight of the longleaf pine litter- and wiregrass-dominated plots, and samples from a 1 m by 2 m area were used to estimate the litter weight of the turkey oak-dominated plots. I sorted the litter samples into three components: longleaf pine litter, turkey oak litter, and unidentified, and obtained oven-dry weights for each.

Litter depth was measured prior to burns in all blocks. Measurements were taken at five points per plot, at plot center and along the plot diagonals, 180 cm from the plot center. Pine and oak litter lodged in turkey oak stems was not considered in litter height measurements, though litter lodged in wiregrass plants was, due to its contact with the

litter bed. Litter depth was measured prior to installing thermocouples for fire monitoring to minimize disturbance of the litter bed before measurements.

Dwarf huckleberry (*Gaylussacia dumosa*), little bluestem, splitbeard bluestem (*Andropogon ternarius*), and longleaf pine cones made up a minimal proportion of the fuels. Their presence was noted, but their weights were not estimated for the study.

Prescribed burns

Study areas were burned by CSNWR staff between February 28 and April 23, 2009. Four of the five burns were ignited aerially, creating several spot fires, as is the common procedure on CSNWR. In these four burns, the study areas were in burn units approximately 200 ha in size. The burn on March 22 was ignited by hand with drip-torches, as CSNWR no longer wished to burn the entire burn unit. A fireline was created around the burn area, and all experimental plots were at least 30 m from the fireline.

Fire weather (temperature, relative humidity, and wind speed) were measured on site during all burns by fire crew members. Hourly weather data was also obtained from a weather station on CSNWR (Mesowest 2008). Burn and weather conditions (from the weather station) are displayed in Table 2.1 for each block.

Table 2.1. A brief summary of prescribed burn and fire weather information.

Block	Burn date	Ignition style	Time of burn	Temp. (°C)	R.H. (%)	Wind speed (kmph)
21-3	2/28/08	Aerial	12:57	6	31	16
21-1a	3/1/08	Aerial	15:40	21	27	14
21-1b	3/1/08	Aerial	15:00	21	27	14
21-2a	3/21/08	Drip-torch	12:56	18	19	8
21-2b	3/21/08	Drip torch	12:40	17	21	6
9-3	3/22/08	Aerial	10:45	13	79	14
15-3	4/23/08	Aerial	14:03	22	67	11

Fire monitoring

I used thermocouple probes (TCPs) and hobo dataloggers (Onset Computer Corporation) to record temperature during burns. The TCPs were 4.8 mm in diameter and 30.5 mm long, with a type K thermocouple at the tip. Five TCPs were placed in each 4 m by 4 m plot, with one at the center, and one on each diagonal, 1.8 m from the plot center (Figure 2.1). TCPs were buried at the base such that the probe tips were 25 cm above the soil (Iverson et al. 2004). Any disturbed litter was replaced following TCP installation to mimic natural conditions. I programmed the dataloggers to record temperature at 1.5 second intervals for a period of 12 hours. TCPs record temperature to within 5 ºC.
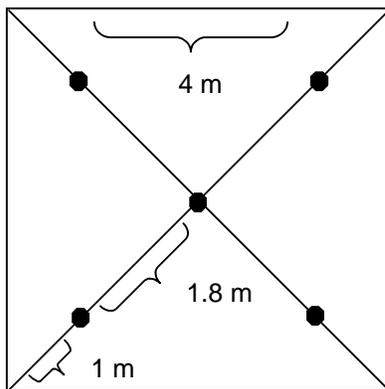
Figure 2.1. Thermocouple layout in 4 m by 4 m plots.

Post-burn fuel measurements

Following burns, litter depth was remeasured at the same locations used for pre-burn measurements. Post-burn measurements were only taken in four of the seven blocks, and made prior to TCP removal to minimize litter disturbance.

Turkey oak stems were resampled after burns to create another set of stem height-to-weight regressions (Figure A-3). The heights of all stems within plots were measured, and the weights of all stems within plots were estimated using the equations from the regression analyses. These weights were used to estimate the post-burn fuel weights per plot and fuel consumption.

Analysis of thermocouple data

TCP data were used to create time-temperature curves, which were analyzed to determine peak temperature, duration above ambient temperature and 60 ºC, area under the time-temperature curve above ambient temperature and 60 ºC, and passage of the flaming front (used for rate of spread calculations). Peak temperature was determined as the highest temperature the TCP recorded. This value is not equal to peak flame temperature, because there is a heating lag time for the probe. The duration, area, and rate of spread calculations were multi-step analyses.

Duration calculations were measured for each TCP as the residence time when temperature was above a designated value. I calculated the duration of burn above ambient temperature as well as above 60 ºC, the temperature at which cells die and a frequently used value in fire ecology studies (Kennard et al. 2005, Wally et al. 2006,

Bova and Dickinson 2008). Ambient temperature varied by block, and occasionally by plot within a block, and was based on the TCP readings, not fire weather data. Because of small temperature fluctuations both before the arrival of the flaming front and after the drop in peak temperature, the start and end times for duration above ambient temperature were determined according to the following procedure. The start time was set as the last time ambient temperature was recorded before the main temperature rise. End time was set as the first time temperature returned to ambient without being followed, within the next 4.5 seconds, by a temperature rise above ambient lasting more than 4.5 seconds. Duration above 60 ºC was determined by using the first and last times where temperature was recorded over 60 ºC. In the case of multiple peaks over 60 ºC, the first (and higher) peak was used.

I calculated heat output (or area under the time-temperature curve) for the time periods used to measure duration of burn by integrating under the time-temperature curve and above the applicable temperature (either ambient or 60 ºC). Integration was done using the trapezoidal rule

Rate of spread was calculated with both a linear and a triangulation method. Linear and triangulation time measurements both assume fire moves across the plot in a straight line, and at a constant direction and rate, however, triangulation does not assume the direction of spread, as linear measurements do. For both analyses I began by determining the time the flaming front passed a TCP location. The arrival of the flaming front is considered the first time in a dataset when a data point is followed by four successive temperature increases (or a constant temperature increase over at least 6

seconds). For the linear method, using the known distance measurements between TCPs in each 16 m^2 plot, and the time difference between the arrival of the flaming front for any two points, I calculated the rate of spread of the fire between every combination of TCPs (ten values total per plot), and used a plot mean for statistical analysis. The triangulation method followed the procedure described by Simard and others (1984), wherein for any three points one can calculate the direction of the fire spread and the rate of spread in that direction based on the time the fire arrives at those three points and the distances between the points. This method produced eight values per plot, and I used a plot mean for statistical analysis.

Statistical analysis

I used PROC REG (SAS Institute Inc. 2008) to determine the relationship between stem height and stem weight for turkey oak stems, and between plant basal area and plant weight for wiregrass. Residual plots and R^2 values were used to determine appropriate transformations.

I used two-way analyses of variance in PROC GLM (SAS Institute Inc. 2008) to test for significant differences in fuel weight, litter depth, fire temperature, duration, heat output, and rate of spread among fuel complexes. For each model, I included a block term to account for location effects, and used weighting to account for the different number of plots in each block. I used least squares means tests in PROC GLM to calculate means and pooled estimates of standard error to make specific comparisons between fuel complexes, and PROC MEANS (SAS Institute Inc. 2008) to calculate the means and

standard error of the mean presented in tables and figures. The pooled estimate of the standard error is also presented at the bottom of each figure. All levels of significance displayed in figures are based on $\alpha = 0.05$.

Weather was considered uniform across a block, due to the close proximity of all plots within a block; thus fire weather data were not included in the statistical analysis, as I used a block term in the two-way analyses of variance to account for location effects.

RESULTS

Fuel Chemistry

Significant differences in energy content were found among the common fuel species ($p < 0.0001$), and mean energy values ranged from 19186 Jg^{-1} (little bluestem, live) to 21725 Jg^{-1} (longleaf pine needles) (Table 2.2). Needle and leaf litter from the woody species contained more energy than the leaves from grass species ($p < 0.0001$). Of the native grass species, wiregrass had higher energy content than little bluestem, whereas the exotic grass species, weeping lovegrass, had a similar energy content as the dominant native grass species, wiregrass.

Mean ash content ranged from 1.36 percent (weeping lovegrass, dead) to 2.58 percent (little bluestem, live) (Table 2.3). I found significant differences among species ($p < 0.0001$), although ash content of leaves and needles from woody species was not significantly different from that of leaves from grass species ($p = 0.4529$).

Table 2.2. Mean energy content (Jg^{-1}) of some sandhills species found on CSNWR. Means with the same letter are not significantly different (model-based SE = 61.3 Jg^{-1}).

Species	Energy Content (Jg^{-1})	
	Mean	Standard error
Longleaf pine, needle litter	21725 A	54.5
Turkey oak, leaf litter	20389 B	64.6
Wiregrass, live	19972 C	39.6
Weeping lovegrass, dead	19658 D	92.7
Wiregrass, dead	19565 D	108.8
Weeping lovegrass, live	19573 D	52.3
Little bluestem, dead	19277 E	97.2
Little bluestem, live	19186 E	51.7

Table 2.3. Mean ash content (%) of some sandhills species found on CSNWR. Means with the same letter are not significantly different (model-based SE = 0.127 %).

Species	Ash Content (%)	
	Mean	Standard error
Weeping lovegrass, dead	1.36 A	0.199
Wiregrass, dead	1.48 AB	0.048
Longleaf pine, needle litter	1.72 BC	0.089
Wiregrass, live	1.97 CD	0.104
Weeping lovegrass, live	2.13 D	0.137
Turkey oak, leaf litter	2.14 D	0.062
Little bluestem, dead	2.53 E	0.195
Little bluestem, live	2.58 E	0.184

Moisture content is significantly different for the fuel types collected at the time of burn ($p < 0.0001$) (Figure 2.2). Turkey oak twigs, the largest diameter fuel, had the highest mean moisture content (26.8 %) and longleaf pine needles, a fine fuel, the lowest (13.2 %). Turkey oak leaves were not significantly different from longleaf pine needles ($p = 0.9735$) or wiregrass ($p = 0.0769$), though wiregrass, a live fine fuel, had higher moisture content than longleaf pine needles, a dead fine fuel ($p = 0.0496$).
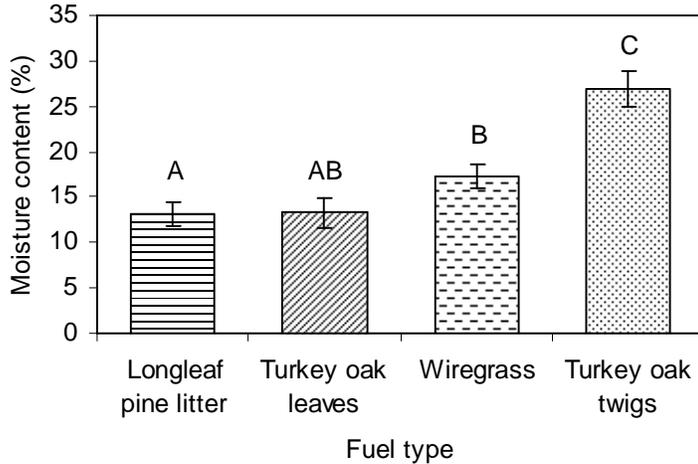
Figure 2.2. Mean fuel moisture content (%) of four fuel types on CSNWR. Means with the same letter are not significantly different, error bars represent standard error of the mean.

Fuel Complexes

I found significant differences in total potential fuel weight among fuel complexes ($p = 0.0006$), with turkey oak-dominated plots containing greater fuel loads than longleaf pine litter- ($p = 0.0009$) or wiregrass-dominated plots ($p = 0.0004$) (Table 2.4).

Table 2.4. Potential fuel weights (Mgha^{-1}) for three fuel complexes on CSNWR. Means with the same letter are not significantly different (model-based SE = 0.89 Mgha^{-1}).

Fuel complex	Potential fuel (Mgha^{-1})			
	Mean	Standard error	Minimum	Maximum
Longleaf pine-dominated	6.98 B	0.64	5.45	10.47
Turkey oak-dominated	12.56 A	1.44	7.57	18.52
Wiregrass-dominated	6.34 B	0.72	4.24	10.08

Mean potential fuel weight for each fuel complex was divided into five categories: turkey oak stems, wiregrass, longleaf pine litter, turkey oak litter, and unidentified litter (Figure 2.3). For the individual fuel components, differences among fuel complexes were significant for turkey oak stems ($p < 0.0001$), wiregrass ($p < 0.0001$), and turkey oak litter ($p = 0.0002$). These differences in fuel components verified our fuel complex designations. For example, the turkey oak-dominated plots had the most turkey oak stems and litter, and the wiregrass-dominated plots had the highest wiregrass weights.
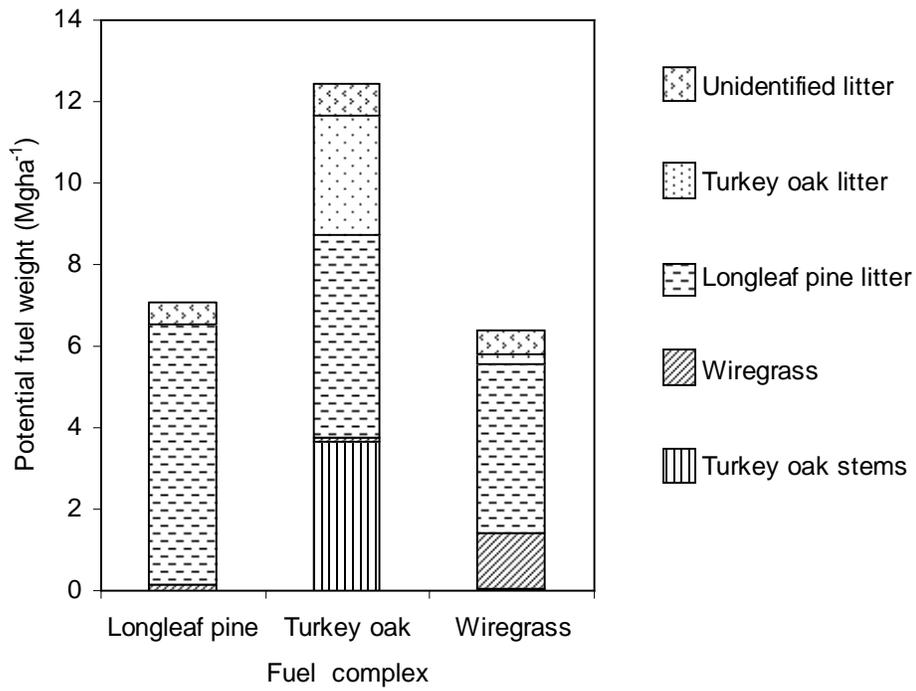
Figure 2.3. Effect of fuel complex on understory potential fuel weight (Mgha^{-1}), including standing turkey oak stems less than 2 m tall, wiregrass plants, and all litter.

Litter depth for each fuel complex is shown in Figure 2.4. Differences among fuel complexes were significant ($p = 0.0214$), with longleaf pine litter-dominated plots having a lower litter depth than either wiregrass- ($p = 0.0088$) or turkey oak-dominated plots ($p = 0.0313$). A density-related measure of litter arrangement is shown in Figure 2.5. The ratio of litter weight to litter depth, used to illustrate the aeration of the fuel bed, was highly significant among fuel complex treatments ($p = 0.0096$). Longleaf pine litter-dominated plots had a denser litter bed than either turkey oak- ($p = 0.0317$) or wiregrass-dominated plots ($p = 0.0031$). No significant difference was found between turkey oak- and wiregrass-dominated plots ($p = 0.2331$).

The combination of fuel chemistry results and differences in fuel weights and litter properties among fuel complexes provides a description for the pre-fire fuel conditions. Longleaf pine-dominated sites had low fuel weights, with a dense fuel bed primarily made up of long-leaf pine needle litter (with relatively high energy content and low moisture content). The wiregrass-dominated sites also had low fuel weights, but a well-aerated fuel bed made up of wiregrass plants (with lower energy content and higher moisture content) and longleaf pine needle litter, both fine fuels. The turkey oak dominated sites had higher fuel weights and a fuel load made up of fine fuels high in energy content and low in moisture content (longleaf pine needles and turkey oak leaf litter) as well as fuels of larger size classes and higher in moisture content (turkey oak stems).
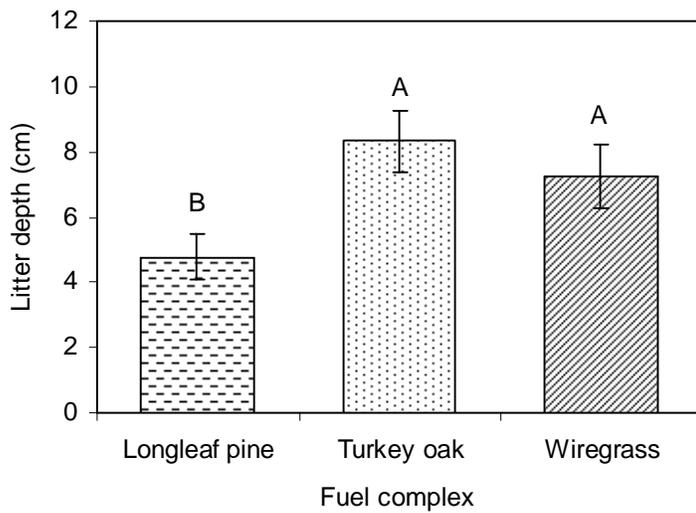
Figure 2.4. A summary of mean litter depth (cm) for three fuel complexes on CSNWR. Means with the same letter are not significantly different, error bars represent standard error of the mean (model-based SE = 0.95 cm).
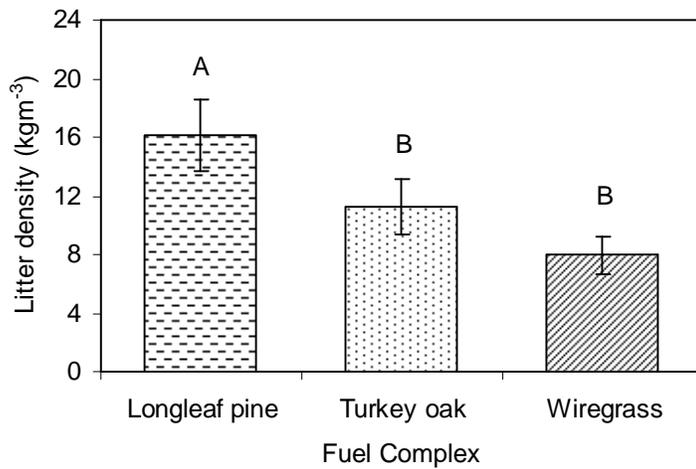
Figure 2.5. A measure of fuel bed aeration (litter density, kgm^{-3}) for three fuel complexes on CSNWR. Means with the same letter are not significantly different, error bars represent standard error of the mean (model-based SE = 1.8 kgm^{-3}).

Litter depth measurements following burns are displayed in Figure 2.6. There was no significant difference among fuel complexes ($p = 0.3906$), with mean depth ranging from 0.2 cm (longleaf pine-dominated) to 0.34 (turkey oak-dominated). There was also no significant difference in percent litter depth consumption ($p = 0.4671$, model-based SE = 1.43 %), which was 93.9 % in longleaf pine-dominated plots, 95.0 % in turkey oak-dominated plots, and 96.5 % in wiregrass-dominated plots. Due to the high litter consumption rates and near-complete consumption of above-ground wiregrass biomass, the end fuel weights used to determine percent consumption of potential fuel are an estimate based on the assumption that the only remaining fuels are turkey oak stems. All turkey oak stems within plots were top-killed by fire.

Mean percent fuel consumption (Figure 2.7) varied among fuel complexes ($p < 0.0001$). Turkey oak-dominated plots (with fuels of larger size classes) had lower consumption rates than longleaf pine- or wiregrass-dominated plots ($p < 0.0001$ for both), in which pre-fire fuels were primarily fine fuels. Figure 2.8 shows the distinct segregation of turkey oak-dominated plots from wiregrass- and longleaf pine-dominated plots when comparing potential fuel to fuel consumed. In all three cases the slope of the best fit line is nearly one ($p = 0.31, 0.16, 0.42$ for longleaf pine, turkey oak, and wiregrass, respectively, for the hypothesis test H_o: slope = 1); showing that, within the range of fuel weights sampled, as potential fuel increases, there is a similar weight of unconsumed fuel remaining in all turkey-oak dominated plots.
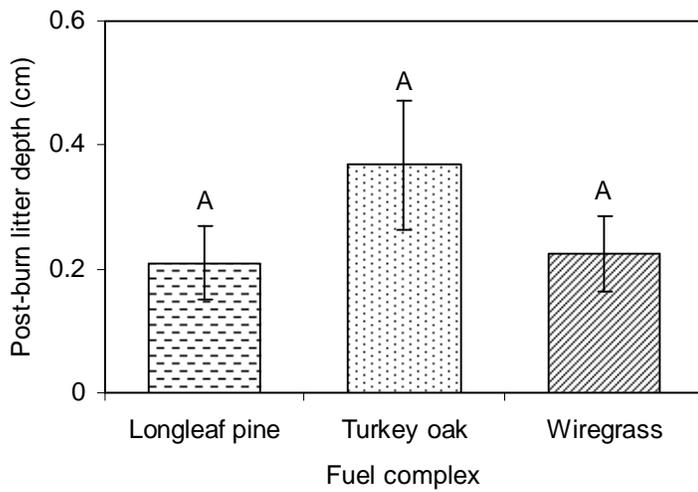
Figure 2.6. Post-burn mean litter depth (cm) for three fuel complexes. Means with the same letter are not significantly different, error bars represent standard error of the mean (model-based SE = 0.07 cm).

Figure 2.7. Mean potential fuel consumption rate (%) for three fuel complexes. Means with the same letter are not significantly different, error bars represent standard error of the mean (model-based SE = 1.6 %).
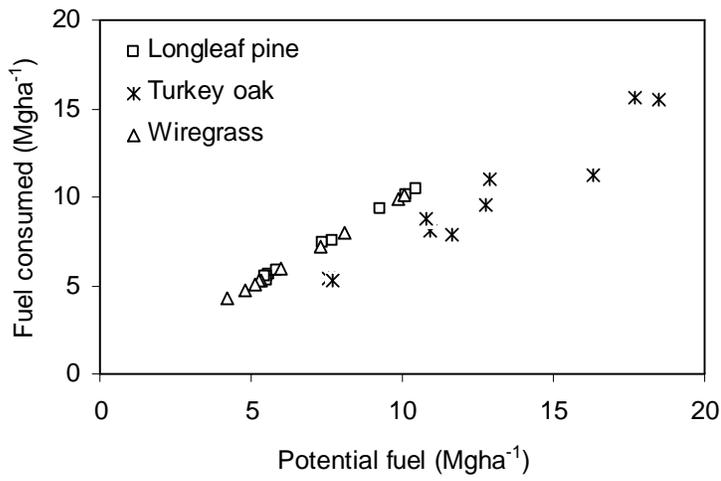
Figure 2.8. Scatterplot of potential fuel (Mgha^{-1}) versus fuel consumed (Mgha^{-1}) for three fuel complexes on CSNWR.

Thermocouples performed well, with only five TCP's failing to record temperature during fires (3 % failure rate). Peak thermocouple temperature, representative of, but not equal to, peak flame temperature, did not vary among fuel complexes ($p = 0.2100$), and mean values ranged from 305 °C (longleaf pine-dominated plots) to 368 °C (turkey oak-dominated plots) (Figure 2.9). There was also no effect of fuel complex treatment on the rate of spread, whether using linear measurements ($p = 0.4560$) or triangulation measurements ($p = 0.5104$) (Figure 2.10). A comparison of methods shows that the values produced from the triangulation calculations are significantly lower than those produced from the linear calculations ($p < 0.0001$).
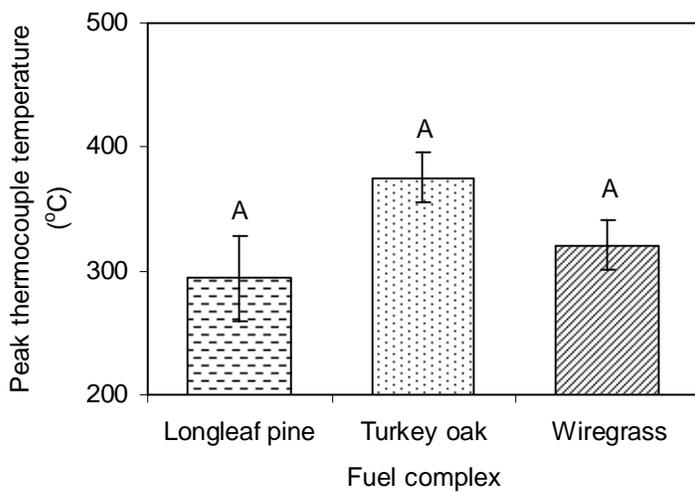
Figure 2.9. Effect of fuel complex on maximum temperature (°C) of thermocouple during prescribed burns. Means with the same letter are not significantly different, error bars represent standard error of the mean (model-based SE = 25.7 °C).
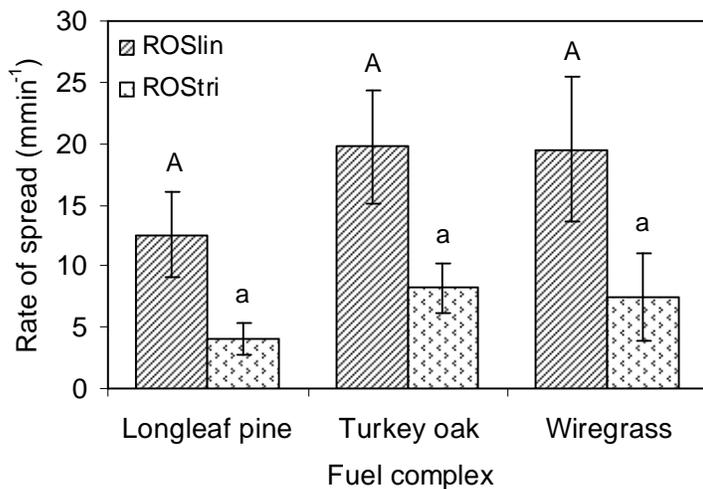
Figure 2.10. Effect of fuel complex on the rate of spread of burn (mmin[-1]), for rate of spread calculated using the linear method (RSOlin) and the triangulation method (ROStri). Means with the same letter are not significantly different, error bars represent standard error of the mean (model-based SE = 5.38 mmin[-1] and 3.08 mmin[-1] for ROSlin and ROStri, respectively).

Duration of burn above 60 °C varied among fuel complexes ($p = 0.0151$), though duration of burn above ambient temperature did not ($p = 0.1158$) (Figure 2.11). The residence time above 60 °C was significantly shorter in wiregrass-dominated plots than in turkey oak-dominated plots ($p = 0.0047$). The difference between wiregrass- and longleaf pine-dominated plots was close to significant ($p = 0.0594$), with mean duration above 60 °C higher in longleaf pine-dominated plots (5.14 minutes) than in wiregrass-dominated plots (3.99 minutes). These results show that the type and arrangement of fuels does influence how quickly the hottest portion of the fire lasts, lasting longest where fuel loads are high, or the fuel bed is denser, and passing quickly through the well-aerated fine fuel bed created by the combination of wiregrass and longleaf pine needles.

Differences in heat output were significant for both the area above 60 °C ($p = 0.0019$) and the area above ambient temperature ($p = 0.0003$) (Figure 2.12). For area above ambient temperature, the least squares means were significantly different among all fuel complexes, with turkey oak-dominated plots having the highest heat output, and wiregrass the lowest heat output. These values reflect the energy content of the fuels and the weight of the fuels consumed. Highest fuel weights were consumed in turkey oak-dominated plots, and though fuel weights were similar in both longleaf pine- and wiregrass-dominated plots, the fuels in the longleaf pine-dominated plots had higher energy content per weight than those in the wiregrass-dominated plots.
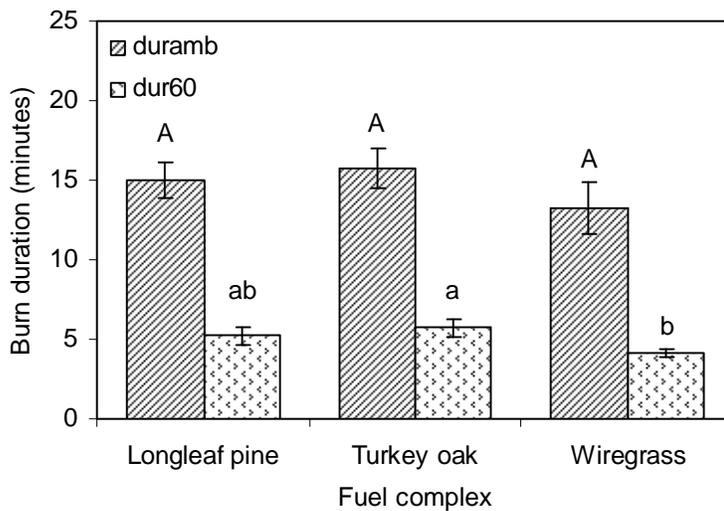
Figure 2.11. Effect of fuel complex on duration of burn (minutes), for duration above ambient temperature (duramb) and duration above 60 °C (dur60). Means with the same letter are not significantly different, error bars represent standard error of the mean (model-based SE = 0.9 min and 0.4 min for duramb and dur60, respectively).
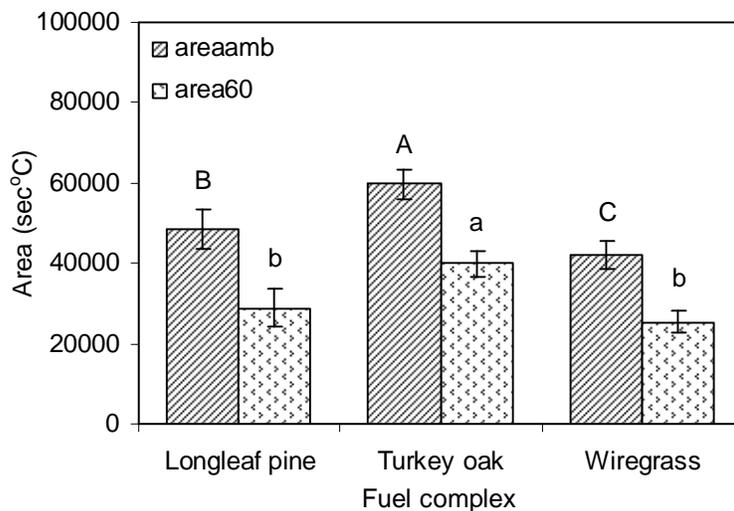
Figure 2.12. Effect of fuel complex on the area under the time-temperature curve (sec°C), for area above ambient temperature (areaamb) and area above 60 °C (area60). Means with the same letter are not significantly different, error b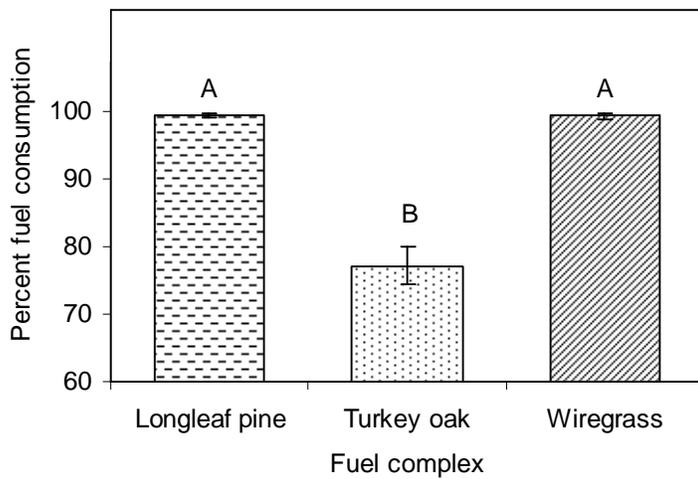ars represent standard error of the mean (model-based SE = 2356 sec°C and 2402 sec°C for areaamb and area60, respectively).

DISCUSSION

My analysis of energy and ash content produced a range of values similar to those found in other studies from longleaf pine ecosystems (Golley 1961, Hough 1969), and within the range reported for other ecosystems (Dickinson and Kirkpatrick 1985, Dimitrakopoulos and Panov 2001, Dibble et al. 2007). However, energy content for the same species can vary by site (Hough 1969) and season (Golley 1961), and my values represent energy contents of sandhills species during the dormant season. It is possible that live tissue sampled mid-summer could vary from that sampled in winter. Additionally, previous research has reported that energy content decreases and ash content increases as litter decomposes (Hough 1969). Because I sampled fresh litter of the woody species (longleaf pine and turkey oak), it is likely that litter deposited lower in the fuel bed may contain less energy and more ash than my reported values.

The energy contents of fuels reported in this study play an important role in fire behavior when those fuels burn. Longleaf pine needles had high energy content, and longleaf pine-dominated plots had higher heat output than wiregrass-dominated plots with similar fuel weights. These findings supports previous field studies that reported increased fire temperatures in areas with higher pine densities (Platt and others 1991, Williamson and Black 1981). Though I did not study field burning properties of little bluestem, the difference in energy and ash content between wiregrass and little bluestem is notable as it may have significant implications on fire behavior. Wiregrass, with higher energy content and lower ash content, is likely to be more readily flammable and generate a higher heat output than little bluestem. These differences could result in an

increased rate of spread and higher fire temperatures in areas dominated by wiregrass as opposed to areas dominated by little bluestem.

The physical properties of fuel complexes at my study sites differed in many ways from sites used in earlier studies on fuels and fire in the sandhills. Williamson and Black (1981) considered only oak-dominated areas without a pine canopy; at CSNWR, turkey oaks are found throughout areas under a longleaf pine canopy. Excluding pine canopy cover would not be representative of the system I studied. In fact, I found that longleaf pine litter was present in similar quantities across the landscape, with other fuel components differentiating the three fuel classes.

Potential fuel weight varied from 4.2 to 18.5 Mgha^{-1} in my plots, falling on the lower end of 2.1 to 59.0 Mgha^{-1} reported by Thaxton and Platt (2006). The smaller range of my values is likely due to the exclusion of sites containing 100-hour or larger pine fuels. The decision to exclude large fuels was made to minimize the influence of confounding factors on fire temperature and behavior; this exclusion is justified because fires are carried by fine fuels in the ecosystem studied.

Plots dominated by turkey oak stems had the highest litter weights. In addition, measures of fuel chemistry and arrangement indicate that the litter in these plots is relatively high in energy content and well-aerated. These results suggest the potential for increased fire intensity and temperature in turkey oak-dominated sites compared to longleaf pine litter-dominated sites. Therefore, it is not surprising that the area under the time-temperature curve was highest in turkey oak-dominated plots. My findings do not support the results of studies noting decreased flammability of oak litter and lower

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temperature burns near oaks as compared to pines (Rebertus et al. 1989b, Williamson and

Black 1981). However, comparisons with those studies are difficult to make because oaks

were isolated from pines in those studies, which is not the case on the CSNWR.

The significant differences in litter arrangement confirmed previous speculations

about variation in litter placement (Rebertus et al. 1989b, Williamson and Black 1981). I

showed that wiregrass- and turkey oak-dominated sites have an aerated fuel bed

compared to longleaf pine litter-dominated sites. Pine needle litter lodges in the

wiregrass, as Hendricks and others (2002) found in a coastal plain longleaf pine

ecosystem. Turkey oak leaves curl and pack loosely, also catching pine needle litter in a

more elevated position. Due to the lack of vegetation in the longleaf pine litter-dominated

plots, a denser litter bed was recognized, in which needles are packed horizontally. Given

similar weights of fuel, a looser arrangement potentially will increase air flow prior to

and during burns, reducing the moisture content of the litter and increasing the rate of

spread of the fire. However, my results do not show significant differences in rate of

spread among fuel complexes. This suggests that either the differences I saw in litter

arrangement are insufficient to affect the rate of spread of the fire, or that the area

dominated by a specific fuel complex is too small to have an effect on rate of spread. In

addition, the aerial method of ignition creates several spot fires which burn on all sides.

Heading, backing, and flanking fires will occur, and rate of spread for each may vary

significantly.

My results suggest that the method of rate of spread analysis can significantly

alter values. Rate of spread fell between 3.7–8.6 mmin^{-1} for triangulation calculations,

and 11.7–20.3 mmin^{-1} for linear calculations. Rate of spread values determined in other parts of the longleaf pine ecosystem (0.5–1.1 mmin^{-1} in the Alabama coastal plain (Kennard et al. 2005), and 1.4–7.8 mmin^{-1} in the Florida sandhills (Lippincott 2000)) suggest that the triangulation method produces more accurate results. The linear method of calculating rate of spread of the fire may overestimate the metric. Our calculations using the linear method were 264 % higher than those found when using the triangulation method. Two points may be hit by the fire almost simultaneously, but by different parts of the flaming front. The linear method assumes they are hit by the same part of the flaming front, as it passes directly from one point to the other. This method will only produce an accurate result if the path of the fire's spread matches the path of a straight line connecting the two points. This cannot happen for every combination of points in our five-point design, and may happen for none, causing our plot mean rate of spread to be higher than actual rate of spread. Iverson et al. (2004) minimized this source of error in their linear calculations by setting maximum rate of spread at 25 mmin^{-1} and excluding any observations with higher values. The triangulation method described by Simard et al. (1984) and used in other studies (Bova and Dickinson 2008) eliminates the error associated with disregarding the direction of fire spread by first determining the angle of the fire spread relative to a side of the triangle, followed by calculating the rate of spread in this direction. There is still error associated with the triangulation method, as it assumes a constant direction and rate of spread. Because results of neither method were conclusive at showing differences among fuel complexes, other measures of fire

behavior, such as duration or residence time, may be better metrics for indicating how fuel complexes on the small scale affect the movement of fire in the sandhills ecosystem.

The fire parameters combining time and temperature variables showed a response to fuel complex while peak temperature failed to show an effect of fuel complex. Molina and Llinares (2001) found similar results in their study in a Spanish shrubland, suggesting that measures related to time and temperature (eg. duration and area under time-temperature curve) are more useful than maximum temperature when comparing fuel complexes and their effects on fire behavior. In addition, measurements which integrate time and temperature minimize the effects caused by the heating and cooling lag times of thick thermocouples, which can affect peak temperature (Kennard et al. 2005).

Duration above 60 ℃ appears to be a better measure than duration above ambient temperature at distinguishing between fuel complexes. The larger variance noticed in the duration above ambient may, in part, be due to the effect of active flaming areas outside the plot boundary (and potentially in a different fuel complex) causing passive heating within the plot and extending the duration of temperatures barely above ambient temperature. The placement of all thermocouples well-within the plot boundaries and the method of determining the end time for duration above ambient were chosen to minimize the chance of passive heating affecting results, however its success is unknown.

The shorter duration of burn above 60 °C in the wiregrass-dominated fuel complex than in the turkey oak-dominated one, suggests that the combination of a well-aerated fuel bed with a low potential fuel weight (as found in the wiregrass fuel complex) affects fire behavior. As the duration of high above-ground temperatures increases, the

period of plant- and soil-heating is extended. Fuel complexes that create a longer residence time of high temperatures (such as the turkey-oak dominated plots) may have the potential to heat the upper regions of the soil to higher temperatures, increasing damage to plants and soil organisms. Both turkey oak and wiregrass withstand fires by sprouting back after burns, but it is unknown what intensity and duration of burn might cause wiregrass plant mortality. Wiregrass sprouts back from the plant crown at ground level, and studies on plant heating of bunchgrasses during fire show that the plant crown heats slowly. Even after several minutes of a high temperature burn, the temperature in the crown may only peak at 50 ºC, and temperature of the soil under the plant will rise only slightly (Robberecht and Defossé 1995). A detailed study within the longleaf pine ecosystem would be necessary to know if wiregrass plants heat in this same manner, and what flame temperature and residence time is required to cause mortality of wiregrass plants.

Fine fuels were almost completely consumed by the prescribed burns, but larger fuel size classes were not. These larger fuels differ from the fine fuels not just in their dimensions, but also in their moisture content and placement. Turkey oak stems have higher moisture content than the litter, and they are in an upright position, removed from the flammable and energy-rich leaf and needle litter layer. These qualities make them a less easily flammable fuel in the sandhills, where fire temperature and burn duration are shorter than in other ecosystems (Molina and Llinares 2001). Though consumption of the standing turkey oak stems was not complete, all stems in the plots were top-killed. Turkey oaks are vigorous resprouters, though, and by May there was fresh growth from

the bases of most stems. I did not determine cover before and after burns, but this rapid regrowth suggests that prescribed burns at the sandhills are not changing the cover of turkey oak in the understory. Reinhart and Menges (2004) also found little effect of fire on the cover of hardwoods already reduced to the understory prior to the burn.

Heterogeneity in vegetation and litter on a small scale has been shown to affect species composition and abundance (Platt and others 2006) and fire effects such as hardwood mortality (Rebertus et al. 1989b, Thaxton and Platt 2006). Fire is used at CSNWR to reduce fuel loads, suppress hardwoods in the understory (especially turkey oak) and maintain the biodiversity of the system. The observed presence of different fuel complexes (with distinct physical and chemical differences), and documented effects of fire behavior parameters such as fuel consumption, duration of burn, and heat output, shows that prescribed fires will burn heterogeneously within longleaf pine stands.

In areas where hardwood cover has increased in the understory, we can expect that fire behavior will reflect the higher fuel loads, creating burns with a longer residence times of high temperatures, and producing a higher heat output over the course of the burn. In contrast, the wiregrass-dominated groundlayer vegetation desired by land managers creates faster-moving fires with low residence times and low heat output. Effects of burns on vegetation were not studied, and the ability of one vegetation complex to create fire effects selecting for or against certain species cannot be determined without further research, though such effects have been suggested in other experiments (Menges and Hawkes 1998, Thaxton and Platt 2006).

CHAPTER 3.

EFFECTS OF BELOW-GROUND COMPETITION AND SURROUNDING

VEGETATION ON WIREGRASS SEEDLING ESTABLISHMENT AND GROWTH

INTRODUCTION

The xeric sandhill plant community exists along the fall-line, running from North

Carolina to Alabama, and includes some of the most nutrient-poor and driest soils within

the longleaf pine ecosystem (Christensen 1981, Peet and Allard 1993). The understory is

dominated by wiregrass (*Aristida stricta* Michx.) in North Carolina and northern South

Carolina (Peet 1993), but herbaceous cover is not continuous and bare sand is exposed at

the soil surface (Peet and Allard 1993). Scattered turkey oak (*Quercus laevis* Walt.) is

present in the understory, but is kept out of the midstory due to frequent burning. The

canopy on these sites is monospecific, with longleaf pine (*Pinus palustris* Mill.) in the

overstory (Christensen 1981). Historically, the structure and species composition of the

system was maintained by frequent, low-intensity surface fires (Frost 1993, Streng et al.

1993, Glitzenstein et al. 1995, Brockway and Lewis 1997, Platt 1999, Sorrie and

Weakley 2006).

In the past century, timber harvest, land use change, and fire suppression have

significantly reduced the dominance of the longleaf pine ecosystem across its range. Of

the three percent which remains, only half has intact understory vegetation (Noss 1989,

Frost 1993). Many dominant species in the ecosystem are dependent on fire to regenerate,

and the loss of this key ecosystem process altered the plant community. Wiregrass only

produces viable seed in large quantities following burns (particularly growing-season burns) (Abrahamson 1984). Because seed production had become so rare following fire suppression, it was once thought by some that wiregrass usually reproduced vegetatively (Clewell 1989). As a result of fire suppression, structurally, the open savannas disappeared: no longer top-killed by fire, hardwoods began to dominate the midstory, and groundlayer vegetation was further impacted (Gilliam et al. 1993, Glitzenstein et al. 2003).

Reestablishing the groundlayer vegetation is crucial for the restoration of the ecosystem. Clewell (1989) suggests that the herbaceous layer functions as a significant fuel component to carry the ground-fires necessary to maintain the ecosystem. In Chapter 2, I demonstrated that herbaceous ground-layer vegetation creates an aerated fine fuel bed with a distinct associated fire behavior. The herb layer is also an important food source for wildlife (Means 2006), and has been associated with increased fitness of the federally protected red-cockaded woodpecker (RCW, *Picoides borealis*) (James et al. 2001). On the Carolina Sandhills National Wildlife Refuge (CSNWR), land management goals include restoration of wildlife habitat (especially for the RCW), and the main management tool is prescribed fire (U.S. Fish and Wildlife Service 2009). Prescribed fire is used to keep turkey oak out of the midstory, and to encourage regeneration of desirable species such as wiregrass. However, as in other xeric sandhill areas with prior fire exclusion, turkey oak cover increased in the understory (Christensen 1981, Rebertus et al. 1989a), and where the soil was disturbed, wiregrass is slow to recover (Clewell 1989). Understanding existing limitations to wiregrass reestablishment will benefit active

management, such as seeding and planting, as well as help encourage natural regeneration.

Vegetation within the longleaf pine stands on CSNWR is heterogeneous at several levels. Stands are distinct based on stand age and history. For example, old plantations may have denser canopy cover and less herbaceous cover than intact, mature stands. Small-scale variation within stands also exists. I have observed small patches dominated by single species in the understory (see Chapter 2), and in the overstory the longleaf pine canopy can be patchy. The patchiness in the longleaf pine ecosystem has also been reported by others (Rebertus et al. 1989a, Thaxton and Platt 2006). This heterogeneity in existing vegetation creates a diverse set of conditions for wiregrass establishment. Above ground, light and litter may vary, and below ground, moisture and nutrients may vary with species composition and structure (Palik et al. 1997, West and Donovan 2004, Pecot et al. 2007). Several studies have addressed the role of above- and below-ground competition on longleaf pine seedling establishment and growth (Palik et al. 1997, Brockway and Outcalt 1998, McGuire et al. 2001, Palik et al. 2003, Pecot et al. 2007), but fewer have examined its effect on herbaceous species (Harrington et al. 2003), wiregrass in particular (Mulligan and Kirkman 2002a, Mulligan et al. 2002), or competition from hardwood species (Kush et al. 1999).

In this chapter, I tested the effect of small-scale variation in understory vegetation on the success of planted wiregrass seedlings and seed, using three vegetation classes visually identified on CSNWR: (1) sites with no understory vegetation (dominated by longleaf pine needle litter), (2) sites dominated by turkey oak stems, and (3) sites

dominated by wiregrass. I use a secondary treatment of root exclusion to test the significance of below-ground competition on seedling and seed success. Environmental variables such as available light, litter, and soil moisture were monitored to describe differences among both vegetation and root exclusion treatments.

MATERIALS AND METHODS

Study Area

The study is located in the upland longleaf pine ecosystem in the xeric sandhills on Carolina Sandhills National Wildlife Refuge (McBee, SC, 34.58N, 80.23W). Elevations on the refuge range from 70 m along Black Creek to 180 m on the highest ridges, while study sites ranged from 122 to152 m. Mean annual precipitation is 110 cm and mean annual temperature is 15.6 °C. All study sites were on excessively drained Alpin sands (Morton 1995), and all were burned by refuge staff in the winter and spring of 2008, prior to planting.

Experimental Design

I used a split-plot design, with the whole-plot-level treatment reflecting the dominant vegetation, and the split-plot treatments limiting below-ground competition. There were three vegetation treatments, one dominated by wiregrass (plant densities ranged from 3–8 wiregrass clumps per square meter prior to burns), one dominated by turkey oak stems (stem densities ranged from 2–5 live stems per square meter prior to burns), and one devoid of vegetation, containing only longleaf pine needle litter. I

selected 4 m by 4 m plots visually, based on the presence of vegetation which fell into one of the three vegetation treatments. I identified vegetation treatments prior to prescribed burns, and though above-ground plant matter was consumed or top-killed in the prescribed burns, both wiregrass and turkey oak are vigorous resprouters, and by the time of experiment installation in mid-May, both species exhibited fresh growth. I used two below-ground competition treatments: one which excluded roots and one with no exclusion. Root exclusion was accomplished by creating a barrier with buried polyvinylchloride (PVC) pipe (Mulligan and Kirkman 2002a). Plots were divided into 36 planting sites, each 50 cm apart. Half of the sites received a PVC pipe root exclusion treatment, while half received no exclusion. Pipe layout was regular, with a row of six planting sites in pipes, alternating with a row without pipes. Where factors interfered with a planting site, such as existing vegetation or pine roots, I chose a new planting site within the plot at least 50 cm from any other site. I had seven blocks, six had one plot of each vegetation treatment, and one had two plots of each vegetation treatment.

Of the 36 planting sites, I assigned 12 to be planted with seedlings to study treatment effects on seedling survival and growth, 12 to receive seeds to study effects on seedling establishment, and 12 as unplanted controls to monitor for natural establishment and recruitment of wiregrass. These were split evenly between the root exclusion and no exclusion treatments and randomly assigned to the planting sites.

Seed Collection and Greenhouse Seedling Production

Wiregrass seed was hand-collected in November 2007 from three sites on CSNWR. Seed was stored outdoors in a dry location until used, and exposed to natural temperature variation though the winter. I conducted germination tests in January 2008 to determine germination rates for each site, and used seed from the site with the highest germination rate (22.5 %, Figure A-4) for the experiment. On March 9, 2008 I sowed seeds in 105-cell flats. Approximately five seeds per cell were sown in a standard germination mix (55 % peat, 45 % perlite). Cells were 3.5 cm deep and hexagonal in shape, with 3.1 cm between opposite sides on the top and 2.1 cm between opposite sides on the bottom. In the event that more than one seed germinated per cell, the later germinates were clipped just above soil-level. Seedlings were kept in a greenhouse at Clemson University for almost two months, then moved outdoors two weeks prior to planting.

Plot Installation and Outplanting

The PVC pipe root exclusion devices were 25.4 cm long and 10.2 cm in diameter. They were hammered into the ground until flush with soil-level so as not to interrupt surface flow of water. All planting sites were located such that the edge of the approximately 10 cm-diameter circular planting zone was at least 5 cm away from existing turkey oak stems, but planting sites were sometimes flush with the base of an existing wiregrass clump.

Seedlings and seeds were planted at study sites from May 13-15, 2008. Seedling treatment sites received two seedlings each, planted approximately 5 cm apart. Seedlings were two months old when planted, and were watered once soon after planting, each set of seedlings receiving approximately 50 mL water). Seed treatments had 100 wiregrass seeds each. The soil surface was disturbed slightly prior to depositing seeds using a common garden hand cultivator. A small quantity of sand and fine litter fragments were thrown over the seeds to keep them in place, but not enough to bury them.

Monitoring Survival, Growth and Germination

Every two to four weeks between planting and November 2008 the study plots were visited to monitor survival and growth of the seedlings and germination of the seeds. The number of green tillers was recorded for all live plants (up to a maximum of 20) as a measure of plant growth. Each seedling in a pair was treated independently when recording survival and tiller number. The number of germinants was recorded at every sampling time in seed treatment sites. This measure does not represent new germinants since the last sampling date, but rather all surviving germinants at that time.

This data was used to determine the number of germinants per 100 seeds, seedling survival, end tiller production per initial investment, and the change in mean tiller number per live plant over time and among treatments.

Monitoring Environmental Factors

The small-scale variation in vegetation present on CSNWR may be associated with several factors. Light availability, soil moisture, and litter may be more useful for describing vegetation treatments than the understory species composition alone. These environmental and physical components are known to affect the growth of species in the herbaceous layer (Kirkman et al. 2001, Mulligan and Kirkman 2002a, Harrington et al. 2003, Pecot et al. 2007) and may be indicators of seed and seedling success.

Available light in the understory, basal area of canopy species and litter weight were measured at the plot level to determine if differences existed in relation to the vegetation treatments, and soil moisture was measured at the seedling level to determine if there was an effect of the root exclusion treatments. Precipitation values were recorded during the growing season from a weather station on CSNWR (Mesowest, station ID JEFS1). The weather station is located at most 12.5 km from a study site, and daily and weekly totals are presented in this study.

Soil moisture

In mid-September I took soil samples from 0–10 cm using a soil corer for moisture content analysis. I randomly chose two control sites for both root exclusion and no exclusion treatments in each plot to collect samples from. Soil samples were immediately transferred to zip-lock plastic bags and placed on ice in a cooler. Within 24 hours, I measured their wet weights, and I measured their dry weights following 48 hours in an oven at 65 ℃. These values were used to determine percent soil moisture by weight.

There had been no precipitation in the three days prior to sampling, and just over 5 cm in the ten days prior to sampling.

Available light

Hemispherical photography and instantaneous measurements of photosynthetically active radiation (PAR) are often used to characterize spatial and temporal patterns in understory light availability (Anderson 1964, Canham 1988, Palik et al. 1997, Battaglia et al. 2002, Battaglia et al. 2003, Valladares and Guzmán 2006). Estimates of seasonal light availability from hemispherical photos are considered a more useful measure than instantaneous measures of PAR with a ceptometer, because the instantaneous measurements do not reflect the seasonal changes in the position and the amount of radiation of the sun, and thus do not represent the light available to the seedlings over the course of the growing season (Canham 1988). However, ground-level measurements are difficult to make using hemispherical photo equipment, while ceptometer measurements can be made flush with the ground at seedling-level. The versatility and ease of ceptometer measurements make them convenient, but their limitations must be recognized. I calculated available light using both methods.

Instantaneous light measurements were made to estimate available PAR, with percent full sunlight calculated at ground-level. Measurements of PAR (wavelengths between 400-700 nm) were taken with an AccuPAR ceptometer (Decadon Devices Inc). Four measurements were taken at the center of each plot, two with the ceptometer pointing east and two with it pointing west. Plot means ($PAR_{seedling}$) were used for further

analysis. Simultaneous to plot measurements, total available sunlight was determined in a nearby open area above all vegetation using a LI-1400 datalogger (LI-COR, Inc.), with values averaged each minute to create means (PAR_{full}). The corresponding PAR_{full} was used to compare with each $PAR_{seedling}$ to determine percent full sunlight reaching the seedlings using equation (1):

$$\text{Percent full sunlight} = (PAR_{seedling}/PAR_{full})*100 \qquad\qquad (1)$$

Hemispherical photos were taken to estimate season light availability through the calculation of gap light index (GLI) and weighted canopy openness (WCO). In September, photos were taken at the center of each plot, at dawn or dusk, with the sun below the horizon. Equipment used was a Nikon Coolpix 4500 camera with a Nikon LC-ER1 fisheye lens. The camera and lens were mounted on a self-leveling mount (Delta-T Devices Ltd) and tripod at a height of 137 cm. One photo was taken per plot, and photos were analyzed using HemiView version 2.1 (Delta-T Devices Ltd 1999).

First, images were classified by determining a threshold gray level for each photo to distinguish between canopy and open sky. For calculations, the hemisphere was divided into sectors, with an azimuth resolution of 8 and a zenith resolution of 18. WCO is determined based on canopy openness in each of these sectors, the size of the sector, and the proximity of the sector to the zenith, with openings closer to the zenith given more weight than those near the horizon (Rich et al. 1999, Battaglia et al. 2003).

GLI is a measure of available light over the course of the year. It takes measures of canopy openness, the location of canopy gaps, the path of the sun, and the seasonal changes in the angle of the sun into account to determine the percentage of incident PAR transmitted to the understory over the course of an entire growing season (Canham 1988). GLI is estimated using equation (2) (Canham 1988):

$$\text{GLI} = [(T_{diffuse}P_{diffuse}) + (T_{beam}P_{beam})]*100 \qquad (2)$$

P_{beam} and $P_{diffuse}$ are the proportions of incident seasonal PAR received at the top of the canopy, as either direct beam or diffuse radiation, respectively. These values must be provided, and I followed other authors in using 0.5 for both P_{beam} and $P_{diffuse}$ (Battaglia et al. 2002, Battaglia et al. 2003). T_{beam} and $T_{diffuse}$ are determined using Hemiview, where T_{beam} is the proportion of direct beam radiation transmitted to the understory, and $T_{diffuse}$ is the proportion of diffuse sky radiation transmitted to the understory. Estimations of T_{beam} and $T_{diffuse}$ are based on several parameters. I used a transmissivity of 0.8, a diffuse proportion of 0.1, a solar constant of 2900 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Rich et al. 1999), and used the uniform overcast sky model, where the intensity of diffuse PAR is assumed uniform across the sky (Canham 1988). I analyzed each photo twice, and used a mean for each photo in further statistical analysis (Vallardes and Guzmán 2006).

Basal area

The basal area of canopy species was estimated at plot center of all plots. Measurements were made using a standard forester's prism.

Litter measurements

Litter weights were estimated for each plot in July, 2008. Litter samples were collected from a 1 square meter area adjacent to each plot, oven-dried, and weighed.

Statistical Analysis

I used PROC MIXED (SAS Institute Inc. 2008) to run analyses of variance (ANOVA) to test for significant differences in the number of tillers per live plant, total tiller production and soil moisture content among vegetation treatments, root exclusion treatments, and interactions between the two. I tested for differences in available light, pine basal area, and ground litter weight just among vegetation treatments using a similar model in PROC MIXED. I compared seedling survival and the number of germinants per 100 seeds among vegetation treatments, root exclusion treatments, and interactions between them using PROC GLIMMIX, assuming a binomial distribution of the data. In all mixed models, block and block*vegetation terms were included as random effects, to account for variation among blocks. In both PROC MIXED and GLIMMIX, I used least squares means tests to determine means and pooled estimates of standard error used to make specific comparisons among treatments, and I used PROC MEANS to calculate

arithmetic means and standard errors presented in figures. All levels of significance

shown in figures are based on α = 0.05.

RESULTS

Seed and Seedling Survival and Growth

The root exclusion treatments caused significant increases in the number of

germinants, the survival of planted seedlings, and the tiller production of live plants

(Table 3.1). Differences among vegetation treatments were only apparent early in the

monitoring period, and there was no interaction between root exclusion and vegetation

treatments at any sampling time.

Table 3.1. A summary of F-values and significant differences among root exclusion
treatments (upper F-value) and vegetation treatments (lower F-value) for the number of
germinants, seedling survival rate, and number of tillers per live plant at all sampling
dates after planting and seed distribution.

Date	# Germinants	Seedling survival	# Tillers per live plant
6/10		$F = 48.38^*$ $F = 6.40^\dagger$	$F = 19.80^*$ $F = 2.78$
6/24		$F = 50.26^*$ $F = 3.98^\dagger$	$F = 5.56^*$ $F = 1.73$
7/14	$F = 19.5^*$ $F = 4.18^\dagger$	$F = 56.27^*$ $F = 2.32$	$F = 23.82^*$ $F = 3.55$
7/24	$F = 29.72^*$ $F = 1.55$	$F = 53.97^*$ $F = 2.72$	$F = 47.36^*$ $F = 3.31$
8/22	$F = 21.44^*$ $F = 1.56$	$F = 53.00^*$ $F = 2.60$	$F = 65.27^*$ $F = 1.33$
9/13	$F = 20.14^*$ $F = 2.20$	$F = 54.52^*$ $F = 3.39$	$F = 70.13^*$ $F = 1.77$
10/4	$F = 19.48^*$ $F = 2.06$	$F = 53.28^*$ $F = 2.33$	$F = 83.27^*$ $F = 1.49$

* signifies significant differences among root exclusion treatments at α = 0.05
† signifies significant differences among vegetation treatments at α = 0.05

Establishment from seed, measured as the number of germinants per 100 seeds in the seed treatments, was much lower than the greenhouse germination rate of the seed (22.5 %), with the final mean rate of surviving germinants not over 1% in any treatment at day 144 (October 4, 2008) (Figure 3.1). Control plots saw no seedling recruitment, so it is assumed all germinants recorded originated from the seed distributed. The number of germinants was significantly different between root exclusion and no exclusion treatments at all sampling times following the onset of germination in early July (Table 3.1) ($p < 0.0001$ for July 14 and all subsequent sampling dates). Differences among vegetation treatments were only significant on July 14 ($p = 0.0418$), with longleaf pine- and wiregrass-dominated plots having higher numbers of germinants than turkey oak- dominated plots.

Seed germination appears closely linked to precipitation, with germination only beginning in July, once rain events became more frequent (Figure 3.1). Though precipitation was more regular for the rest of the growing season, many of the original germinants died before the end of July, and only minimal additional germination was recorded later in the season.

Survival of planted seedlings showed a similar response to root exclusion and vegetation treatments as did the number of germinants (Figure 3.2, Table 3.1). Seedling survival differed between root exclusion treatments at all sampling times following planting ($p < 0.0001$ for all), with root exclusion increasing the survival rate. Seedling survival only varied among vegetation treatments at the first two sampling times following planting ($p = 0.0128$ on June 10, and $p = 0.0474$ on June 24); again, longleaf

pine- and wiregrass- dominated plots had higher survival rates than the turkey oak-dominated plots. Survival decreased until late June, but stabilized before significant precipitation accumulation began in July.

The mean number of tillers per live plant was significantly greater where competing roots were excluded at all sampling times following planting ($p = 0.0196$ for 6/24 and $p < 0.0001$, for all others), though no significant difference was found among vegetation treatments at any sampling time (Table 3.1, Figure 3.3). Tiller number is a good approximation of plant biomass for wiregrass (Mulligan and Kirkman 2002a), and I used it not only to measure the size of live seedlings, but also to measure the end production per initial plant investment (measured as the mean number of tillers per plant investment) (Figure 3.4). This value is a measure of the biomass produced, incorporating both the number and size of surviving seedlings. The number of tillers per original plant invested was not significantly different among any treatments at the time of planting, confirming no conscious selection during planting. At the end of the growing season, the number of tillers per initial plant investment was significantly different between root exclusion treatments ($p < 0.001$), with the mean tiller number per original seedling rising from 1.44 to 4.99 over the first 144 days where competing roots were excluded, and dropping from 1.39 to 0.67 where root competition was not excluded. There was no difference among vegetation treatments ($p = 0.49$) and no interaction between the vegetation and root exclusion treatments ($p = 0.94$).
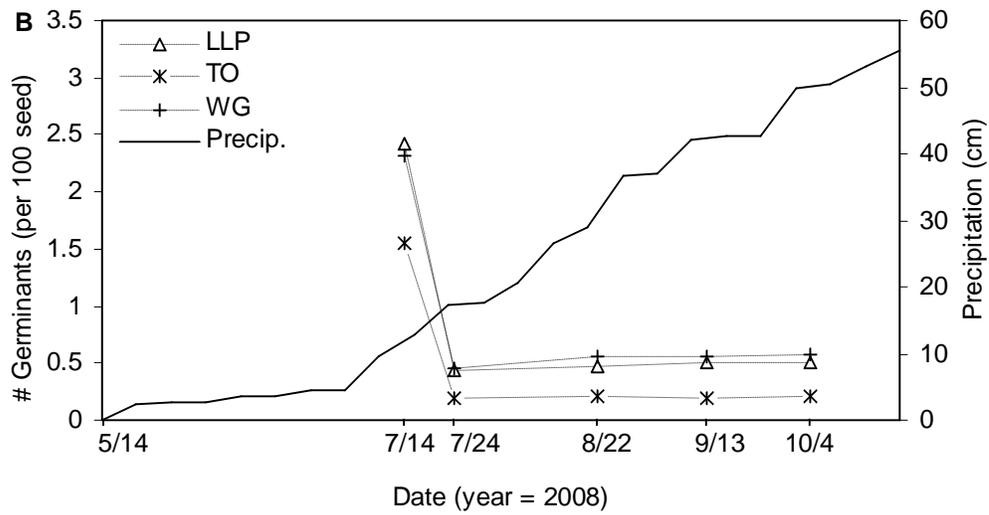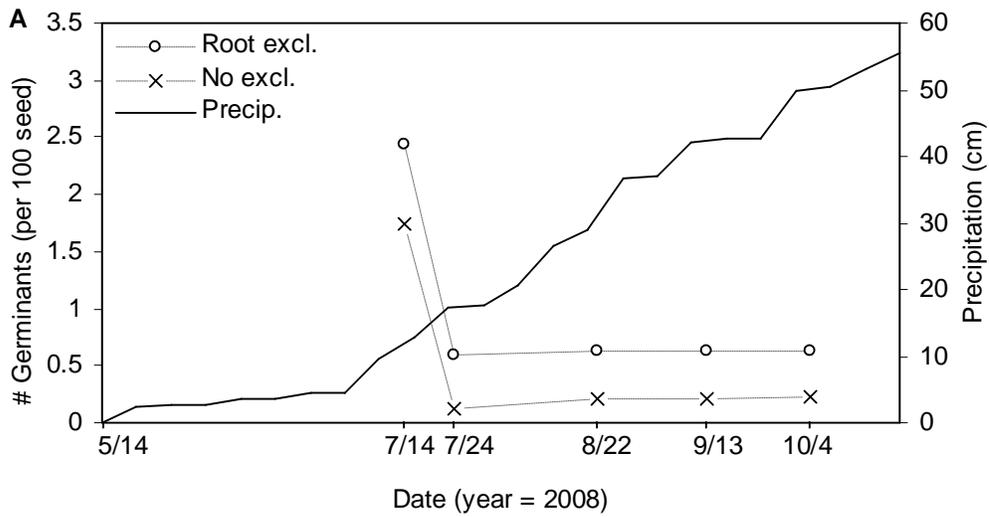
Figure 3.1. Establishment rate from seed, as a measure of the number of germinants per 100 seeds, among (A) root exclusion treatments and (B) vegetation treatments (LLP = longleaf pine, TO = turkey oak, and WG = wiregrass), with seasonal accumulated precipitation beginning from seed distribution on May 14, 2008.
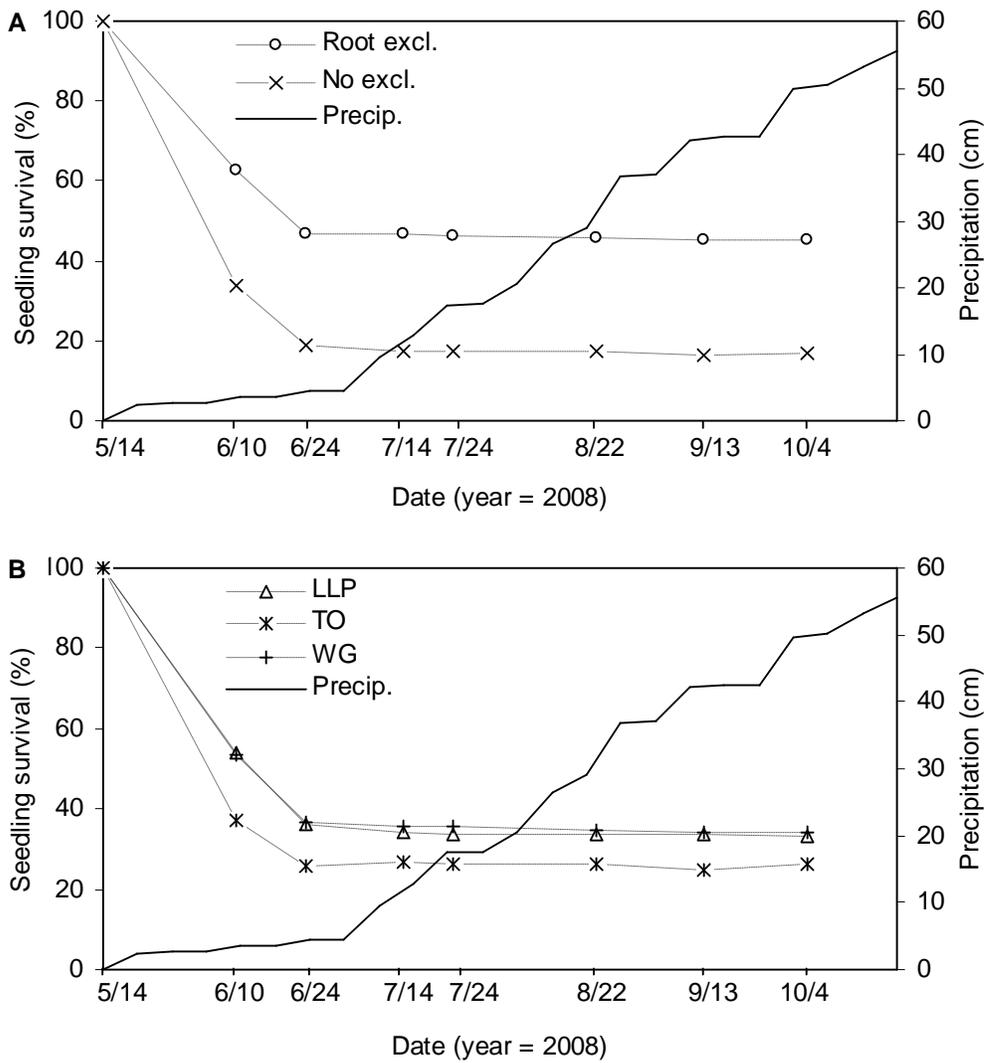
Figure 3.2. Seedling survival rate (%) of planted seedlings among (A) root exclusion
treatments and (B) vegetation treatments (LLP = longleaf pine, TO = turkey oak, and WG
= wiregrass), with seasonal accumulated precipitation beginning from planting on May
14, 2008.
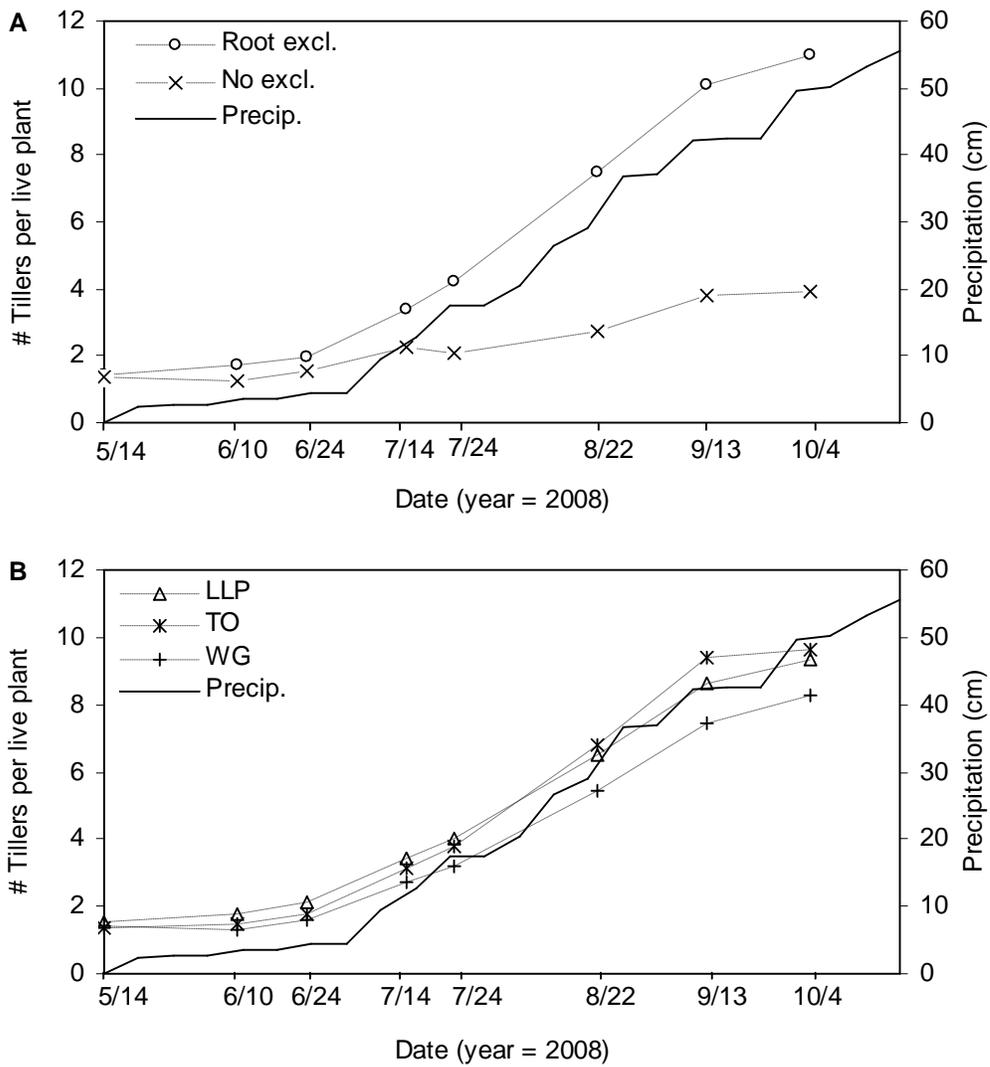
Figure 3.3. Mean number of tillers per live plant among (A) root exclusion treatments and (B) vegetation treatments (LLP = longleaf pine, TO = turkey oak, and WG = wiregrass), with seasonal accumulated precipitation beginning from planting on May 14, 2008.

Figure 3.4. Tiller production per initial plant at day 1 (May 14) and day 144 (October 4) among (A) root exclusion treatments and (B) vegetation treatments, and (C) interactions between vegetation and root exclusion treatments at day 144. Means with the same letter are not significantly different, error bars represent standard error of the mean.

Environmental Variables

Soil moisture content was measured at the seedling level, and can be used to compare effects of both sets of treatments (Figure 3.5). Mean soil moisture content (by weight) was greater where root exclusion occurred than where there was no exclusion (p = 0.0206), suggesting that soil moisture is a resource affected by below-ground competition on CSNWR. There was no effect of vegetation treatment on soil moisture (p = 0.5382) or interaction between the vegetation and root exclusion treatments (p = 0.2193). However, the mean soil moisture content is nearly identical for both root exclusion and no exclusion treatments in wiregrass-dominated plots, while it is higher where roots are excluded in the longleaf pine- and turkey oak-dominated plots.

Difference among vegetation treatments were not highly significant for any of the three measures of light availability (Figure 3.6) (p = 0.1061, 0.0991 and 0.0605 for percent full sunlight, WCO and GLI, respectively), though results are marginally significant for WCO and GLI. Mean available light was lowest at 137 cm in longleaf pine-dominated plots, and at ground-level, it was lowest in turkey oak-dominated plots. I cannot conclude that wiregrass seedlings were exposed to different levels of light competition, though, because for percent full sunlight, measured at seedling level, differences among treatments were not even marginally significant. Estimation of pine basal area confirms these results; as basal area did not differ among vegetation treatments (p = 0.2540) (Figure 3.7). Ground litter was primarily made up of fine fuels (longleaf pine needle litter), and the comparable basal area of pines also explains the similar litter weights (p = 0.6727) (Figure 3.8).
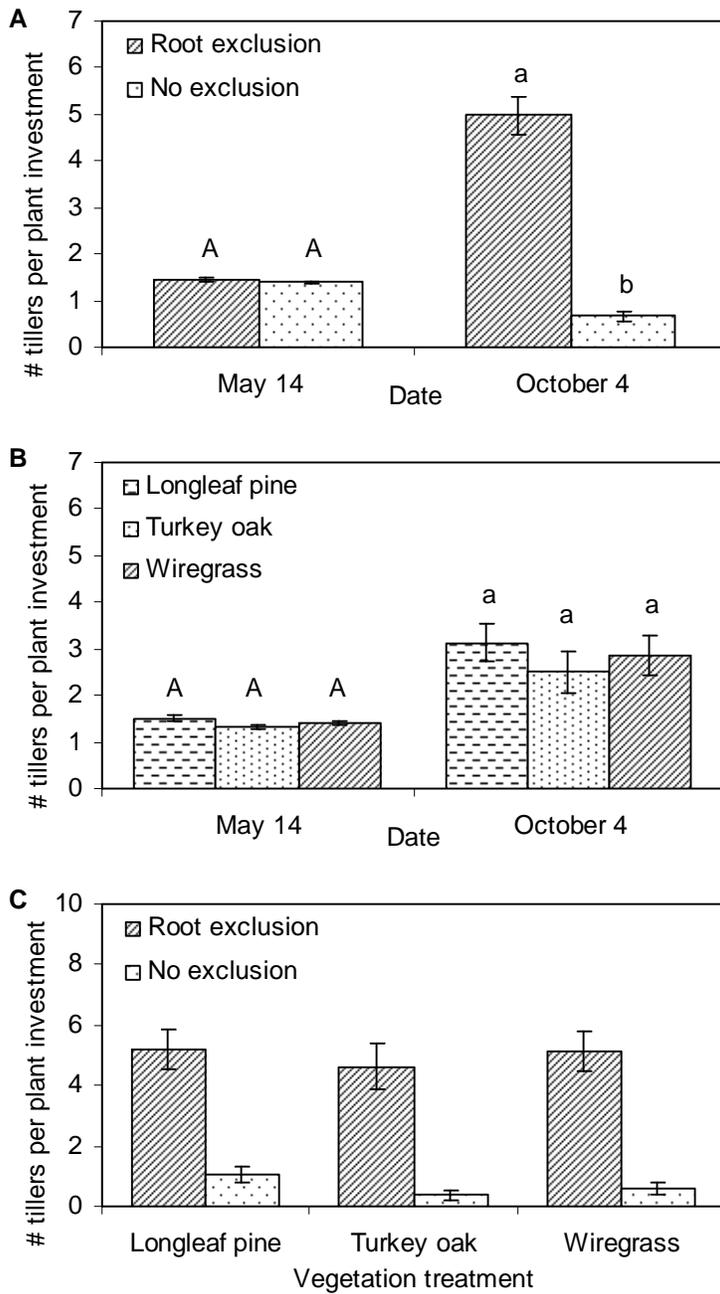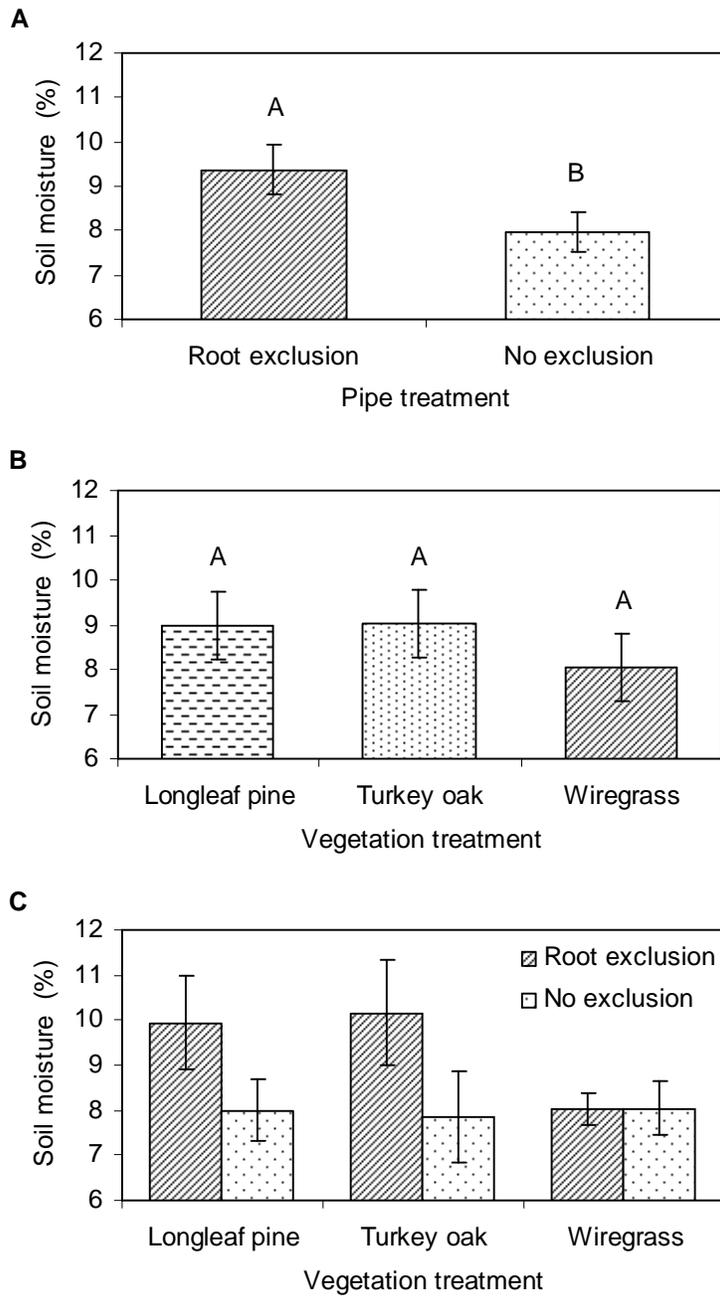
Figure 3.5. Soil moisture content (% by weight) among (A) root exclusion treatments, (B) vegetation treatments, and (C) interactions between root exclusion and vegetation treatments. Means with the same letter are not significantly different, error bars represent standard error of the mean (model-based SE = 0.57 %, 0.76 % and 0.90 % for (A), (B) and (C), respectively).
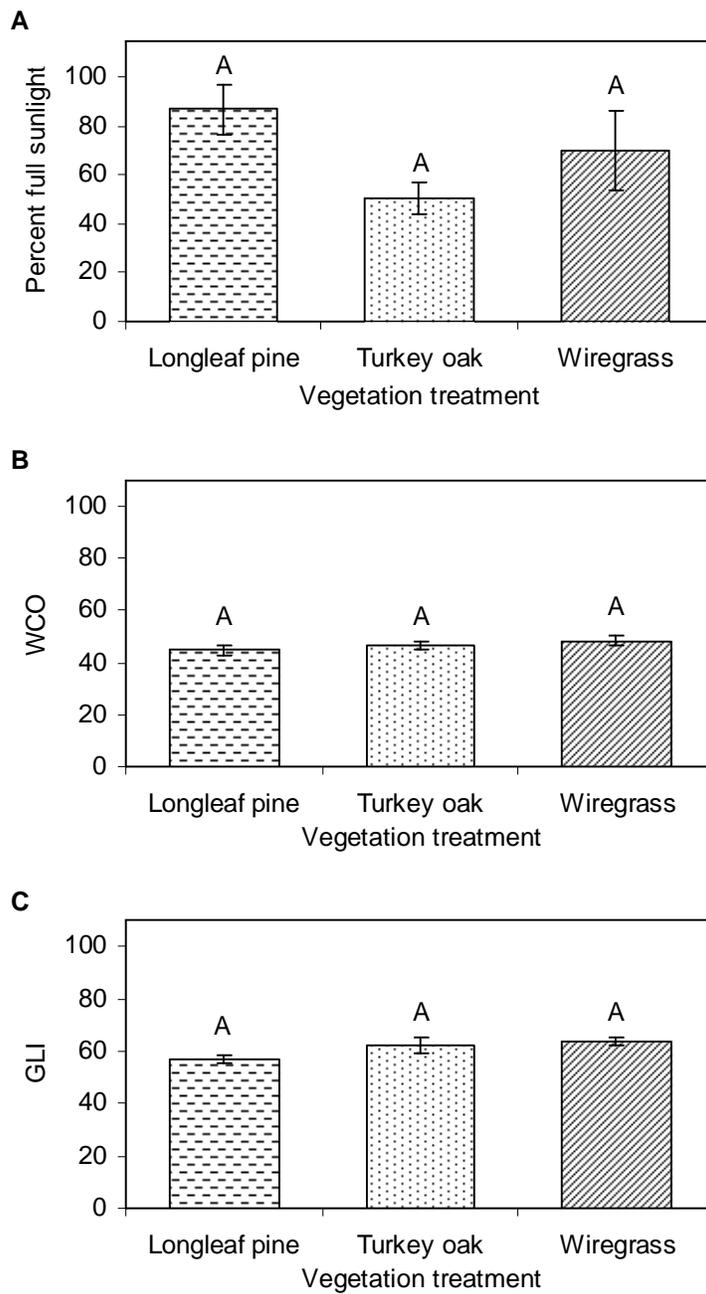
Figure 3.6. Available light measured as (A) percent full sunlight at ground-level, (B) weighted canopy openness (WCO) at 137 cm, and (C) gap light index (GLI) at 137 cm. Means with the same letter are not significantly different, error bars represent standard error of the mean (model-based SE = 12.1 %, 2.0 % and 1.3 % for percent full sunlight, WCO and GLI, respectively).
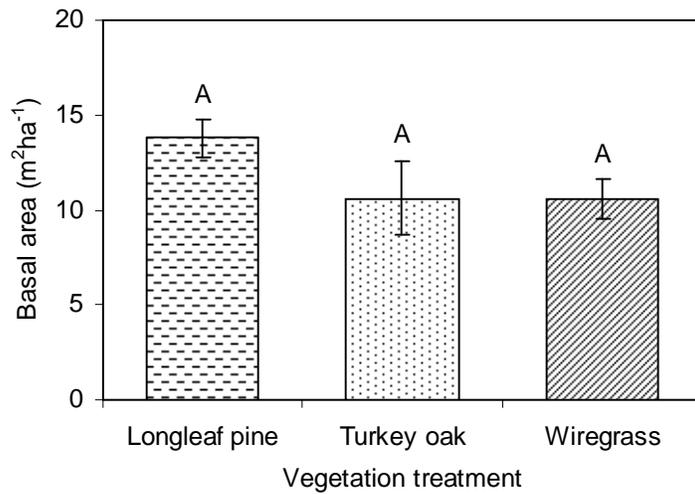
Figure 3.7. A description of basal area (m^2ha^{-1}) in each vegetation treatment. Means with the same letter are not significantly different, error bars represent standard error of the mean (model-based SE = 1.55 m^2ha^{-1}).
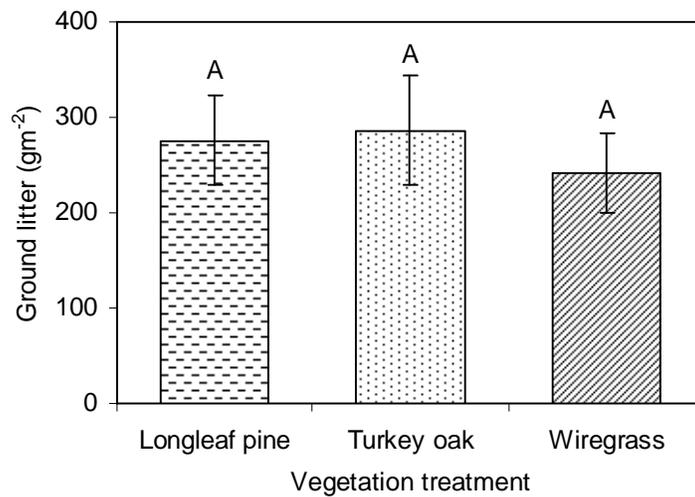
Figure 3.8. A description of ground litter (gm^{-2}) in each vegetation treatment. Means with the same letter are not significantly different, error bars represent standard error of the mean (model-based SE = 52.5 gm^{-2}).

DISCUSSION

My findings of increased number of germinants, seedling survival, and tiller production of wiregrass in root exclusion sites suggest that below-ground competition is a significant factor affecting the establishment and growth of wiregrass. However, the source of the below-ground competition (e.g. dominant species present) did not significantly affect wiregrass success by the end of the season, and neither did the surrounding understory vegetation show any correlation with the environmental and physical variables, above- or below-ground, I measured.

If differences in above-ground competition existed among vegetation treatments, they would be best estimated from the measures of available light or basal area of canopy species. My results suggest only a slight correlation between available light and understory vegetation, with the lowest available light at 137 cm found in the plots without existing understory vegetation (longleaf pine-dominated). The greater pine canopy cover may, in part, be responsible for the lack of groundlayer vegetation. But at ground level, longleaf-pine dominated plots had higher available PAR than either of the other vegetation treatments. Variation in light levels in a longleaf pine stand was found to be important in gap studies (Palik et al. 1997, Battaglia et al. 2002, Pecot et al. 2007), and increased understory production has been measured where there is more available light (Pecot et al. 2007). All my plots were under a scattered longleaf pine canopy, and the presence of, or proximity to gaps was not taken into account when deciding on plot placement, perhaps leading to the lack of highly significant differences in available light.

My results suggest that the combination of the pine canopy and understory vegetation may alter light levels at the ground level in a different way than the pine canopy does alone. At 137 cm, the lowest mean available light level was found in longleaf pine-dominated plots, while at ground level, the highest mean available light level was found in longleaf pine-dominated plots, suggesting that the lack of ground-layer vegetation in the longleaf pine-dominated plots may increase the light available to seedlings, proportional to the other vegetation treatments. However, Mulligan and Kirkman (2002a) found no effect of above-ground competition by neighboring wiregrass plants on wiregrass seedling success, so light limitations caused by understory vegetation are likely less significant than those caused by the longleaf pine canopy, which has been implicated in determining herbaceous biomass and species richness in several different locations (Harrington and Edwards 1999, Mulligan et al. 2002, Platt et al. 2006, Pecot et al. 2007).

Soil moisture is an important factor in determining herbaceous and, specifically, wiregrass biomass at the landscape level, with biomass increasing along a xeric-to-mesic gradient (Mitchell et al. 1999, Glitzenstein et al. 2001, Kirkman et al. 2001). I found higher survival and growth on sites with higher soil moisture (root exclusion sites), suggesting that soil moisture is a limiting resource for wiregrass establishment and seedling growth in the upland longleaf pine forests on CSNWR. However, at this small scale, where all plots were on excessively drained sands on the xeric end of the moisture gradient, differences in soil moisture among the vegetation treatments were insignificant. Several factors other than soil moisture may help determine which understory species is

present, and it is possible that the size of a patch dominated by a specific understory species may be too small to create its own set of environmental conditions.

Seed and seedling success also showed little effect of vegetation treatment. Seedling survival and establishment from seed only varied among vegetation treatments early on, with survival and establishment lowest in turkey oak dominated plots, suggesting that when exposed to harsh conditions, such as the dry spell in May and June of 2008, the immediate environment may play a role, with turkey-oak dominated sites inhibiting survival more than wiregrass- or longleaf pine-dominated sites. Soil moisture was not measured at the beginning of the growing season, so I do not know if a comparison in soil moisture among vegetation treatments would produce different results in drought conditions than it did in September after several rain events. A series of data on soil moisture content during the dry-down period following a rain event is necessary to see if the vegetation treatments create different levels of soil moisture depending on drought stress. Early work comparing water uptake by turkey oak and wiregrass in sandhills soils showed that soil moisture content dropped to the wilting point in an equal amount of time whether turkey oak was present or not, while the removal of wiregrass greatly increased the amount of time it took for the same reduction in soil moisture content (Woods 1958). This suggests that the presence of turkey oak does not affect below-ground competition for water, while the presence of established wiregrass plants does, which further fails to explain the differences in seedling survival and establishment I saw among vegetation treatments in June and July.

The strong demand of wiregrass for soil moisture (Woods 1958) may explain the nearly identical soil moisture content in wiregrass-dominated plots regardless of root exclusion, while in both longleaf pine- and turkey oak-dominated plots soil moisture was higher where roots were excluded. Though the majority of wiregrass roots are found in the top 10 cm of soil (Saterson and Vitousek 1984), the rooting zone is described as being 50 cm deep (West et al. 2003). Wiregrass may be capable of creating a region of such negative water potential, that even at a 25 cm depth, water can be pulled down from the soil within the PVC pipe and into the soil accessible by roots of existing wiregrass plants.

I studied wiregrass establishment both from seed, as well as from planted seedlings. Germination from seed was much lower than the laboratory germination rate, and the survival rate of germinants was even lower. Wiregrass seeds have a short dormancy period; Coffey and Kirkman (2006) found a two-year viability period in the seed bank, and Mulligan and Kirkman (2002b) found seeds germinating in their first and second years in the seed bank. I found seed produced the previous fall to be successful at germinating any time during the next growing season when rainfall is sufficient. I observed natural seedling recruitment in April 2009 from seed produced the previous fall (data not presented), and new seedling germination as late as October 2008 during the course of this experiment. These results confirm what is known about the pros and cons of direct seeding: it can be done in the winter when labor is more available, but because establishment is unreliable, large quantities of seed are required (Walker and Silletti 2006).

My results suggest that for direct seeding or planting containerized seedlings, limiting below-ground competition will increase the rate of seedling establishment and survival. Reducing below-ground competition in practice can be difficult. It has been shown that reducing canopy cover through the creation of gaps, or reducing basal area, will increase existing herbaceous vegetation growth, the survival of planted seedlings, and the natural recruitment rate of wiregrass in the longleaf pine ecosystem (Harrington and Edwards 1999, Mulligan et al. 2002, Harington et al. 2003, Pecot et al. 2007). Reducing root competition is only partially achieved through a reduction in canopy cover, though. A canopy reduction in a Ponderosa pine ecosystem did not increase herbaceous biomass as much as root reduction did (Riegel et al. 1995), though Harrington and others (2003) found similar increases in herbaceous biomass in a longleaf pine plantation whether the reduction in competition was above or below ground. It would be necessary to determine the amount of canopy cover, and reduction thereof needed, in order to cause an increase in herbaceous biomass with canopy removal only. At the low-to-intermediate pine basal areas in my study area (comparable to the 50 % basal area reduction treatment in Harrington et al. 2003), competition from pine roots was sufficient to lower the survival and growth of wiregrass seedlings. My results do not suggest that hardwoods in the understory, and at densities between 2–5 stems per square meter, inhibit the survival and growth of wiregrass any more so than the other surrounding vegetation does. Effort is often put into reducing understory woody vegetation as a means to increase grass and herbaceous species cover (Kush et al. 1999, Freeman and Jose 2009),

but may only be necessary where hardwood cover is denser, or where hardwoods are invading the midstory.

Wiregrass was present but patchy in the stands I included in this study; in some areas wiregrass cover was dense, but nearby it could be sparse. The stands included mature trees and had more open canopies than many on CSNWR. Though ideal for studying whether local conditions will affect the success of wiregrass establishment, it is possible that on sites such as these, where longleaf pine stand and age structure are representative of that desired by CSNWR management, and where frequent burning keeps hardwoods in the understory, wiregrass cover may be at the upper limit of its expected density. CSNWR also has several sites where longleaf pine stand and age structure are not at desirable levels, and where wiregrass densities are sparse throughout stands. On these sites, reducing below-ground competition may be necessary to establish higher wiregrass densities, either through the removal of overstory pines, or through the aggressive removal (herbicide or mechanical) of competing, less-desirable understory vegetation.

Only the first year's survival and growth rates are presented in this study. It is possible that the growth and survival rates may be affected by treatments in different ways in subsequent years. Extended monitoring is also necessary to see if below-ground competition or surrounding vegetation affect the seed production of wiregrass. Together, such results could determine limiting factors on the long-term viability of a restored wiregrass population.

APPENDIX

A Preburn dead 0-70 cm

$y = 10^{\wedge}(-0.621 + 0.033x)$

$R^2 = 0.6752$

B Preburn dead > 70 cm

$y = (-8.834 + 0.201x)^2$

$R^2 = 0.7845$

C Preburn live 0-70 cm

$y = 10^{\wedge}(-0.585 + 0.029x)$

$R^2 = 0.8965$

D Preburn live > 70 cm

$y = (-3.639 + 0.124x)^2$

$R^2 = 0.9268$

Figure A- 1. Turkey oak stem length-to-weight regressions used to estimate turkey oak stem weights before burns. (A) dead stems 0-70 cm, (B) dead stems >70 cm, (C) live stems 0-70 cm, and (D) live stems >70 cm.

Figure A- 2. Wiregrass basal-area-to-weight regression used to estimate plant weights before burns.
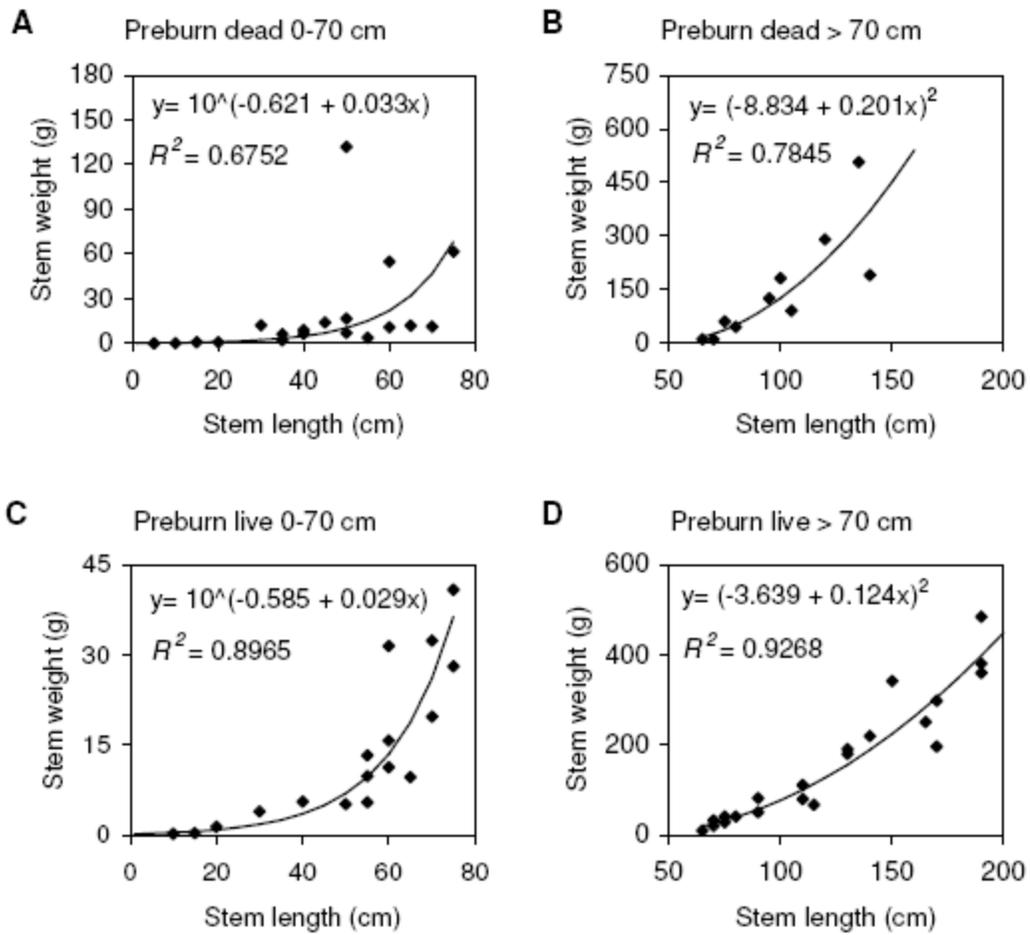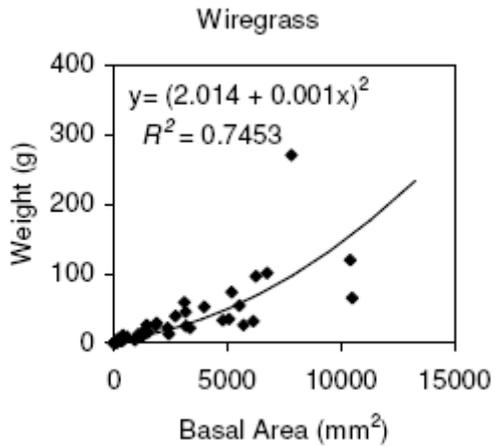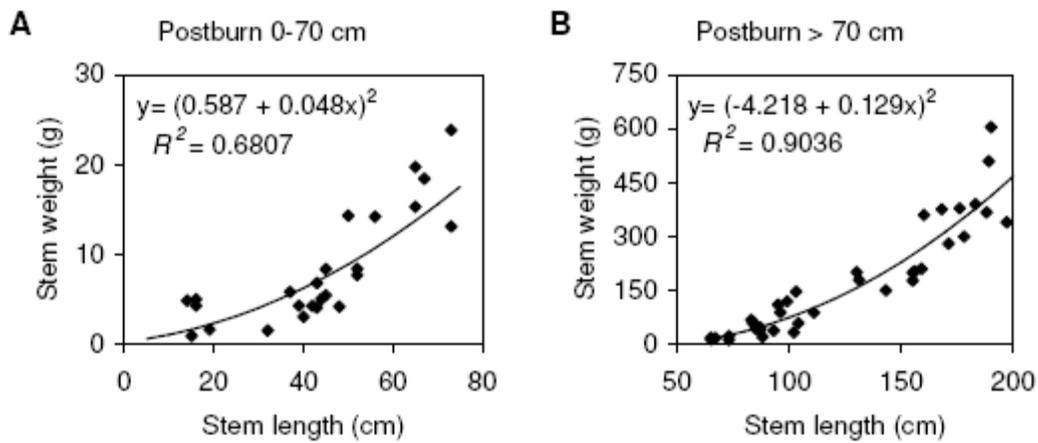

Figure A- 3. Turkey oak stem length to stem weight regressions used to estimate turkey oak stem weights after burns. (A) post-burn stems 0-70 cm, and (B) post-burn stems >70 cm.

Figure A- 4. Greenhouse germination rates (%) of wiregrass seed collected in November, 2007. Error bars represent standard error of the mean.

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