MAUREEN KAY MULLIGAN
Wiregrass (*Aristida beyrichiana* Trin. and Rupr.) Recruitment, Establishment and Growth
(Under the direction of L.K. KIRKMAN)

The once dominant longleaf pine-wiregrass ecosystems of the southeastern United States are now extremely rare. Because wiregrass is often considered a keystone species in these communities, recent restoration efforts have focused on its regeneration; however, little information is available on wiregrass population dynamics. In this study, wiregrass establishment and recruitment was assessed in several restoration situations including longleaf pine plantations and formerly cultivated fields.

Low canopy densities were shown to be necessary for successful wiregrass recruitment and establishment although wiregrass can persist in closed canopy situations. Prescribed burning in the first two years following seed germination resulted in higher seedling mortality than no-burn, particularly for small seedlings in the first summer. Weedy competition decreased wiregrass growth regardless of seedling age. However, seedling survival increased only for 3-week-old and 1-year-old individuals in the absence of weedy competition. Root competition resulted in smaller seedlings and lower survival regardless of seedling age.

INDEX WORDS: Wiregrass, Aristida beyrichiana, Longleaf pine, Seedling Establishment, Competition

WIREGRASS (*ARISTIDA BEYRICHIANA* TRIN. AND RUPR.) RECRUITMENT, ESTABLISHMENT AND GROWTH

by

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CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW

The longleaf pine (*Pinus palustris*) and wiregrass (*Aristida* spp.) communities of the southeastern United States require frequent fire for maintenance of stand structure. In the absence of periodic fire disturbance, a dense midstory of shrubby vegetation forms (Wells 1931, Lemon 1949, Monk 1968, Peet & Allard 1993). With further fire suppression, the highly diverse, herb dominated vegetation is eventually replaced by hardwood species (particularly *Quercus* spp.) (Heyward 1939, Rebertus et al. 1993, Glitzenstein et al. 1995, Brockway & Lewis 1997) with eventual canopy closure (Heyward 1939, Glitzenstein et al. 1995). Therefore, in degraded longleaf pine and wiregrass systems, the reintroduction of fire is critical to habitat restoration. It has been suggested that wiregrass plays a keystone role in these communities by increasing pyrogenicity of the system through its role as an excellent fine fuel source (Means & Grow 1985, Platt et al. 1988, Clewell 1989, Noss 1989, Seamon et al. 1989, Glitzenstein et al. 1995, Van Eerden 1997). Thus, current restoration efforts have focused interest on the regeneration and establishment of *Aristida stricta* (Michx) and *Aristida beyrichiana* (Trin. and Rupr.) (wiregrass), the dominant understory vegetation of the longleaf pine-wiregrass communities in the Southeastern United States Coastal Plain, as a means to re-establish ecological function and structure of the ecosystem.

There are several problems associated with wiregrass restoration and regeneration. First, successful reproduction occurs only following growing season fires (Parrott 1967, Seamon & Myers 1992, Streng et al. 1993, Outcalt 1994, Van Eerden 1997). This seasonal fire requirement for reproductive success may be due to elevated maximum temperatures that occur in summer burns relative to cool season burns (Van Eerden 1997, Walker & Van Eerden 1997). Management for the past several decades has utilized dormant season burns (i.e., months prior to March) for optimum quail habitat management (Outcalt 1994, Smith & Atkinson 1997, Van Eerden 1997). However, growing season prescribed burns are increasingly implemented as a management option (Smith & Atkinson 1997). Secondly, wiregrass does not recover from intense soil perturbations (Clewell 1989, Outcalt & Lewis 1990, Outcalt 1992, Walker & Van Eerden 1997). The lack of re-invasion in abandoned fields adjacent to stands of wiregrass is most likely due to a lack of propagules as a result of dormant season burns. Furthermore, current efforts to establish wiregrass have proven to be costly with unpredictable germination rates that can fall below 10%. Finally, anecdotal evidence suggests that wiregrass vigor decreases with fire exclusion and increasing canopy cover (Clewell 1989, Outcalt 1994, Means 1997). High litter levels can negatively affect wiregrass seedling establishment whereas no litter or light litter can be favorable for seedling growth and survival (Van Eerden 1997).

As a result of incomplete knowledge of wiregrass population biology, many questions remain in terms of the optimal and practical reintroduction techniques for this species. Limited experimental studies of wiregrass establishment exist (direct seeding (Seamon & Myers 1992, Bissett 1996, Seamon 1998); planted seedlings (Seamon et al. 1989, Van Eerden 1997, Outcalt et al. 1999) and site preparation (Outcalt 1994)). However, several important questions remain unanswered including the most favorable successional stage in the restoration process in which to introduce propagules (e.g., old field, young plantation, thinned canopy) and the optimal burn regime following recruitment (e.g., season, time since esta t). Similarly, seed dispersal distances and potential rate of expansion of wiregrass stands from both planted and established plants have not been examined.

In species rich communities such as longleaf pine and wiregrass, where environmental conditions are likely stressful for establishment of young seedlings due to drought, regeneration niches may play an important role in determining community composition. A regeneration niche exists where a particular species experiences regenerative advantages over other species in a given habitat as a result of microsite differences in biotic or abiotic factors (Grubb 1977). Seedling establishment in natural environments is one important stage where the regeneration niche may play an important role. This niche may vary with stages of development resulting in both positive and negative interactions between and among species (Grubb 1977, Holmgren et al. 1997).

Facilitation and competition refer to the net effect of changes in the environment of a plant, caused by the presence of other plants (Holmgren et al. 1997). Facilitation occurs when positive interactions occur among plants (Callaway 1995). For example, interactions can occur through favorable microclimate changes, decreasing predation, attracting appropriate dispersal agents, etc. (Hunter & Aarssen 1988). Negative effects (competition) occur when limited resources that are required by one organism are usurped by another organism (Keddy 1989). Facilitation and competition do not occur in isolation and, therefore, it is likely that a balance between negative and positive effects occurs (Callaway 1997, Holmgren et al. 1997). Furthermore, the interactions between facilitation and competition may shift over time, through environmental gradients, or through indirect effects resulting in complex relationships between facilitative and negative influences (Callaway 1997, Callaway & Walker 1997, Holmgren et al. 1997).

Effects of facilitation and competition have been documented in many environments (Carlsson & Callaghan 1991, Aguiar & Sala 1994, Bertness & Leonard 1997, Morgan 1997). The relationship in the Patagonian steppe between shrubs and grass exemplifies the shift through time from facilitation to competition (Aguiar et al. 1992, Aguiar & Sala 1994). Shrubs initially provide microclimatic benefits to grasses (Aguiar et al. 1992). However, with the increase in grass seedling age and densities, competition begins to outweigh the benefits of neighbors (Aguiar et al. 1992, Aguiar & Sala 1994, Aguiar et al. 1996). Bunchgrasses in the shortgrass steppe were found to facilitate establishment of other vegetation through increasing nutrient levels in the soil at the base of grasses (Kelly & Burke 1997). Once plants become established at grass bases, the relationship probably shifts towards one of competition, depending on environmental stress and age of the plant (Greenlee & Callaway 1996).

Vegetation gaps may be suitable environments for the study of facilitative and competitive influences on seedling establishment. Gaps are important to the regeneration of many different systems including grasslands and forests (Runkle 1989, Denslow et al. 1990, Reader & Bricker 1992, Ryser 1993, Belsky & Canham 1994, Berkowitz et al. 1995, Morgan 1997). Differences in abiotic resources (light, nutrients, moisture) and biotic factors (colonizing species) created by gaps can lead to differences in plant establishment in gaps versus non gap areas (Belsky & Canham 1994, Denslow et al. 1990, Berkowitz et al. 1995). Gaps in grasslands can benefit seedling establishment (Aguilera & Lauenroth 1993, Morgan 1997). Larger gaps improved seedling emergence (excluding root competition) as well as increased survival and emergence of *Bouteloua gracilis* in the central prairie (Aguilera & Lauenroth 1993, Aguilera & Lauenroth 1995, Morgan 1997). In other grassland situations, however, gaps have not been shown to improve seedling establishment (Ryser 1993). Gaps may not improve survival in times of drought in stressful systems, as facilitation may play a larger role in establishment (Greenlee & Callaway 1996). Similar processes have been reported in hardwood forests with tree and herbaceous establishment (Collins et al. 1985, Lorimer 1989, Reader & Bricker 1992). Gaps in forests create forest heterogeneity (Whitmore 1989) and many forest species have adapted to various light regimes (Brokaw & Scheiner 1989, Canham 1989). In tropical forests, large areas with decreased canopy density resulted in increased irradiance and woody plant densities, but smaller areas with thinned canopies show increases in herb frequency (Reader & Bricker 1992). However, not all forest herbs respond positively to thinning and gaps (Collins et al. 1985).

Due to the successional processes affecting gap structure, similarities are also seen in old field experiments regarding competition. Differences in species emergence, survival and growth occurred with varying diameter openings in gaps created in old field successional vegetation (Goldberg & Werner 1983, Goldberg 1987, De Steven 1991a & b). Moreover, old field establishment experiments in the southeastern United States initially showed a facilitative relationship between seeds and weedy vegetative cover in early successional communities (De Steven 1991a). However, once seedlings became established, the relationship with weedy vegetation became competitive (De Steven 1991b).

Because longleaf pine-wiregrass systems are sometimes recognized as grasslands with trees, it may be expected that gaps in canopy structure as well as gaps in understory structure may influence species composition and interactions (Robbins & Myers 1992). However, little is known of establishment and recruitment dynamics of most species in the longleaf pine and wiregrass system.

This thesis examines the establishment phase of wiregrass (*Aristida beyrichiana* Trin. and Rupr.) life cycle through a series of experimental field studies in recently abandoned fields, five-year-old longleaf pine plantations, and twenty-year-old longleaf pine plantations. Chapter 2 of this thesis assesses canopy effects on survival and growth of planted wiregrass individuals and the resulting seedling recruitment following fire. Chapter 3 investigates burn effects on naturally recruited wiregrass seedling survival. Competitive interactions that occur during wiregrass seedling establishment are evaluated in chapter 4. Finally, chapter 5 synthesizes the findings of these studies and provides management suggestions gleaned from this research.

CHAPTER 2: *ARISTIDA BEYRICHIANA* TRIN. AND RUPR. (WIREGRASS) ESTABLISHMENT AND RECRUITMENT: IMPLICATIONS FOR RESTORATION[1]

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[1] Mulligan, M.K., L.K.Kirkman, and R.J. Mitchell. 1999. Submitted to Restoration Ecology.

ABSTRACT

Restoration of the longleaf pine ecosystems of the southeastern United States has focused interest on the regeneration and establishment of *Aristida* spp. (wiregrass) as a means to re-establish ecological function and structure of the ecosystem. This study examined dispersal distance from planted adults and canopy cover and density effects on establishment and reproduction. In 1994, wiregrass plugs were planted in two densities (500 seedlings/100 m^2 and 49 seedlings/100 m^2) and three canopy thinning treatments (25 m^2 basal area/ha, 16 m^2 basal area/ha and 8 m^2 basal area/ha) were implemented in a 20 year old longleaf plantation in southwestern Georgia. Due to the intense site preparation and the density of pines planted, virtually no understory vegetation was present. The site was burned in June 1995, which promoted seed production of the planted wiregrass. Results indicate that the 8 m^2 basal area/ha treatment results in larger plants that in turn produce a greater number of seedling recruits. No seedling recruitment occurred in control plots. Dispersal distances of up to 594 cm were recorded. Natural seedling recruitment occurred at low density transplanting (5 plants per 10 m^2), denoting that high density planting similar to natural density (5 plants per m^2) is not required for successful establishment or reproduction. However, overstory thinning in dense pine plantations is required for reproduction and increases the survival of individual plants due to changes in the environmental conditions at the forest floor.

Key words: *Aristida beyrichiana*; wiregrass; *Pinus palustris*; longleaf pine; canopy thinning; plantation forestry; restoration

INTRODUCTION

At the time of European settlement, *Pinus palustris* Mill. (longleaf pine) was the predominant overstory vegetation of southeastern North America stretching from southern Virginia, south to central Florida, and west to eastern Texas (Means & Grow 1985, Noss 1989, Ware et al. 1993). Along the southern portion of the Coastal Plain (from southern South Carolina south to southern Florida and west to Mississippi), these longleaf pine stands are associated with the dominant understory grass, *Aristida beyrichiana* Trin. & Rupr. (wiregrass) (Peet & Allard 1993). Changing land use in the southeastern United States over the past 200 years has led to the exclusion of fires in longleaf-wiregrass systems as well as conversion of naturally forested land to plantation forests and cropland. Only a fraction of the 770,000 hectares of natural longleaf pine that persists has intact understory vegetation (Ware et al. 1993). With less than approximately 3% of its original area remaining, longleaf pine-wiregrass is one of the world's most endangered ecosystems (Simberloff 1993, Ware et al. 1993). The continued deterioration and loss of longleaf-wiregrass savannas is presently one of the most critical challenges to conservation biology in the southeastern United States (Ware et al. 1993).

Wiregrass (*Aristida stricta* (Michx.) and *Aristida beyrichiana* (Trip. & Rupr.)) is considered by many to be a keystone component in this fire dependent community (Clewell 1989, Hardin & White 1989, Platt et al. 1989) because of its structural dominance (Noss 1989, Glitzenstein et al. 1995) and its function as a high quality fuel source (Clewell 1989, Outcalt 1992, Outcalt et al. 1999). An abundance of wiregrass clumps presumably increases pyrogenicity due to the vertical arrangement of the grass tillers which uphold accumulated pine litter and consequently decrease fuel moisture content (Means & Grow 1985, Clewell 1989, Noss 1989, Platt et al. 1989, Seamon et al. 1989, Glitzenstein et al. 1995, Van Eerden 1997). Thus, recent efforts to restore characteristic structure and function to longleaf systems include the reintroduction of wiregrass as a primary objective.

Wiregrass restoration and regeneration is problematic for several reasons. First, successful wiregrass reproduction has been observed to occur only following growing season fires (Parrott 1967, Seamon & Myers 1992, Streng et al. 1993, Outcalt 1994, Van Eerden 1997). However, management on remaining stands of longleaf pinelands for the past several decades has utilized dormant season burns (i.e., months prior to March) for optimum quail habitat management (Outcalt 1994, Smith & Atkinson 1997, Van Eerden 1997). These dormant season burns, which occur during cooler months, do not often result in successful wiregrass flowering and seed production (Parrott 1967, Brockway & Lewis 1997, Van Eerden 1997). Secondly, wiregrass does not recover from intense soil perturbations (Clewell 1989, Outcalt & Lewis 1990, Outcalt 1992). Thus, the loss of wiregrass from vast areas due to disturbance as well as management practices that have diminished seed production are factors contributing to the lack of wiregrass re-invasion of old fields and other disturbed areas. Growing season prescribed burns are increasingly implemented as a management option (Smith & Atkinson 1997) and successful germination and wiregrass establishment has been documented (Seamon et al. 1989, Seamon & Myers 1992), although rates of recruitment and recruitment distances are unknown. Finally, current efforts at wiregrass restoration have proven to be costly (Bissett 1996, Seamon 1998). Rates of germination are unpredictable and frequently fall below 10% (Parrott 1967, Outcalt 1994, Van Eerden 1997). As a result of limited knowledge of wiregrass biology, many questions remain in terms of the optimal and practical reintroduction techniques for this species.

Although it may be desirable to establish wiregrass in planted pine stands, it is unknown if establishment will be hampered by high overstory density. Mature longleaf pine stands have an average canopy closure approximating 50% (as low as 20%) (Palik & Pederson 1996, Palik et al. 1997, McGuire 1999). Thus, wiregrass is adapted to high light environments and appears to have greater vigor in open canopy situations (Parrott 1967, Means 1997, personal observation). Most wiregrass restoration has been attempted in open fields and areas lacking longleaf pine overstory (Seamon & Myers 1992, Bissett 1996, Means 1997, Seamon 1998, Outcalt et al. 1999). Consequently, wiregrass dependence on an open canopy during establishment is uncertain. Furthermore, natural populations of wiregrass occur in high densities averaging 5 plants per m^2 across a regional moisture gradient (Clewell 1989). It is unclear if naturally occurring densities represent a critical threshold for successful seedling recruitment or if population growth is possible with fewer initial individuals.

This study examines wiregrass establishment and growth in a 20-year-old longleaf pine plantation, as influenced by density of planted wiregrass individuals and percent canopy cover over a 5 year period. Specifically, the following questions are addressed: How does canopy cover affect planted wiregrass seedling establishment, vigor and seedling recruitment? Does the density of transplanted individuals affect successful establishment and recruitment of wiregrass? What is the maximum dispersal distance of successful propagules derived from planted individuals?

METHODS

This study was conducted at Ichauway (31^{o} 15’ latitude, 84^{o} 30’ longitude), an ecological reserve of the Joseph W. Jones Ecological Research Center. Ichauway is located on the Dougherty Plain in Baker County, Georgia (Figure 1). The study site was a 20-year-old, 49 ha longleaf pine plantation. The soils in the pine plantation are classified as loamy, siliceous, thermic Arenic Paleudults (Wagram loamy sands) (USDA 1986). Average annual rainfall for the area is 131 cm which is distributed fairly evenly throughout the year (National Climate Data Center, Asheville, NC). Previous land use of this plantation was for agricultural crops. Prior to implementation of the study (1994), tree density consisted of 1184 trees/ha and an average basal area of 25 m^2/ ha. The high density of pines resulted in canopy closure and very little understory vegetation.

Experimental plots were established in a split-plot, randomized complete block design. Three overstory thinning treatments were randomly assigned to plots within each of five blocks for a total of fifteen, 25 m x 25 m overstory removal plots. Canopy removal treatments included: a) control with no overstory removal (25 m^2/ha), b) 33% reduction in overstory basal area (16 m^2/ha), and c) 66% reduction in overstory basal area (8 m^2/ha). Trees were randomly selected for removal from within each 25 m x 25 m plot. We will refer to these thinning treatments as 1/3 and 2/3 canopy removal.

Two densities of wiregrass were planted within each 25 m x 25 m plot in a 10 m x 10 m split-plot design (Figure 2). High density subplots were planted at 5 seedlings/m^2 based upon natural wiregrass density reported by Clewell (1989). Low density subplots were planted at 5 seedlings/10 m^2. Wiregrass plugs (approximately six-month-old seedlings grown in tubes) were planted in April 1994. Initial measurements of seedling survival, tiller number and above ground dry weights were made the following February (1995). Number of tillers and clipped dry weights were recorded for 5 individual clumps in the low density subplots and 10 clumps in the high density subplots in each treatment plot. Aboveground biomass was oven dried at 70^{o}C for 72 hours and weighed. Percent survivorship and growth parameters were measured again in March 1996, April 1998, and April 1999.

Soil moisture, soil temperature, litter weights, and canopy cover were measured in 1998 and 1999. Time Domain Reflectometry (TDR) soil moisture readings were recorded using a Tektronic cable tester (model #1502C) approximately every month at two points to a 15 cm depth within each subplot (for a total of 60 readings/sample period) beginning in September 1998 (Topp & Davis 1985). Soil temperature was recorded in conjunction with TDR measures using a 15 cm thermocouple (Omega Engineering, Inc. Stanford, CN). Litterfall biomass was assessed by collecting all pine needle litter within three randomly located 1 m^2 sampling areas from the forest floor for each plot in May 1999. The litter was dried at 70^{o}C for 72 hours and weighed. Percent canopy cover was measured with LAI 2000 canopy analyzer (Li-Cor Inc., Lincoln, NE) by taking 36 readings across 8 diagonal transects within each plot in November 1999.

A low-intensity prescribed burn performed across the entire pine plantation in June 1996 induced wiregrass flowering and seed production. Natural seedling recruitment rates following this seed production were determined in June 1998 within each 10 m x 10 m planted subplot. Within a 1 m x 5 m transect in each subplot, we marked all seedlings with aluminum nails and censused the cohort of new seedlings (Figure 2). We also measured the density of new seedlings as a function of distance from adult plants.

Recruitment distances were recorded in 1 m wide, concentric bands located outside of each 10 m x 10 m planted subplots (Figure 2) for a minimum distance of 3 m or until no additional seedlings were located (maximum 7 m). Each seedling was marked with an aluminum nail and counted.

Data analysis

General Linear Models Procedure (Proc GLM; SAS Institute Inc. 1989) for a randomized complete block, split-plot design was performed on percent survivorship and plant vigor measures (dry weights and tiller numbers) of transplanted individuals, soil moisture measurements, and soil temperature values. General Linear Models Procedure (Proc GLM; SAS Institute Inc. 1989) for randomized complete block design was used for analysis of variance on gap fraction measurements and litter weights. Tukey's multiple comparison test was employed to test for differences among treatment means in all cases. Due to skewness of the data, we used the Kruskal-Wallis one-way analysis of variance by ranks test to compare recruitment populations for the data from the first three concentric 1 m bands for each subplot (Proc NPAR1WAY; SAS Institute Inc. 1989).

RESULTS

Transplant survival and vigor

Initial survivorship of planted seedlings (1 year post planting) did not differ among overstory removal treatments or planting densities ($F= 0.10$, $p>0.05$) (Figure 3a). However, by 1996 and 1998 the environmental conditions in the control plots had negatively affected transplant survival (1996, $F=11.25$, $p<0.01$ and 1998, $F=22.35$, $p<0.01$). By 1999, percent survivorship differed among all canopy cover treatments

(F=39.61, $p<0.01$). Survival of transplants in control plots was 20%, in 1/3 thinning plots 52% and in 2/3 thinning plots 70%.

Mean dry weight and tiller number per plant were strongly affected by canopy treatment in all years. By 1999, mean tiller number was 12 times greater in 2/3 and 6 times greater in 1/3 treatment plots than controls. (F=15.86, $p<0.01$) (Figure 3c). Similarly, the mean canopy gap fractions (LAI readings) associated with tree removal (2/3 removal plots=32%, 1/3 removal plots=27% and control plots=25%) was significantly related to plant growth (tiller numbers) ($R^2=0.43$, $p<0.01$) (Figure 4). For 1999, the wiregrass dry weight in 2/3 overstory removal plots was 20 times more than in control plots and 1/3 overstory removal plots had 8 times more than control plots. The overall reduction in biomass between 1998 and 1999 was due to the prescribed burn that was performed in August 1998 (Figure 3b).

Environmental factors

Percent volumetric soil moisture ranged from 5% (September 1998) to 14% (July 1999) (Figure 5a). For all months except October 1998 and July 1999, no difference in percent soil moisture among overstory removal treatments occurred. However, a marginal difference in mean annual (average for 12 months) soil moisture was seen with overstory removal (F=4.35, $p=0.05$) with lower mean percent soil moisture in 2/3 overstory removal plots (8.8%) than in control plots (9.7%).

Soil temperature ranged from a minimum of 10.5^{o}C in February 1999 to a peak temperature of 27.7^{o}C in August 1999 (Figure 5b). Both extremes in temperature were recorded in plots with 2/3 overstory removal. From April 1999 through September 1999, soil temperatures differed among all canopy removal treatments (F=5.86, $p<0.05$). Mean annual soil temperatures increased with percent canopy removal (F=18.45, $p<0.01$) (Figure 5b).

Pine needle accumulation is related to tree density. Mean pine needle litter biomass differed among overstory removal treatments (F=3.86, $p<0.05$) with greater biomass accumulation in the control plots (924.35 ± 83.5 g) than in the 2/3 overstory removal plots (589.07 ± 87.3 g). The 1/3 removal plots were intermediate (751.07 ± 87.3 g) and did not differ from the extremes.

Seedling recruitment

Wiregrass seedling recruitment occurred both within and outside of the planted subplots. No seedling recruits were found in control plots (Table 1). Nearly 85% of the total recruitment occurred within the high density (500 plants/100 m^2), 2/3 overstory thinning treatment. Recruitment distances of up to 596 cm from nearest adult plant were recorded.

Recruitment density within subplots varied widely (Table 1). The number of seedlings per m^2 diminished (χ^2 =57.448, $p<0.01$) and wiregrass density declined (χ^2 =18.954, $p<0.01$) as canopy cover increased. The mean number of seedlings per adult plant similarly decreased with increasing canopy cover (χ^2 =15.844, $p<0.01$). However, the initial density of adult, transplanted individuals did not affect the ratio of seedlings to adult plants (χ^2 =1.2633, $p>0.26$).

Similarly, recruitment outside of the subplots was variable (Table 1). The mean number of seedlings per m^2 rapidly declined with distance from transplanted individuals (χ^2 =9.0640, p= 0.0108) (Figure 6). Density of transplantation (χ^2 = 40.483, $p<0.01$) and overstory removal treatment (χ^2 = 82.407, $p< 0.01$) affected seedling recruit totals (Figure

6). However, only overstory removal ($\chi^2 = 10.653$, $p<0.01$) appeared to play a significant role in the number of seedling recruits per adult plant ($\chi^2 = 1.4988$, $p>0.22$).

DISCUSSION

This study demonstrates that although wiregrass growth and reproduction is enhanced in open canopy conditions, wiregrass can survive in dense canopy environments. Because natural longleaf pine-wiregrass savannas typically have open canopies (Palik & Pederson 1996, Palik et al. 1997, Noel et al. 1998, McGuire 1999), this response to canopy opening is not surprising. Numerous studies have documented increased herb growth with decreasing overstory basal area in a variety of natural stand conditions (Collins et al. 1985, Reader & Bricker 1992, Kush et al. 1999) and pine plantations (Gaines 1954, Halls 1955, Wolters 1973, Wolters 1982, Harrington & Edwards 1999, McGuire 1999).

The observed increase in growth that accompanied overstory removal is correlated with increased availability of light. Although, decreasing below ground competition with the removal of trees could also affect successful establishment (Aarssen & Epp 1990, Belsky 1994, Aguilera & Lauenroth 1995), our observations suggest that moisture differences were not a major factor. Any gains in soil moisture from lowered competition were likely offset by high soil temperatures as a result of decreased litter accumulation as well as greater light to the ground surface (Collins et al. 1985, Facelli & Pickett 1991, Van Eerden 1997, Harrington & Edwards 1999). Soil moisture was measured only in year 5, a year of low rainfall. It is possible that greater differences in soil moisture among treatments may have occurred in prior years with greater rainfall. We propose that establishment of wiregrass in plantation pine forests is possible particularly in thinned stands due to the changes in understory conditions that accompany tree removal. Furthermore, the persistence of wiregrass in closed canopy situations may be evidence of adaptive attributes of the plant that allow it to survive for long periods of time without fire and subsequent shading by hardwoods. Thus, restoration opportunities may exist for locating suppressed remnant patches of wiregrass in areas with undisturbed soils that have not been burned for long periods of time.

Our finding that establishment and relative recruitment rates (number of seedlings per adult) were unaffected by density suggests that restoration of wiregrass with subsequent expansion is possible with lower densities of transplantation than found in natural populations, although recruitment rates would undoubtedly be slower. Pollination may not be limited at lower densities (Ims 1990, Smith et al. 1990, Tisch & Kelly 1998); however, to further address the relationship of density and reproductive success, the number of viable seeds produced per individual should be examined.

The evidence that plant growth is also independent of density indicates that planting with fewer than 5 plants per m^2 would not provide advantageous survivorship or growth; however, further study of density effects on establishment, vigor and recruitment are needed for planted densities >5 per m^2 to examine the role of intraspecific competition. Nonetheless, the outcome of the density effects in this study indicates that lower density plantings may provide a cost effective option for restoration prescriptions. Recommended transplant densities of 1 plant per m^2 (Outcalt et al. 1999) would most likely result in high survival and successful reproduction which would likely lead to potential expansion from transplanted areas at a lesser cost than planting at natural wiregrass densities. Additionally, direct seeding may be a low cost option for filling in spaces between low density planted individuals as well as establishing plants in areas lacking wiregrass.

These results, coupled with the persistence of wiregrass in low light situations and greater dispersal distances than previously reported, indicate that wiregrass restoration attempts may be more feasible and less costly than previously predicted.

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Table 1. Wiregrass seedling recruitment rates in 1998

Outside Transplanted Subplots

Removal treatment	Density treatment	Seedling total	Seedlings/adult (mean ± SE)	Seedlings/m^2 (mean ± SE)
0	49	0	0	0
0	500	0	0	0
33	49	1	0.006 ± 0.009	0.007 ± 0.008
33	500	207	0.114± 0.585	1.530 ± 0.560
66	49	34	0.172 ± 0.108	0.250 ± 0.102
66	500	473	0.233 ± 0.732	3.504 ± 0.646

Inside Transplanted Subplots

Removal treatment	Density treatment	Seedling total	Seedlings/adult (mean ± SE)	Seedlings/m^2 (mean ± SE)
0	49	0	0	0
0	500	0	0	0
33	49	2	0.012 ± 0.08	0.027 ± 0.005
33	500	40	0.022 ± 0.443	0.533 ± 0.044
66	49	31	0.160 ± 0.393	0.413 ± 0.041
66	500	410	0.2012 ± 4.015	5.467 ± 0.361

Figure 1. Historical range of longleaf pine and wiregrass.

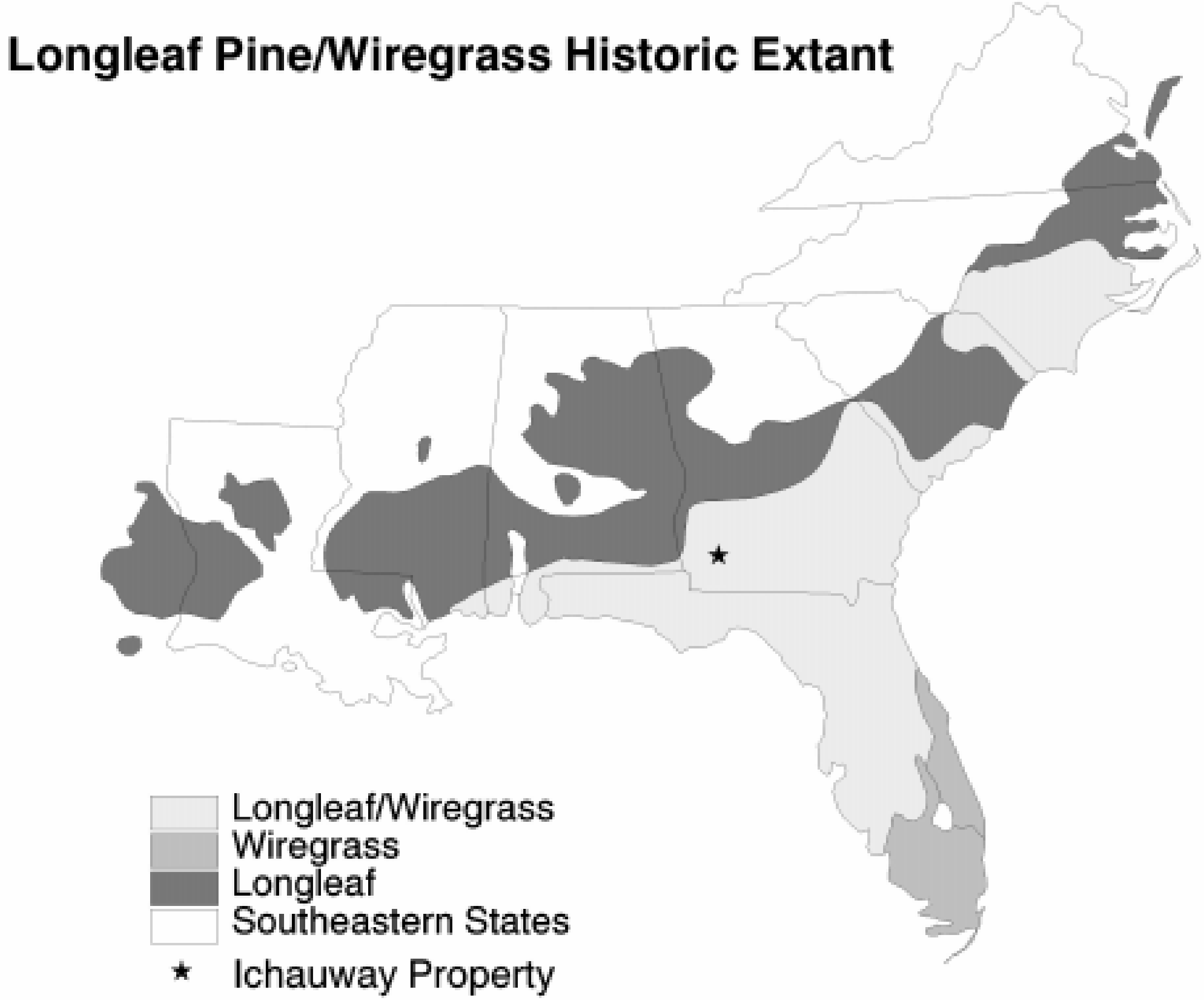

Longleaf Pine/Wiregrass Historic Extant
Longleaf/Wiregrass
Wiregrass
Longleaf
Southeastern States
★ Ichauway Property

Figure 2. Experimental plot layout in longleaf pine plantation.

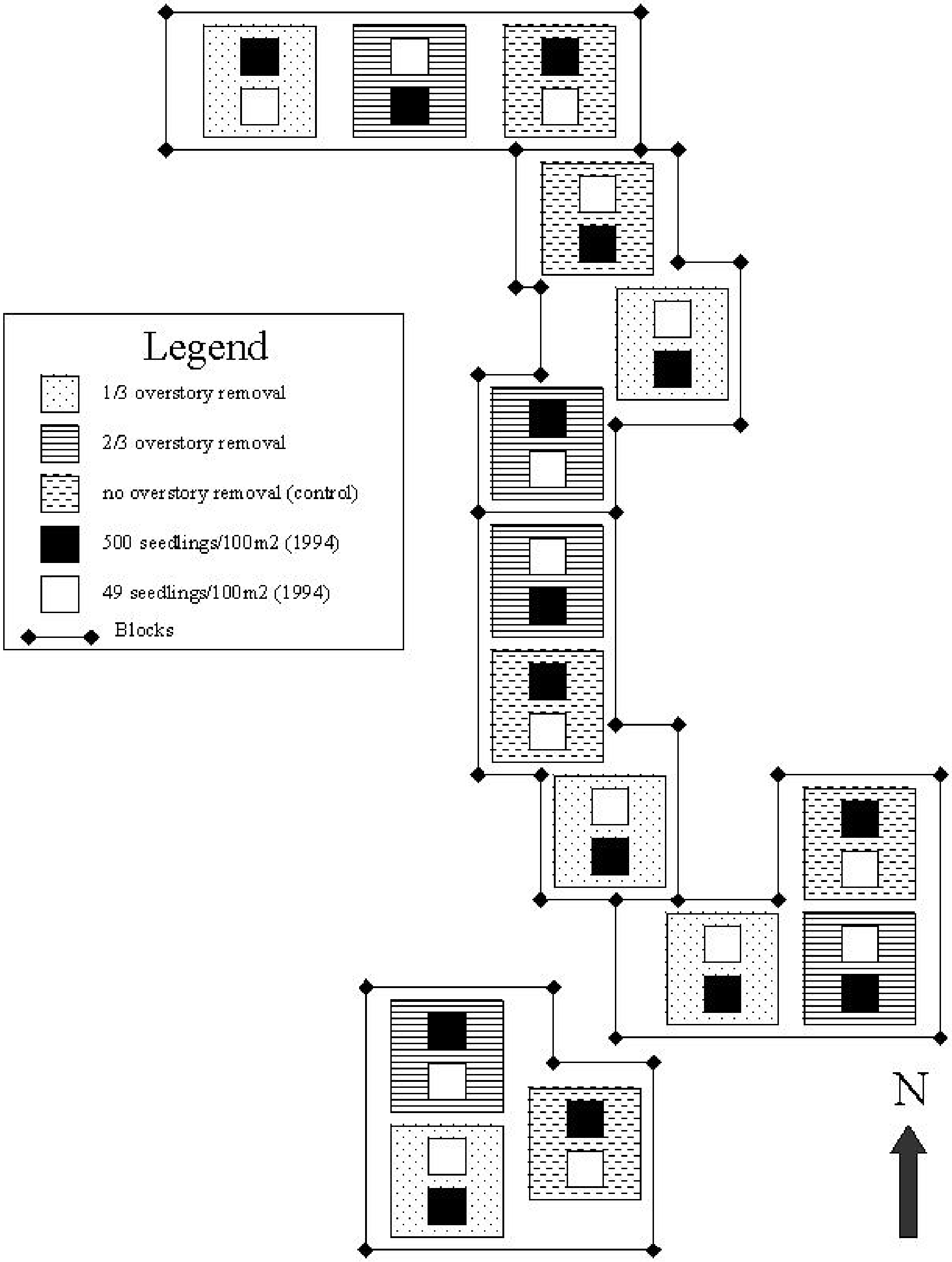
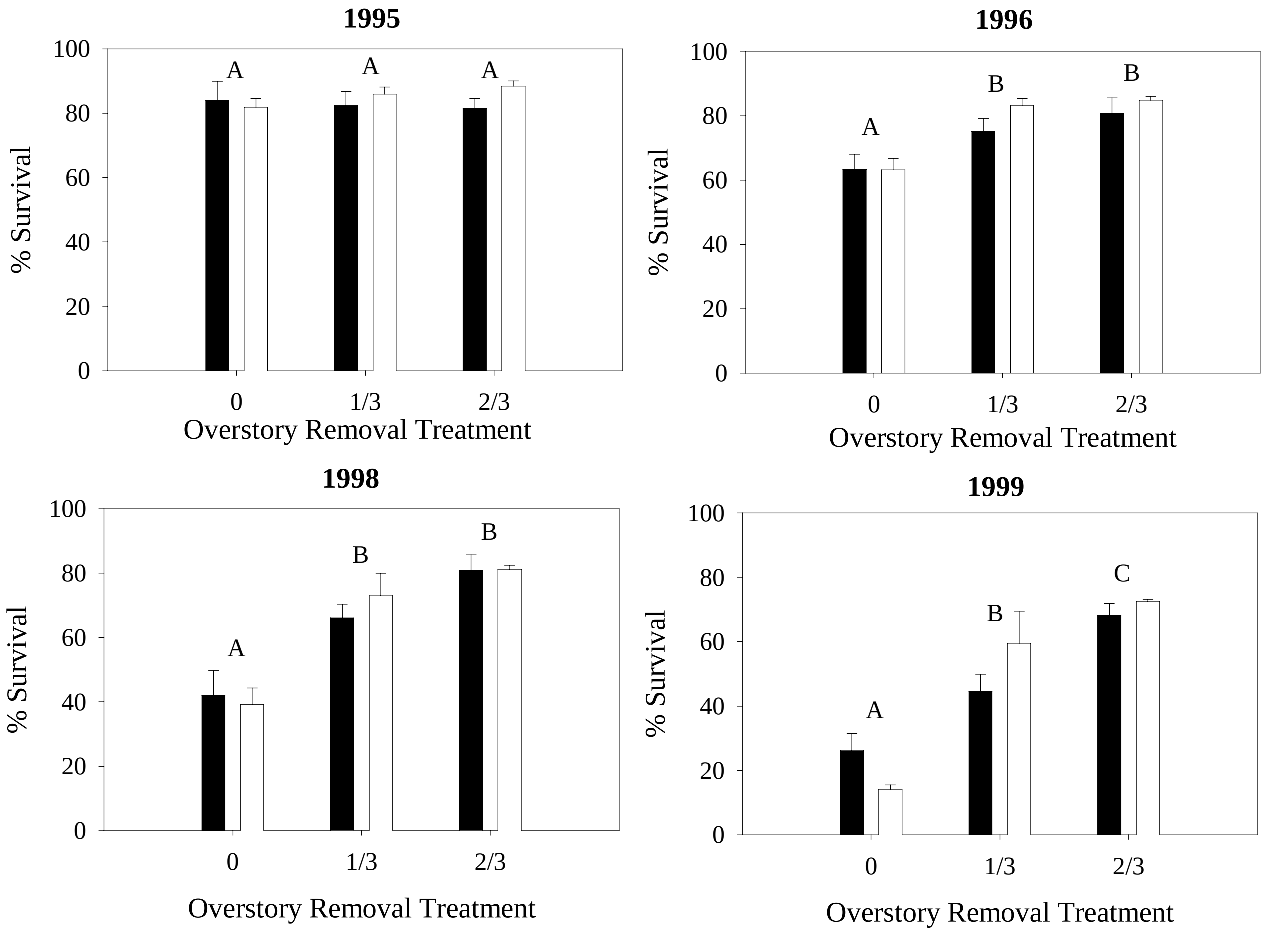
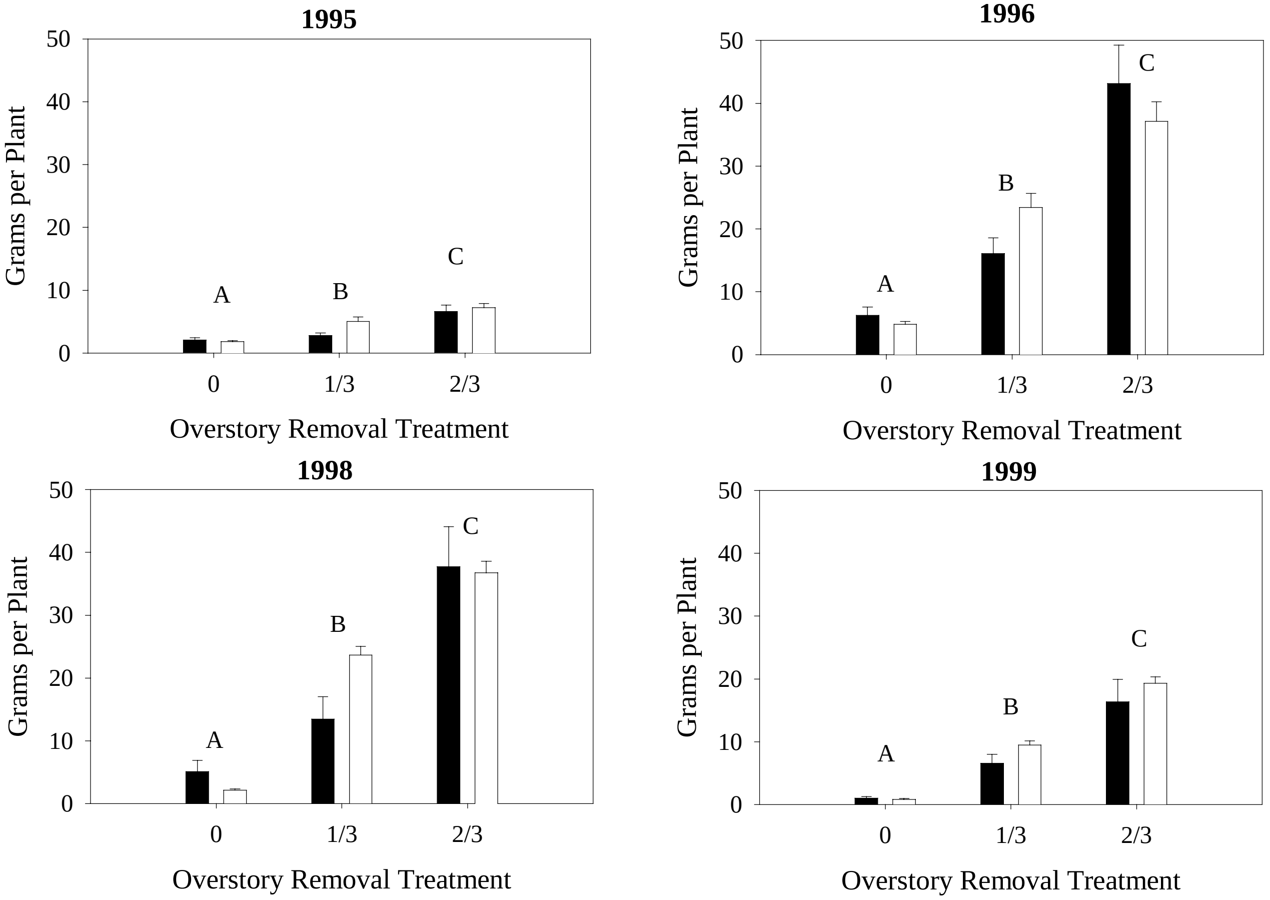

Legend
1/3 overstory removal
2/3 overstory removal
no overstory removal (control)
500 seedlings/100m2 (1994)
49 seedlings/100m2 (1994)
Blocks
N

Figure 3. Survivorship and vigor of transplanted wiregrass (a) %survival (mean ± SE) (b)tiller number (mean + SE) (c) above ground dry weight (mean +SE). Canopy treatment means with different letters significantly differ ($p<0.05$).

a.


1995
A
A
A
1996
A
B
B
1998
A
B
B
1999
A
B
C
% Survival
100
80
60
40
20
0
0
1/3
2/3
Overstory Removal Treatment

b.


1995
1996
1998
1999
Grams per Plant
Overstory Removal Treatment
0
1/3
2/3
0
10
20
30
40
50
A
B
C

c.

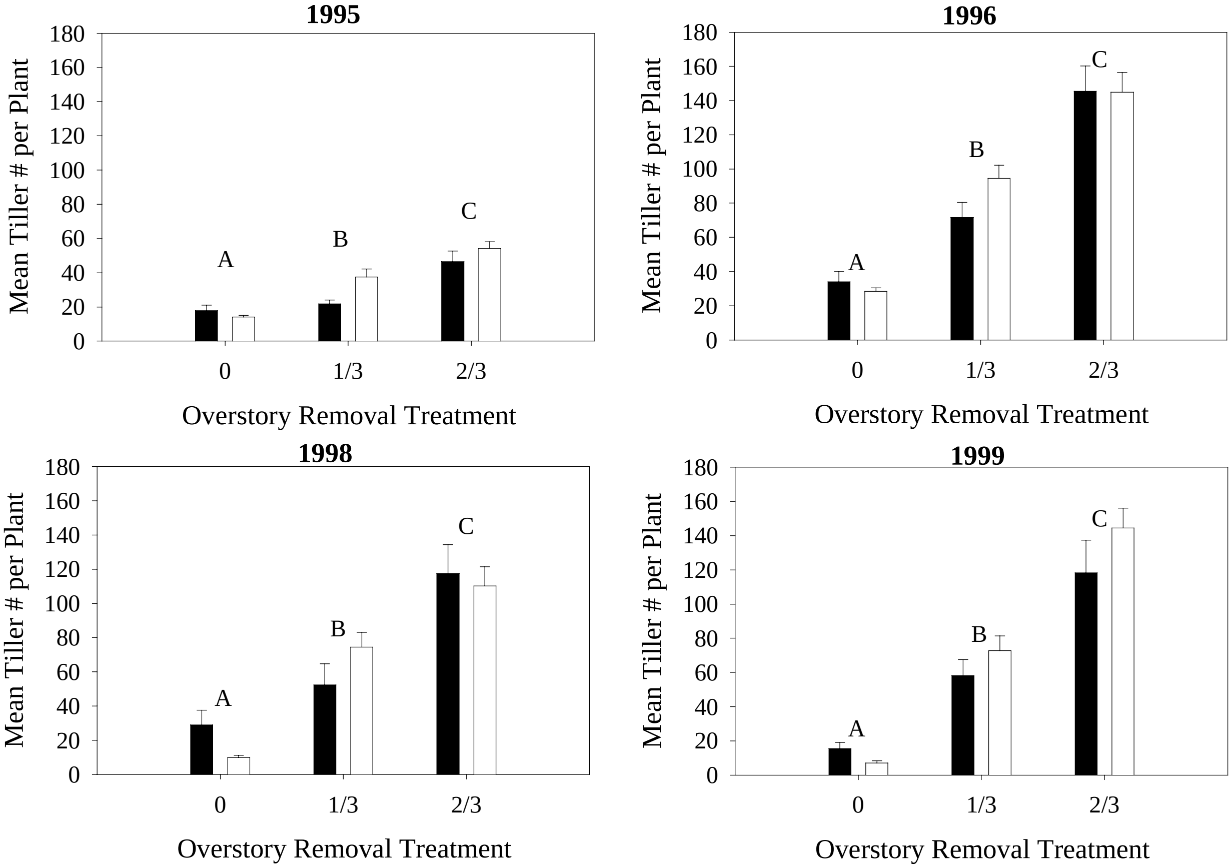

1995
1996
1998
1999
Mean Tiller # per Plant
0
20
40
60
80
100
120
140
160
180
A
B
C
0
1/3
2/3
Overstory Removal Treatment

Figure 4. Plant size (mean tiller number) and canopy gap fraction (LAI 2000).

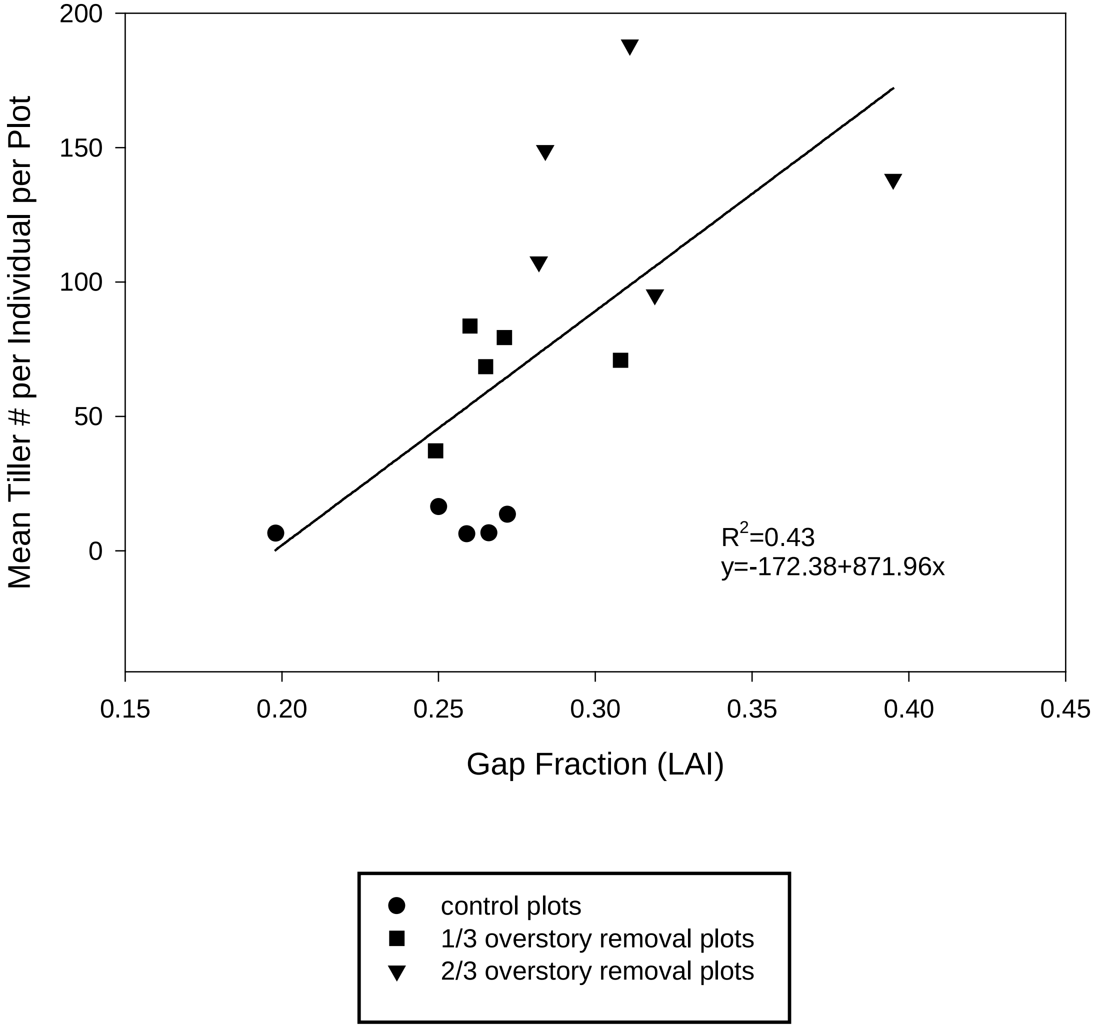
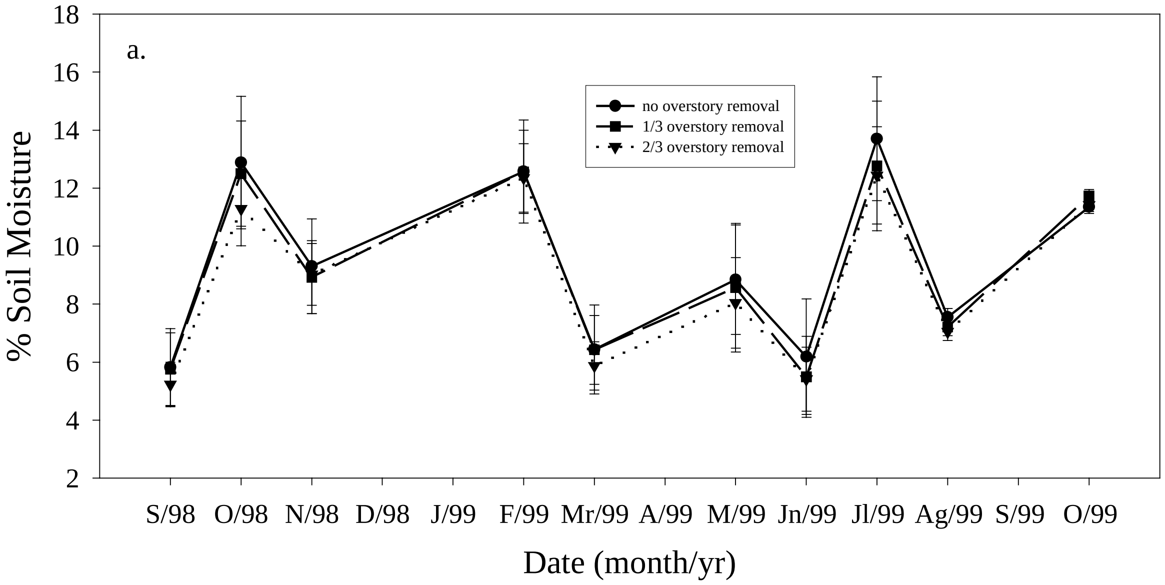

200
150
100
50
0
Mean Tiller # per Individual per Plot
0.15
0.20
0.25
0.30
0.35
0.40
0.45
Gap Fraction (LAI)
R2=0.43
y=-172.38+871.96x
● control plots
■ 1/3 overstory removal plots
▼ 2/3 overstory removal plots

Figure 5. Seasonal soil conditions (a) percent volumetric soil moisture (mean + SE) (b) soil temperature (mean + SE).


a.
no overstory removal
1/3 overstory removal
2/3 overstory removal
% Soil Moisture
18
16
14
12
10
8
6
4
2
S/98
O/98
N/98
D/98
J/99
F/99
Mr/99
A/99
M/99
Jn/99
Jl/99
Ag/99
S/99
O/99
Date (month/yr)

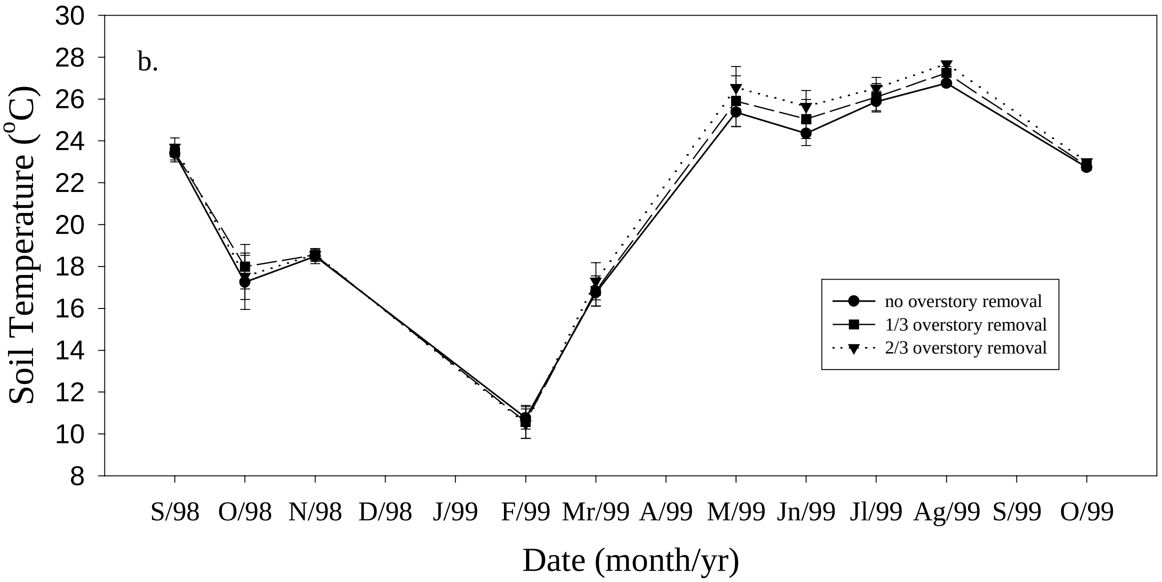
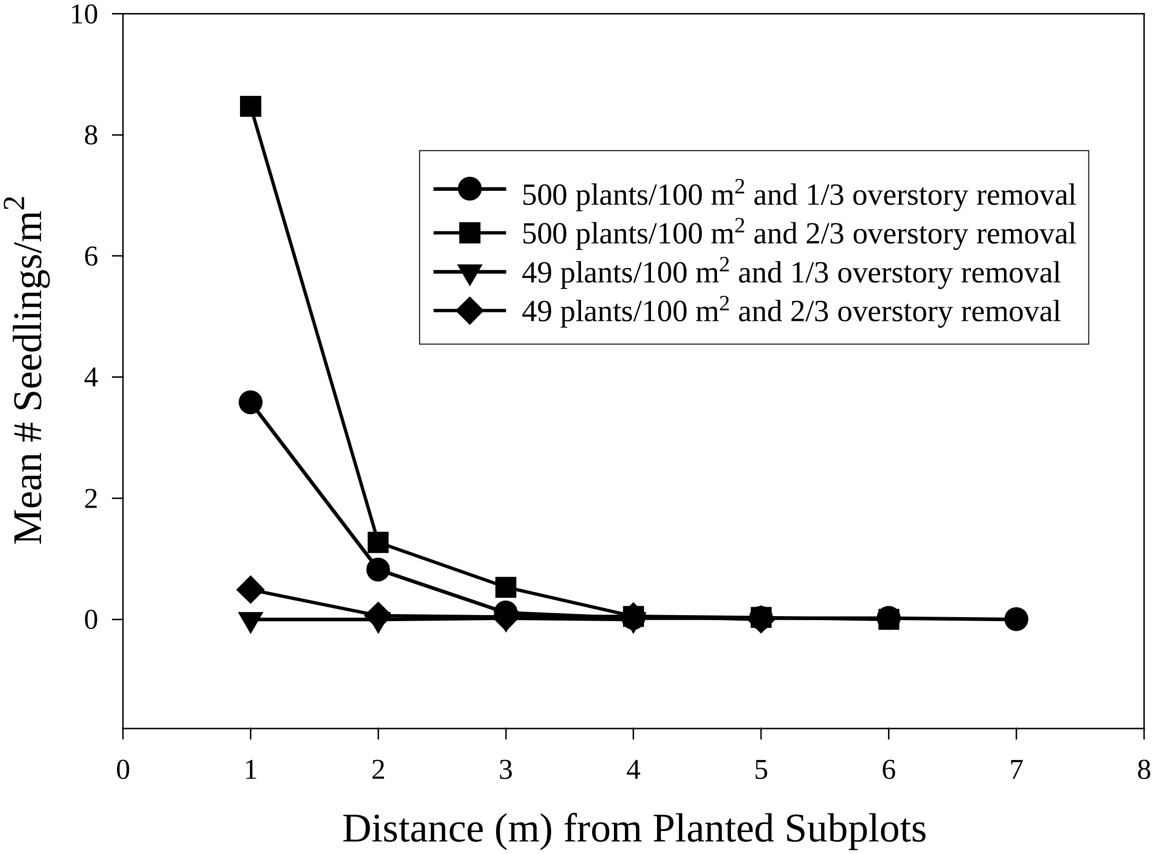

b.
Soil Temperature (°C)
30
28
26
24
22
20
18
16
14
12
10
8
S/98
O/98
N/98
D/98
J/99
F/99
Mr/99
A/99
M/99
Jn/99
Jl/99
Ag/99
S/99
O/99
Date (month/yr)
no overstory removal
1/3 overstory removal
2/3 overstory removal

Figure 6. Seedling recruitment rate with distance from nearest adult.



10
8
6
4
2
0
0
1
2
3
4
5
6
7
8
Mean # Seedlings/m²
Distance (m) from Planted Subplots
500 plants/100 m² and 1/3 overstory removal
500 plants/100 m² and 2/3 overstory removal
49 plants/100 m² and 1/3 overstory removal
49 plants/100 m² and 2/3 overstory removal

CHAPTER 3: TO BURN OR NOT TO BURN: SEEDLING SURVIVAL AND RECRUITMENT OF WIREGRASS (*ARISTIDA BEYRICHIANA* TRIN. AND RUPR.)[1]

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[1] Mulligan, M.K., and L.K.Kirkman. 2000. Submitted to Restoration Ecology.

ABSTRACT

Regeneration and expansion of *Aristida beyrichiana* and *Aristida stricta* (wiregrass) populations in remaining fire maintained *Pinus palustris* (longleaf pine) stands of the southeastern United States has become a focus of land managers. Although growing season fire is required for successful seed production, studies examining naturally occurring wiregrass seedling dynamics are few. This study investigates how seedling survivorship is affected by season of fire, seedling size, time since germination and proximity to adult plants. Restoration at this research site was begun in 1992 with the planting of containerized longleaf pine and wiregrass seedlings in a field previously cultivated as a wildlife food plot. Study plots were established in November 1997 following a growing season prescribed-fire (June 1996) that resulted in successful seed production and seedling recruitment. Burn treatment plots included: No burn (control), fire in the dormant season of the first year following germination (March 1998), fire in the growing season of the first year following germination (August 1998), and fire in the growing season of the second year following germination (July 1999). Specifically, we found that seedling mortality increases with growing season burning and close proximity to adult plants. Natural seedling recruitment continued into the second year following initial seed-drop in all plots but was highest in the no burn (control) plots demonstrating a persistent seed bank. Where wiregrass management objectives include population expansion, seedling recruits should be allowed 1-2 years post-germination without growing season fire for successful establishment.

Key words: *Aristida beyrichiana*, wiregrass, *Pinus palustris*, restoration, fire ecology, seedling survivorship, seedling recruitment

INTRODUCTION

Longleaf pine-wiregrass is a fire-evolved system that is characterized by frequent fire (every 1-5 years) (Christensen 1981, Means & Grow 1985, Noss 1989, Glitzenstein et al. 1995). *Aristida beyrichiana* Trin. and Rupr. (wiregrass) is considered a keystone species in this ecosystem (Clewell 1989, Platt et al. 1989, Hardin & White 1989) owing to its high pyrogenecity (Clewell 1989, Outcalt 1992, Outcalt et al. 1999) and its structural dominance (Noss 1989, Glitzenstein et al. 1995). The presence of wiregrass is often used to indicate relatively undisturbed longleaf pine-wiregrass communities because wiregrass is not known to re-establish dominance on previously cultivated sites and is less vigorous without periodic fire disturbance (Clewell 1989). Due to the perceived importance of wiregrass to the structure and function of longleaf pine-wiregrass systems, information concerning wiregrass regeneration is now of particular interest for southeastern land managers with restoration objectives.

Historically, fires have resulted from both natural and anthropogenic sources (Platt et al. 1988, Platt et al. 1989, Robbins & Myers 1992, Landers et al. 1995). The greatest incidence of lightning coincides with increased frequency of fires in the months of May through August (henceforth referred to as the growing season) (Robbins & Myers 1992). However, prescribed fires for increased pine production and game management are habitually performed during November through April (henceforth referred to as the dormant season) (Robbins & Myers 1992, Smith & Atkinson 1997). Wiregrass responds with a mast reproductive effort following growing season fire (Seamon et al. 1989, Streng et al. 1993, Outcalt 1994, Van Eerden 1997). It appears that the high intensity of growing season fires elicits successful wiregrass flowering and seed production (Outcalt

1994, Van Eerden 1997). The strong dependence of wiregrass on burning season for successful reproduction has led to debate over how modification in disturbance regime through management practices (i.e. primarily dormant season burns) affects population responses of individual species (Platt et al. 1988, Streng et al. 1993, Brewer & Platt 1994, Glitzenstein et al. 1995).

Species within fire-maintained habitats vary in response to fire season (Collins & Wallace 1990, Robbins & Myers 1992, Bond & van Wilgen 1996, Knapp et al. 1998). Likewise, longleaf-wiregrass species exhibit contrasting population patterns with alteration in seasonal fire applications (Streng et al. 1993, Brewer & Platt 1994, Glitzenstein et al. 1995, Kirkman et al. 1998, Heirs 1999). For some species, the importance of burning outweighs the significance of the season of the burn for maintenance and growth of populations (Kirkman et al. 1998, Heirs 1999). Other species vary in growth and reproductive success depending on season of burn (Robbins & Myers 1992, Streng et al. 1993, Brewer & Platt 1994, Glitzenstein et al. 1995). Additionally, a single species may respond differently to fire at distinct stages in its life cycle (Bond & van Wilgen 1996). In fact, the timing of fire following germination may play a critical role in survivorship of wiregrass seedlings, although little information regarding optimal conditions for seedling establishment is available (Mulligan et al. in review). Knowledge of wiregrass seedling survivorship through fire is particularly important where restoration and management efforts depend on population expansion of this species.

This study examines several aspects of wiregrass seedling population dynamics. In particular, we investigate the following: Does the season of burning influence the survivorship of wiregrass seedling recruits? How does the initial size of a wiregrass seedling and the age of a wiregrass seedling affect survivorship? Does the distance to the nearest adult wiregrass plant affect survival?

METHODS

The study site is located within an on-going longleaf-wiregrass restoration project at the Joseph W. Jones Ecological Research Center in Baker County, Georgia, USA. In 1992, restoration efforts began on a small field previously cultivated as a wildlife food plot (200 m x 50 m) with the planting of longleaf pine seedlings and wiregrass seedlings. Uneven pine densities of 469-1054 trees/ha were deliberately obtained by planting in spiral patterns. Containerized wiregrass seedlings were planted at an average density of 3 plants/m^2. Surrounding vegetation is natural longleaf pine-wiregrass that is maintained with frequent prescribed fire. In June 1996, the study site was prescription-burned for the first time since planting. This fire resulted in flowering and seed production of the wiregrass in 1996 and subsequent seedling germination in 1997.

We divided the planted field into eight plots (20 m x 50 m) and randomly assigned the following four burn treatments: 1) no burn, 2) fire in dormant season-first year following germination (March 1998), 3) fire in growing season-first year following germination (August 1998), and 4) fire in growing season-two years following germination (July 1999). There were two replications of each burn treatment. Prior to burn treatments, 2 m wide fire breaks were created by mowing vegetation which reduced fuel loads and protected adjacent plots from fire. Within each plot, we established two sampling transects (1 m x 40 m) with a 5 m buffer on the field edges (Figure 1). In November 1997, we censused wiregrass seedling recruitment. Each transect was divided into two potential sampling sections (1 m x 20 m) and two of the 4 sections were randomly chosen to be censused per treatment plot. Each seedling was counted and tagged with an aluminum nail. To determine size-specific mortality, we measured size of seedlings in a $5m^2$ subsection of one randomly selected transect from each plot. Seedlings were marked with numbered, aluminum tags in the $5m^2$ subsection. These numbered seedlings were scored in one of three size classes based on the longest tiller length (small $\leq$ 3 cm, 3 cm < medium $\leq$ 15 cm, large >15 cm) and the distance to nearest adult plant was recorded.

March 1998 burn treatment plots and a $10m^2$ subsample from the no burn plots were re-sampled for survivorship in August 1998 (Figure 2). Seedlings in the August 1998 burn treatment plots and a $20m^2$ subsample of no burn plots were re-sampled in January 1999. A final census was collected for all sample plots in October 1999.

Data analysis

Means and standard errors (Proc MEANS; SAS Institute Inc. 1989) were calculated for size class data, second year seedling recruitment, and distance to nearest adult. A one-way analysis of variance was performed using General Linear Models Procedure (Proc GLM; SAS Institute Inc. 1989) to determine if a) distance to adult wiregrass plant differed among size classes, and b) percent survivorship of the final census differed among treatments for medium size seedlings. We used Tukey's multiple comparison test to determine differences in survivorship and distance among treatment means. Due to the patchiness of wiregrass recruitment and low numbers of replicates, post hoc tests of mean differences of seedling survival according to size class were performed on second year seedling recruitment data only where feasible (medium size class) (Proc GLM, SAS Institute Inc. 1989).

RESULTS

Initial recruitment across all plots prior to treatments averaged 20.43 ± 2.09 seedlings/m^2, but the density varied widely (range = 0-359 seedlings/m^2). At the time of the initial census (1997), over 80% of the seedlings were from the medium size class (Table 1). The average distance from the nearest adult wiregrass plant across all treatments was approximately 47 cm (range = 9-100 cm). Furthermore, at initial sampling, wiregrass seedling size decreased with increasing proximity to adult plants (F=11.43, $p<0.05$) (Figure 3).

In 1999, the percent survivorship of the initial cohort of seedlings differed by burn treatment (F=25.13, $p<0.01$). The no-burn treatment (55.7%) and first year dormant season burn treatment (43.3%) had nearly twice the survivorship than either first (17.1%) or second year (26.9%) growing season burn treatments. Regardless of burn treatment, few small size seedlings survived and a greater probability of mortality occurred with close proximity to adult plants for small and medium seedlings (Table 1). Seedlings classified as medium in the 1997 census had greater mortality with growing season fires (F=8.47, $p<0.05$) than with dormant season fire (4 months after initial census), even though seedlings were likely to be larger in size by the time of the growing season fires (9 months and 20 months after initial census) (Figure 4). Patterns of survivorship by seedling size within treatments are inconclusive due to the low initial numbers of individuals in large and small size classes and patchy recruitment. However, percent mortality decreased with increasing seedling size (Table 1).

New seedling recruitment continued through the second year following initial seed-drop for all plots (Figure 5), but was most abundant in the absence of fire. The first year growing season burn treatment (August 1998) and second year growing season treatment (July 1999) resulted in profuse flowering and seed production of wiregrass. For first year burn plots, recruitment from this event was evident in subsequent sampling. By the 1999 census, the number of new seedling recruits in the first year growing season treatment plots increased from < 1 seedlings/m^2 to > 8 seedlings/m^2 (Figure 5). Continued sampling would likely show a similar increase in seedling recruits in the second year growing season burn plots (July 1999) due to a second successful seed production event that followed the burn treatment. Although first year dormant season treatments (March 1998) did not result in reproduction there was a small increase in the number of seedlings. However, this increase was not as great as that experienced in the first year growing season burn plots (Figure 5).

DISCUSSION

This study indicates that mortality of wiregrass seedlings increases with growing season burns in the first and second years following germination and establishment. Although age and size of seedlings confound differences in survivorship that are seen with variation in season of burn (Brewer & Platt 1994, Bond & van Wilgen 1996), our findings of greater seedling mortality in both first and second year summer burns than first year dormant season burns suggests that season of burn may be more important to wiregrass seedling survival than age at this early stage of development. The elimination of seedlings with growing season fire could be the result of high ambient temperatures (Robbins & Myers 1992, Glitzenstein et al. 1995, Van Eerden 1997) or low but variable winds (Robbins & Myers 1992) which frequently accompany growing season fires and can raise temperatures to fatal levels for seedlings (Hare 1961). Below average rainfall for the two years of this study, accompanied by high air temperatures in 1998 may have resulted in particularly high fire intensities (National Climatic Data Center, Asheville, NC, USA).

If growing conditions had allowed for optimal plant growth and development, seasonal differences in survivorship may not have been evident (i.e., larger wiregrass seedlings may have survived regardless of the burn season). Successful plant establishment and rapid growth is especially critical for re-sprouting species found in fire-dependent communities because recovery from fire depends largely on the stage of development (Silva et al. 1991, Robbins & Myers 1992, Grace & Platt 1995, Hartnett & Keeler 1995, Bond & van Wilgen 1996, Fordyce et al. 1997, Spier & Snyder 1998). Because a majority of wiregrass plant biomass is located in root tissues (75-80% below ground surface and 55-60% in the top 5 cm of soil) (Parrott 1967), root biomass development is likely vital to wiregrass seedling survival through fire. However, the vertical distribution of wiregrass (root to shoot biomass ratios) through time since germination has not been studied. Below average precipitation during the summers of 1998 and 1999 provided less than optimal growing conditions and likely resulted in an overall smaller statured seedling cohort with increased vulnerability to growing season fire.

Examples of facilitation are predominantly found in stressful environments (i.e. deserts, dunes, and salt marshes) (Callaway 1995), Holmgren et al. 1997). Because extreme heat and drought conditions occurred throughout this study period, we expected to see facilitation of wiregrass seedling establishment by adult wiregrass plants (Callaway 1995, Holmgren et al. 1997, Callaway & Walker 1997). However, we found no evidence that close proximity to adult clumps offered increased establishment and survival. Rather, our findings of greater mortality of small seedlings in conjunction with evidence that large seedlings occur further from adult plants, indicate that seedling establishment patterns were more likely influenced by competition with adult plants. Additionally, the presence of adult wiregrass plants may have elevated fuel levels and, consequently, increased fire temperatures to lethal levels for seedlings in the immediate vicinity of adult plants (Hare 1961, Grace & Platt 1995). Further study of competitive interaction effects on wiregrass establishment is needed to fully understand this relationship.

Seedling recruitment subsequent to the initial census was expected with growing season treatments which elicited seed production. However, seedling recruitment in years subsequent to initial seed drop has not been well documented. Our results support recent observations by Seamon (1998) indicating that a persistent seed bank exists for wiregrass for at least 2 years. Decreased recruitment with burn treatment suggests that seed survival declined with exposure to fire.

These observations indicate that timing (season) and frequency of prescribed burns greatly influence successful wiregrass seedling establishment. Optimal burn regimes for wiregrass expansion include variation in the timing and frequency of fire to permit greater opportunities for successful natural recruitment and establishment of wiregrass. In particular, a growing season burn for seed production followed by 1-2 years without another growing season fire will likely increase survival of natural wiregrass recruits.

ACKNOWLEDGEMENTS

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Table 1. Transition matrix of size class and % mortality of wiregrass seedlings from a subsample 1997-1999.
Bold values indicate frequency of individuals (all treatments combined) **/** mean distance to adult ± SE.

	1999 size class					
1997 size class	small	medium	large	dead	row total	% mortality
small≤3 cm	0	**2 /** 67.5±11.50	**7** / 52.4±3.89	**76** / 38.8±1.88	**85** / 40.6±1.82	89
3 cm<medium≤15 cm	6	**22** / 46.2±3.21	**189** / 54.2±1.25	**482** / 44.4±0.74	**699** / 47.1±0.64	69
large>15 cm	1	0	**29** / 51.3±2.06	**34** / 56.1±2.88	**64** / 53.8±1.81	53
column total	7	24	225	592	848	

Fig. 1. Experimental plots in longleaf-wiregrass restoration site located in former wildlife food plot.

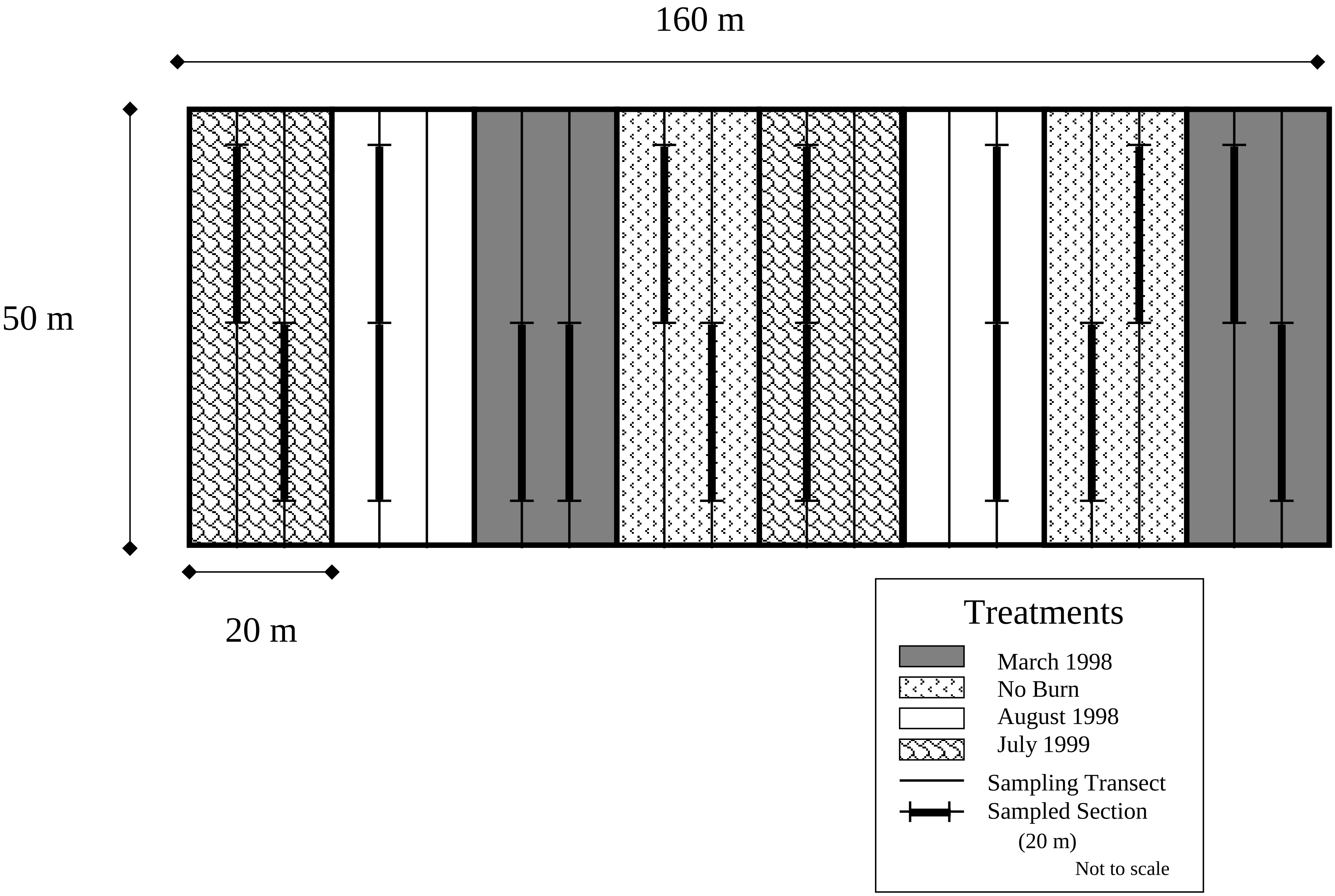
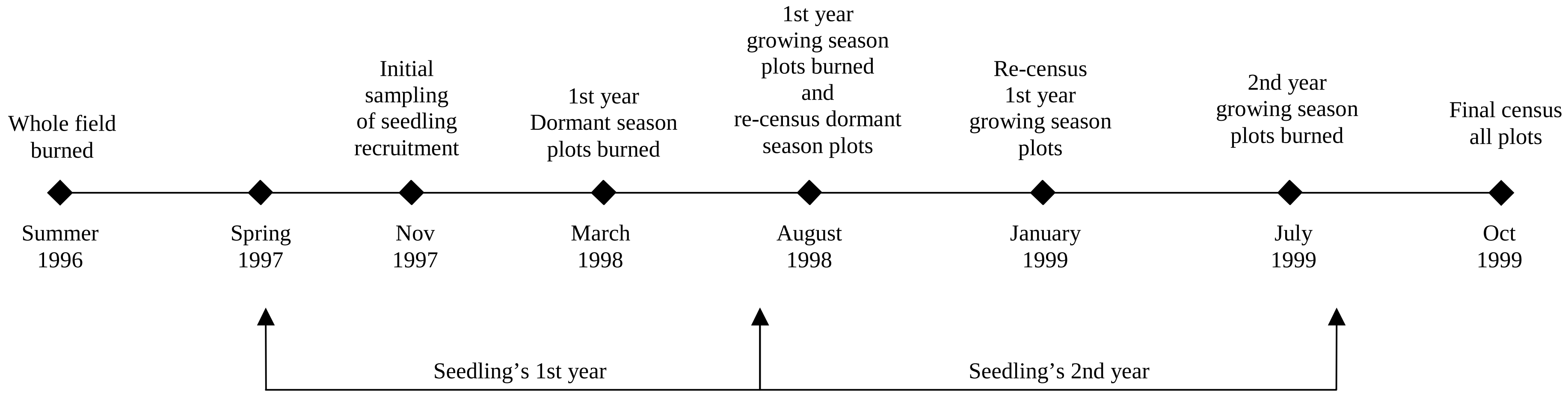

160 m
50 m
20 m
Treatments
March 1998
No Burn
August 1998
July 1999
Sampling Transect
Sampled Section
(20 m)
Not to scale

Fig. 2. Sampling and treatment time line (1997-1999).



Whole field burned
Initial sampling of seedling recruitment
1st year Dormant season plots burned
1st year growing season plots burned and re-census dormant season plots
Re-census 1st year growing season plots
2nd year growing season plots burned
Final census all plots
Summer 1996
Spring 1997
Nov 1997
March 1998
August 1998
January 1999
July 1999
Oct 1999
Seedling’s 1st year
Seedling’s 2nd year

Fig. 3. Relationship of size class and distance to adult plant (1997) (mean ±SE). Significant differences ($p<0.05$) among size classes are indicated by different letters.

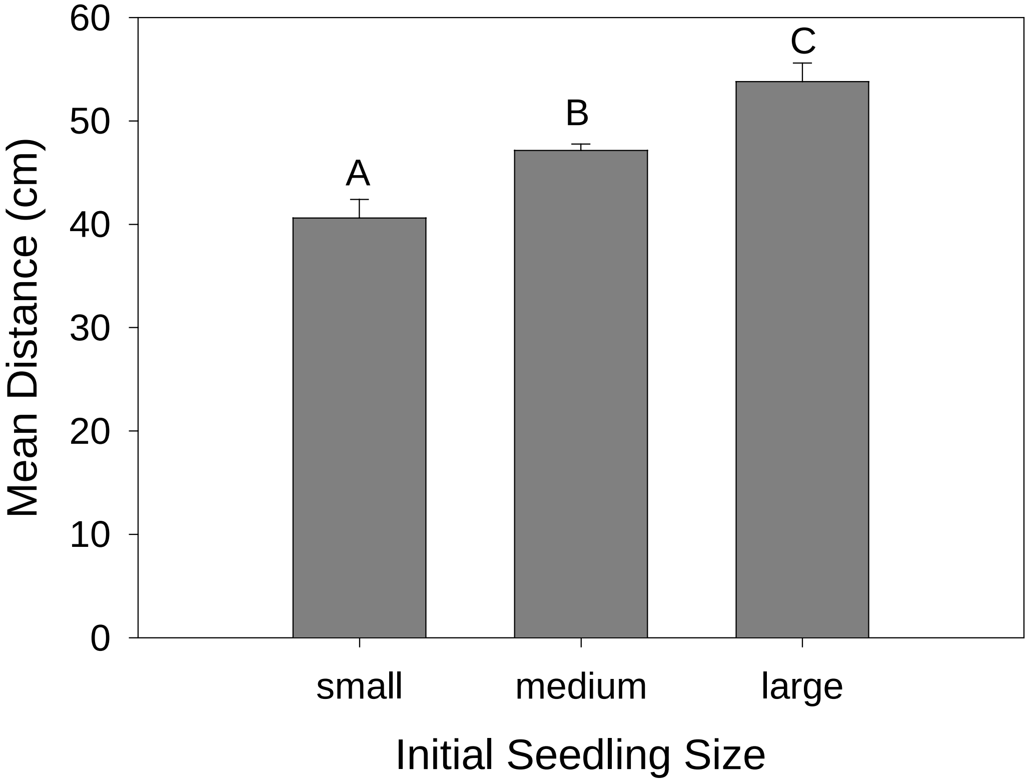

Mean Distance (cm)
0
10
20
30
40
50
60
A
B
C
small
medium
large
Initial Seedling Size

Fig. 4. Initial seedling size class survivorship of wiregrass seedlings by burn treatment (1997-1999) (mean ± SE). Significant differences ($p<0.05$) among treatments in percent survival are indicated only for the medium size class by different letters.

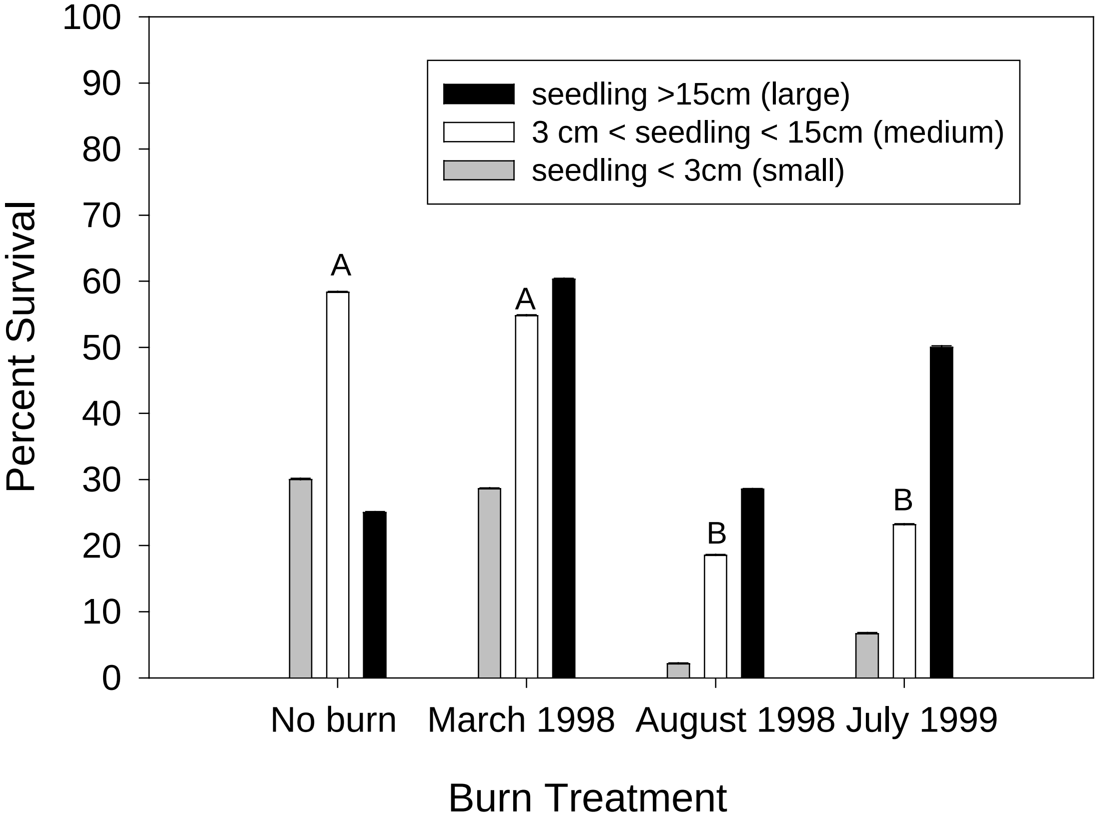
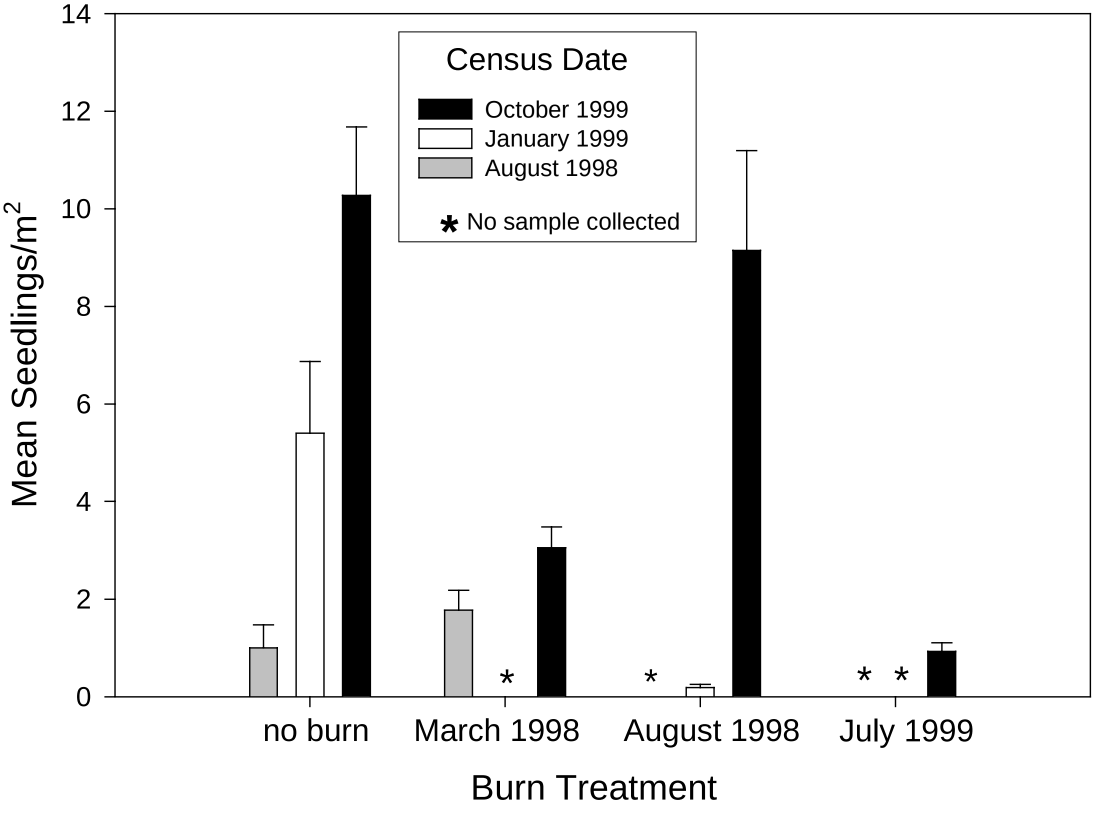

100
90
80
70
60
50
40
30
20
10
0
Percent Survival
seedling >15cm (large)
3 cm < seedling < 15cm (medium)
seedling < 3cm (small)
A
A
B
B
No burn
March 1998
August 1998
July 1999
Burn Treatment

Fig. 5. Cumulative seedling recruitment following burn treatment application subsequent to the 1997 initial seedling count (mean ± SE).


Census Date
October 1999
January 1999
August 1998
* No sample collected
Mean Seedlings/m2
0
2
4
6
8
10
12
14
no burn
March 1998
August 1998
July 1999
Burn Treatment
*
*
*
*

CHAPTER 4: COMPETITION EFFECTS ON WIREGRASS GROWTH AND SURVIVAL

Mulligan, M.K. and L.K.Kirkman. 2000. To be submitted to Plant Ecology

Key words: Plant interactions, facilitation, seedling establishment, age gradient, drought

ABSTRACT

We investigated plant interaction effects (competition and facilitation) on wiregrass establishment in two frequently encountered restoration situations of former longleaf pine and wiregrass habitats in the Southeastern United States: pine plantation and previously cultivated fields. In the plantation experiment, we specifically examined canopy removal, neighboring wiregrass density, and aboveground and belowground interaction effects on establishment and growth of wiregrass seedlings at three different ages (3week, 6 months, and 1 year) with 3 competitive exclusion treatments (aboveground exclusion, belowground exclusion, or no exclusion). Competition treatment effects were age dependent for survivorship and growth. Survival of six month old seedlings was unaffected by competition treatment; whereas, one year and three week old seedlings were larger where roots were excluded. Seedling size increased with root exclusion except in the case of the three week old seedlings in plots lacking neighboring wiregrass which did not change in size regardless of exclusion device. In old fields, fertilizer treatments did not benefit seedling survival or growth. Seedlings were smaller where neighboring old field, weedy vegetation was present regardless of wiregrass seedling age; whereas, survival was dependent on seedling age. Six month old seedling survivorship remained high regardless of weeding treatment. Water limitation on seedling establishment was exacerbated due to a second consecutive year of severe drought that occurred during this study. Our results suggest that wiregrass dominance in the longleaf

and wiregrass ecosystem does not rely solely on frequent fire disturbances. Rather, changing environmental conditions (ie varying rainfall) through time may allow for episodic shifts in successful establishment and recovery events.

INTRODUCTION

Interactions between organisms occur regularly in natural environments and may even be critical to the persistence of a particular species in a certain habitat (Hacker & Gaines 1997). Facilitation and competition refer to the net effect of the interactions experienced by an organism as a result of the presence of neighboring organisms (Holmgren et al. 1997). Facilitation occurs when the net effect of these interactions is positive (Callaway 1995). For example, positive interactions can occur as a result of microclimate changes (Sans 1998, Holzapfel & Mahall 1999), decreasing predation (Rousset & Lepart 2000), or attracting appropriate dispersal agents (Hunter & Aarssen 1988). Alternatively, competition occurs when these interactions lead to negative net effects on associated species (Tilman 1988, Keddy 1989).

Plant interactions can be further divided into aboveground and belowground elements. Belowground interactions involve the acquisition of nutrient resources as well as water and physical space (McConnaughay & Bazzaz 1991, Casper & Jackson 1997), whereas aboveground interactions mainly involve changes in light intensity or availability due to limits in physical space (Belcher et al. 1995, Wilson & Tilman 1995, Casper & Jackson 1997). It is possible for negative interactions (competition) to occur above or belowground when neighboring plants usurp resources and lower plant growth rates, survivorship or reproductive success (Cook et al. 1993, Belcher et al. 1995, Wilson

& Tilman 1995, Cahill 1999, Haugland & Froud-Williams 1999). Inversely, above and belowground positive interactions (facilitation) can result in increased plant growth rates, survivorship or reproductive success (Bertness & Callaway 1994, Hacker & Bertness 1999).

Facilitation and competition do not occur in isolation and it is, therefore, likely that a balance or interplay between negative and positive effects occurs (Callaway & Walker 1997, Holmgren et al. 1997). Experiments examining the effects of both facilitation and competition executed across a wide range of habitat types, have demonstrated shifts in interactions from positive to negative net effects and vice versa (De Steven 1991b, De Steven 1991a, Aguiar & Sala 1994, Bertness & Leonard 1997, Sans et al. 1998, Levine 1999, Tielborger & Kadmon 2000). For instance, mature grasses and shrubs in the Patagonian steppe and shortgrass steppe initially provide microclimatic benefits to grasses and annuals during establishment (Aguiar et al. 1992, Aguiar & Sala 1994). However, with the increase in age and densities of the new recruits, competition begins to outweigh facilitation (Aguiar et al. 1992, Aguiar & Sala 1994, Greenlee & Callaway 1996, Kelly & Burke 1997). Similarly, seeds in old field establishment experiments in North Carolina initially benefited from weedy vegetative cover (De Steven 1991a). However, once seedlings became established, the relationship with weedy vegetation became competitive (De Steven 1991b). Furthermore, environmental conditions may affect plant interactions as in desert communities where increased rainfall allowed for facilitation to occur in the establishment of annuals beneath perennial shrubs; however, dry years resulted in competition between perennial shrubs and establishing annual species (Holzapfel & Mahall 1999, Tielborger & Kadmon 2000). Overall, net effects of plant interactions (facilitation or competition) appear to vary with species, stages of plant development, environmental gradients, and seasonal changes (Callaway 1995, Wilson & Tilman 1995, Callaway & Walker 1997, Holmgren et al. 1997, Chambers et al. 1999, Rousset & Lepart 2000, Tielborger & Kadmon 2000). These shifts appear to follow observable patterns of increasing facilitation in extreme habitats (Holmgren et al. 1997, Brooker & Callaghan 1998)

Plant interactions during seedling establishment may be vital to the maintenance of some species and knowledge of these dynamics may be particularly useful in developing reintroduction strategies for targeted species. The restoration of ground cover in longleaf pine (*Pinus palustris*) and wiregrass (*Aristida* spp.) ecosystems of the southeastern Coastal Plain of the United States is one example where increasing our understanding of plant interactions during establishment may improve management techniques.

Longleaf and wiregrass habitats have an open understory with dense grass cover that appears monospecific at first glance. However, these communities have species diversity that rivals any plant community in the temperate zone (Walker & Peet 1983, Peet & Allard 1993) with up to 40 plant species per square meter (Peet & Allard 1993). Moreover, many rare plant taxa are associated with the longleaf pine wiregrass savannas (Hardin & White 1989). With less than 3% of the original area occupied by longleaf and wiregrass remaining and an even smaller proportion retaining intact understory vegetation (Simberloff 1993), restoring degraded habitat is of particular interest (Seamon et al. 1989, Seamon & Myers 1992, Bissett 1996, Van Eerden 1997).

Wiregrass is often referred to as a keystone species of the longleaf pine community (Platt et al. 1988, Clewell 1989, Hardin & White 1989) because of its structural dominance in undisturbed areas (Noss 1989, Glitzenstein et al. 1995) and its function as a high quality fine fuel source (Clewell 1989, Outcalt 1992). An abundance of wiregrass clumps presumably increases pyrogenicity due to the vertical arrangement of the grass tillers which uphold accumulated pine litter and consequently decrease fuel moisture content (Means & Grow 1985, Clewell 1989, Noss 1989, Platt et al. 1989, Seamon et al. 1989, Glitzenstein et al. 1995, Van Eerden 1997). Thus, recent efforts to restore longleaf systems include the reintroduction of wiregrass as a primary objective.

There are several problems associated with wiregrass restoration and regeneration. First, successful reproduction occurs only following growing season fires (Parrott 1967, Seamon & Myers 1992, Streng et al. 1993, Outcalt 1994, Van Eerden 1997). This seasonal fire requirement for wiregrass reproductive success may be due to elevated maximum temperatures that occur in summer burns relative to those earlier in the season (Van Eerden 1997, Walker & Van Eerden 1997). Region-wide management for the past several decades has utilized dormant season burns (i.e. months prior to May) for optimum quail habitat management (Outcalt 1994, Smith & Atkinson 1997, Van Eerden 1997). However, growing season prescribed burns are increasingly implemented as a management option (Smith & Atkinson 1997). Secondly, wiregrass does not recover from intense soil perturbations (Clewell 1989, Outcalt & Lewis 1990, Outcalt 1992, Walker & Van Eerden 1997). The lack of re-invasion in abandoned fields adjacent to stands of wiregrass is most likely due to a lack of propagules as a result of dormant season burns. Furthermore, the rates of germination of existing propagules are unpredictable and can fall below 10%. Anecdotal evidence suggests that wiregrass vigor decreases with fire exclusion and increasing canopy cover (Clewell 1989, Outcalt 1994, Means 1997). Similarly, high pine litter levels can negatively affect wiregrass seedling establishment whereas no litter or light litter can be favorable for seedling growth and survival (Van Eerden 1997).

The limited knowledge of wiregrass biology and natural establishment processes precludes the development of optimal and practical re-introduction techniques for this species. Although some experimentation with direct seeding (Seamon & Myers 1992, Bissett 1996, Seamon 1998), containerized seedlings (Seamon et al. 1989, Van Eerden 1997, Outcalt et al. 1999, Mulligan et al. in press) and site preparation (Outcalt 1994) has occurred, questions regarding the best point in the successional process in which to introduce propagules (e.g., old field, thinned canopy plantations) and how wiregrass establishment is affected by plant interactions remain unanswered. Since longleaf pine and wiregrass communities are highly disturbed communities that are characterized as having low productivity and low nitrogen availability (Christensen 1977, Mitchell et al. 1999, Wilson et al. 1999), we hypothesized that early stages of wiregrass seedling establishment (3 week) would benefit from neighboring vegetation through the amelioration of poor site conditions.

This study examines the effects of plant interactions on wiregrass seedling establishment across an age gradient in two commonly encountered initial restoration site conditions: longleaf pine plantations and recently abandoned fields. Our study focuses on the following questions: 1) Is wiregrass establishment positively or negatively influenced by neighboring pines and wiregrass? 2) Are patterns similar for above and belowground interactions? 3) Is wiregrass establishment positively or negatively influenced by neighboring early successional vegetation? 4) Do nutrient additions modify interactions? 5) Do responses vary with the age of seedling?

METHODS

Study sites

Study sites are located at the J.W. Jones Ecological Research Center at Ichauway near Newton, Georgia, USA. For the plantation competition study we selected a 20-year-old, 49 ha longleaf pine plantation with an initial planted tree density of 1184 trees/ha (average basal area of 25 m^2/ ha). The soils in this pine plantation are classified as loamy, siliceous, thermic Arenic Paleudults (Wagram loamy sands) (USDA 1986). The combination of the closed canopy and deep sandy soils resulted in little, if any, understory vegetation or ground cover in the plantation. Old-field competition sites included six cultivated wildlife food plots. The outer perimeter (15-20 m) of each field has been chopped annually for several decades to reduce shrub encroachment, but left fallow. This fallow field perimeter was used for experimental plots to avoid elevated residual soil nutrients from recent fertilizer applications in the cultivated field sections. Prior food plot management included annual field disking with rotations of fallow, corn and Egyptian wheat strips with annual fertilizer (5-10-15 NPK) application at a rate of 2722 kg/ha. Average annual rainfall for the area is 131 cm, which is distributed fairly evenly throughout the year (National Climate Data Center, Asheville, NC, USA).

Wiregrass seedling cohorts were grown in a greenhouse at the Jones Ecological Research Center from seed collected in December 1997 following same year summer burns at nearby sites on the Ichauway property. Seeds were sown at appropriate time intervals to establish 3 age groups of seedlings (1 year, 6 month, and 3 week) at the time of planting.

Plantation competition

Experimental plots were established in 1994 in a randomized complete block design for canopy removal and wiregrass density treatments. Within each of 10 blocks, three, 25 m x 25 m plots were established (Figure 1). We randomly assigned one of the following canopy removal treatments to a single plot in each block: a) control with no overstory removal (25 m^2/ha), b) 33% reduction in overstory basal area (16 m^2/ha), and c) 66% reduction in overstory basal area (8 m^2/ha). Trees were randomly selected for removal within each treatment plot. We will refer to these thinning treatments as 1/3 removal, 2/3 removal and no canopy removal.

We examined competitive interactions on young seedlings with and without adult wiregrass present using two separate experimental setups. In five of the blocks we further divided each plot into two, 10 m x 10 m split-plots (Figure 1A). In April 1994, we transplanted six-month old wiregrass plants into each split-plot subplot at either high density (5 seedlings/m^2 based upon natural wiregrass density reported by Clewell (1989) or low density (5 seedlings/10 m^2). Wiregrass seedling survival and vigor were periodically monitored and results are reported elsewhere (Mulligan et al. in review). The remaining five experimental blocks had no wiregrass transplants (Figure 1B).

We installed two types of exclusion devices in January 1999 to eliminate competition. Polyvinylchloride (PVC) pipe (30 cm diameter PVC SDR 35 (.91cm in thickness)) was driven into the soil to a depth of 30 cm to eliminate belowground competition with neighboring wiregrass and pines. We used a sharpened, metal soil core of the same dimensions as the PVC tubes (30 cm x 30 cm) to sever all roots. PVC pipes were then driven with sledgehammers into the groove created by the corer until the PVC was flush with the ground surface. This method was used to minimize soil disturbance. To eliminate competition for light by neighboring adult wiregrass plants, cone collars made of hardware cloth (10 cm diameter at soil surface and 30 cm height) were installed to prevent adjacent adult wiregrass foliage from overlapping planted seedlings.

We used a split-split plot design to examine below ground and above ground competition effects on wiregrass seedling growth and survival across an age gradient in the presence of adult wiregrass. Main factors included adult wiregrass density (DENS = high and low), seedling age at planting (AGE = 1 year, 6 month, and 3 week), competitive exclusion (COMP = root exclusion, above ground wiregrass exclusion, and no exclusion) and overstory removal treatment (OTRT = no removal, 1/3 removal and 2/3 removal). Within each block, each combination of age and competition exclusion was randomly assigned to 1m^2 in each adult wiregrass density subplot (AGE*COMP*OTRT = 27 treatment combinations per density subplot (810 seedlings total)).

To examine belowground competition effects on wiregrass seedling growth and survival across the age gradient in the absence of adult wiregrass, we randomly assigned all combinations of seedling age class (AGE = 1 year, 6 month and 3 week at transplantation) and competitive exclusion (COMP = no exclusion and root exclusion) to 1 m^2 compartments within overstory removal plots (AGE*COMP*OTRT = 18 treatment combinations per plot (270 seedlings total)).

In March 1999, we planted one seedling in each predetermined treatment compartment in all plots. Initial seedling tiller numbers were recorded for each seedling.

All plants were watered immediately after transplantation and within the first week, dead seedlings were immediately replaced. We weeded plots in a 30 cm diameter area around each seedling weekly. Severe drought occurred in the first two months following the transplantation of wiregrass seedlings. Based on weekly precipitation during this period, plants were watered for the months of April and May equal to ½ the average weekly rain amount as calculated using monthly precipitation averages (1895-1996, National Climatic Data Center, Asheville, NC, USA). We hand watered all plants five times in the months of April and May. Tiller numbers and survivorship were recorded in October 1999 for each seedling.

Old field competition

In October 1998, all field sites were triple harrowed. Four blocks were established in each field for a total of 24 blocks (Figure 2). Each block contained 12, 1m^2 treatment plots arranged in 3 rows and 4 columns. We examined three factors: fertilization (FERT), weeding (WEED) and age at planting (AGE). Age cohorts at planting included 1 year, 6 month and 3 week old seedlings as previously described. Fertilizer applications consisted of a one-time application of 5-10-15 NPK fertilizer (March 1999) at a rate of 272 g/m^2 as is used in food plot management. All vegetation was removed by hand from half of the weeding treatment 1 m^2 plots prior to planting and was maintained weekly thereafter. Within each block, every 1 m^2 plot was randomly assigned a treatment combination (FERT*WEED*AGE = 12 treatment combinations per block). Five seedlings per 1 m^2 treatment plot were planted for a total of 1440 seedlings. Plants were watered immediately following planting. Seedling mortality that occurred within the first week following transplantation was assumed to be due to transplantation stress and dead seedlings were replaced. Hand watering was implemented using the same criteria as was used in the plantation competition study. Initial tiller numbers were recorded for all transplanted seedlings. In October 1999, tiller numbers and survivorship were recorded for each seedling.

Statistical analyses

For plantation plots lacking adult wiregrass, analysis of variance, via General Linear Models procedure (Proc GLM;SAS Institute Inc. 1989), for a randomized complete block design was used to test for treatment effects on wiregrass seedling survivorship and growth. At the time of the plantation competition study initiation, previously established adult wiregrass plants in the 2/3 overstory removal plots were larger than the wiregrass in plots with less canopy removal (Mulligan et al. in review). Therefore, where adult wiregrass was present, General Linear Models procedure (Proc GLM; SAS Institute Inc. 1989), for a randomized complete block, split-split plot design was used to test for treatment effects on wiregrass seedling survivorship and growth. Tukey's multiple comparison test was used to test for differences among main plot treatment means in all cases. Where crosswise comparisons of significant interactions were made, Bonferroni corrections were applied.

For old field manipulations, analysis of variance, via General Linear Models procedure (Proc GLM; SAS Institute Inc. 1989), for a randomized complete block design was performed to test for treatment effects on wiregrass seedling survivorship and wiregrass seedling size. Tukey's multiple comparison test was used to compare treatment means in both cases. Bonferroni corrections were applied where crosswise comparisons of interactions were made.

RESULTS

Plantation competition

Seedling age at planting significantly affected wiregrass seedling survival regardless of the canopy thinning treatment or adult wiregrass density (Table 1). Overall, 6 month old seedlings had the highest survivorship (Figures 3, 4) Where wiregrass was present, percent survival (mean ± SE), for 1 year seedlings was 43.7 ± 3.0, 6 month seedlings was 90.7 ± 1.8 and 3 week seedlings was 32.2 ± 2.8. In the absence of wiregrass percent survival (mean ± SE) for 1 year seedlings was 64.4 ± 5.1, 6 month seedlings was 86.7 ± 3.6 and 3 week seedlings was 16.7 ± 4.0. Competition treatment effects on survival were age dependent (TRMT*PLTAGE) (Table 1). The competitive exclusion treatments had no effect on the six month old seedling survival; whereas, root exclusion significantly increased the survival of both 1 year old seedlings and 3 week old seedlings (Figures 3, 4).

Where adult wiregrass was lacking, increasing tree density reduced seedling size (Table 2B). Mean seedling size (± SE) in 2/3 overstory removal plots was 15.6 (± 2.1), 1/3 overstory removal plots was 9.1 (± 1.5) and plot with no overstory removal was 10.2 (± 1.8). Tree density did not affect plant size where adult wiregrass was present; however, seedlings planted in high wiregrass density subplots were significantly smaller than the wiregrass seedlings planted in low density subplots (high density mean ± SE = 7.1 ± 0.6, low density mean ± SE = 9.5 ± 0.7) (Table 2A). Competitive exclusion treatment effects on seedling size were age dependent (TRMT*PLTAGE) both with and without wiregrass understory. Root exclusion devices consistently resulted in larger plants regardless of the presence of adult wiregrass plants (Figure 5, Figure 6 and Table

2). However, the magnitude of the increase in size for the six month old seedlings in plots containing adult wiregrass plots was significantly greater than either 3 week or 1 year seedling size increase (Figure 5). Furthermore, in plots lacking adult wiregrass, root exclusion significantly increased 6 month and 1 year seedling size while no differences occurred between root exclusion and no exclusion for 3 week old seedlings without neighboring adult wiregrass (Figure 6).

Old field competition

Weeding increased overall wiregrass seedling survivorship (% survival) in old fields (Table 3A) (treatment means ± SE: weeded = 73.3±1.7; not weeded = 63.8±1.8) Whereas, with the exception of one year old seedlings, fertilizers had no affect on seedlings. Survivorship also varied by age at planting (Table 2A) (treatment means ± SE: 1 year = 62.7±2.2, 6 month = 91.5±1.3, 3 week = 51.5±2.3). The effect of weeding on percent survival was age dependent (WEED*AGE). Weeding significantly increased survivorship for both 3 week and 1 year old seedling cohorts, whereas, six month old seedling survivorship was unaffected by weeding (Table 3A, Figure 7).

Mean wiregrass seedling size (tiller number) was significantly affected by all main treatments (WEED, FERT and AGE)(treatment means ± SE: weeded = 38.88±0.92; not weeded = 6.61±0.92; fertilized = 21.17±0.92; not fertilized = 24.32±0.92; 1 yr = 28.04±1.13; 6 month = 32.13±1.13; 3 week = 8.06±1.13) (Table3B). However, the highly significant interaction term (WEED*FERT*AGE) indicated that treatment effects differed for the one-year-old seedling cohort. In particular, fertilizer application resulted in decreased seedling size for the one-year-old seedlings in weeded plots relative to the one-year-old seedlings in unweeded plots. Three week and 6 month seedling sizes were not significantly altered by the fertilizer application regardless of weeding treatment (Table 3B, Figure 8).

DISCUSSION

Contrary to our predictions, our results demonstrate that facilitation of wiregrass is not occurring even at early stages of development. A second consecutive year of severe drought took place during the sample period, which, according to predicted trends (Holmgren et al 1997, Brooker and Callaghan 1998), would seem to increase the likelihood of the occurrence of facilitation. Nevertheless, our results did not support the hypothesis that wiregrass seedling establishment is facilitated by neighboring vegetation under harsh environmental conditions.

This study suggests that wiregrass is not a superior competitor for resources in either early successional communities or plantation forests. More accurately, as with other long lived, frequent fire disturbance species, wiregrass relies on quick, early establishment followed by frequent disturbance to obtain and maintain dominance in the understory (Robbins & Myers 1992, Bond & van Wilgen 1996, Fordyce et al. 1997). In previous studies, increasing pine density had an immediate, negative impact on wiregrass plant size; however, changes in survivorship due to neighboring pines were apparent over time (Mulligan et al. in press). In this study, competition with pines results in decreased growth of wiregrass regardless of pine density yet different patterns may emerge in the long term. Furthermore, natural stand densities of neighboring adult wiregrass does not appear to affect seedling size and survivorship; however, it is possible that employing wiregrass densities greater than those found in natural stands would establish a threshold of changing wiregrass-wiregrass interactions. This may be especially appropriate given that proximity to adult wiregrass plants affects seedling size (Mulligan and Kirkman in review). Wiregrass competition occurs primarily belowground since root exclusion treatment consistently resulted in larger plants; whereas, seedlings removed from neighboring adult plant shading did not differ in size or survival from seedling with no exclusion treatment. In our experiment, nutrients did not appear to be limiting wiregrass growth or survival for 3 week or 6 month old seedlings; rather, competition for water directed growth and survival patterns. Conversely, highly stressed plants (as with one year old, root bound plants) may be more susceptible to drought when fertilizers are applied. Therefore, wiregrass has no difficulty becoming established in dense canopy situations especially if adequate water is available. However, canopy thinning (by prescribed burning, mowing or tree removal) is required for continued vigor and seedling recruitment (Mulligan et. al. in review).

Although we found no evidence supporting facilitation in these experiments, three week old seedlings grown in root exclusion devices within plots containing neighboring adult wiregrass appeared larger than the 3 week old, root exclusion seedlings in pine only plots. Therefore, it may be possible that neighboring adult wiregrass plants provide a slight advantage to wiregrass during early developmental stages. However, due to our experimental design, it was not possible to statistically compare plots with wiregrass to plots without wiregrass. Old field plots showed no sign of facilitation from neighboring vegetation.

Our findings that three week old seedlings consistently experience higher mortality than six month old seedlings was not surprising. The difference in size and survival across an age gradient affirms that the competitive ability of seedlings increases with age. Seemingly, by 6 months of age, wiregrass seedlings have reached some key developmental stage that allows for high survivorship (albeit at decreased growth) regardless of neighboring plants.

One explanation for the poor growth and survival of 1 year old seedlings is that they were not in optimum condition for transplantation. Specifically, the one year old seedlings were root bound in the seedling containers. As a result, one year old seedling data was confounded by the amplification of negative interactions on seedlings of poor quality. If larger containers had been used for the one year old seedlings prior to planting, results may have been different. For this reason, we did not use the data associated with the one year old seedlings as the upper limit of an age gradient, but rather as an example of how neighboring vegetation interactions affect the establishment of initially weakened wiregrass seedlings. Three week old and six month old seedlings were in excellent health and had no apparent, similar confounding effects. Therefore, assessments of shifts in survivorship and growth across an age gradient were limited to the six month and the 3 week old cohorts

Recent studies in harsh environments have found that typical environmental conditions (e.g. average rainfall) lead to observable positive effects (facilitation) in harsh environments; whereas atypical conditions (e.g. prolonged drought) result in an increase in the observable negative effects (competition) among plants (Holzapfel & Mahall 1999, Tielborger & Kadmon 2000). It is possible that average rainfall amounts would have caused neighboring plants to facilitate seedling establishment, chiefly that of the three week old seedlings. Long term monitoring may reveal shifts in observed plant interactions with varying environmental conditions (Wilson & Nisbet 1997, Tielborger and Kadmon 2000, Rebele 2000). Similarly, investigation of earlier plant developmental stages (e.g. germination and emergence) or examination of additional parameters (e.g. plant biomass or reproductive success) may indicate changes in plant fitness (Goldberg et al. 1999)

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Table 1

GLM for the effects of competition treatment (trmt) seedling age at transplantation (pltage) on percent survival

A. Wiregrass understory present (completely randomized block, split-split plot)

Source	df	F	P
OTRT (overstory removal)	2	0.83	0.4710
DENS (wiregrass densities)	1	1.67	0.2211
TRMT	2	17.75	0.0003
PLTAGE	2	179.44	0.0001
TRMT*PLTAGE	4	3.56	0.0390
Model Error	731		

B. No wiregrass (completely randomized block)

Source	df	F	P
OTRT (overstory removal)	2	2.19	0.1144
TRMT	1	20.25	0.0001
PLTAGE	2	86.36	0.0001
TRMT*PLTAGE	2	5.58	0.0044
Model Error	180		

Table 2

GLM table for the effects of competition treatment (TRMT) seedling age at transplantation on mean tiller number per individual

A. Wiregrass understory present (completely randomized block, split-plot)

Source	df	F	P
OTRT (overstory removal)	2	0.14	0.8748
DENS (wiregrass densities)	1	5.89	0.0319
TRMT	2	46.46	0.0001
PLTAGE	2	90.65	0.0001
TRMT*PLTAGE	4	13.32	0.0002
Model Error	731		

B. No wiregrass understory present (completely randomized block)

Source	df	F	P
OTRT (overstory removal)	2	6.25	0.0024
TRMT	1	73.61	0.0001
PLTAGE	2	46.71	0.0001
TRMT*PLTAGE	2	15.51	0.0001
Model Error	180		

Table 3

A. Partial GLM table of the effects of weeding (WEED), fertilizing (FERT) and seedling age at planting (AGE) on wiregrass seedling survival

Source	df	F	P
WEED	1	19.88	0.0001
FERT	1	14.54	0.0001
AGE	2	122.57	0.0001
WEED*FERT	1	0.00	0.9453
WEED*AGE	2	4.18	0.0155
FERT*AGE	2	2.11	0.1221
WEED*FERT*AGE	2	0.30	0.7317
Error	287		

B. Partial GLM table of the effects of weeding (WEED), fertilization (FERT), and seedling age at planting (AGE) on wiregrass seedling size (tiller#)

Source	df	F	P
WEED	1	616.18	0.0001
FERT	1	5.85	0.0158
AGE	2	130.79	0.0001
WEED*FERT	1	2.56	0.1096
WEED*AGE	2	49.15	0.0001
FERT*AGE	2	5.61	0.0037
WEED*FERT*AGE	2	4.91	0.0075
Error	287		

Fig. 1 Experimental design in longleaf plantation. A. Block containing wiregrass in the understory: completely randomized block, split-plot design (replicated 5 times). B. Block without wiregrass in the understory: completely randomized block design (replicated 5 times).

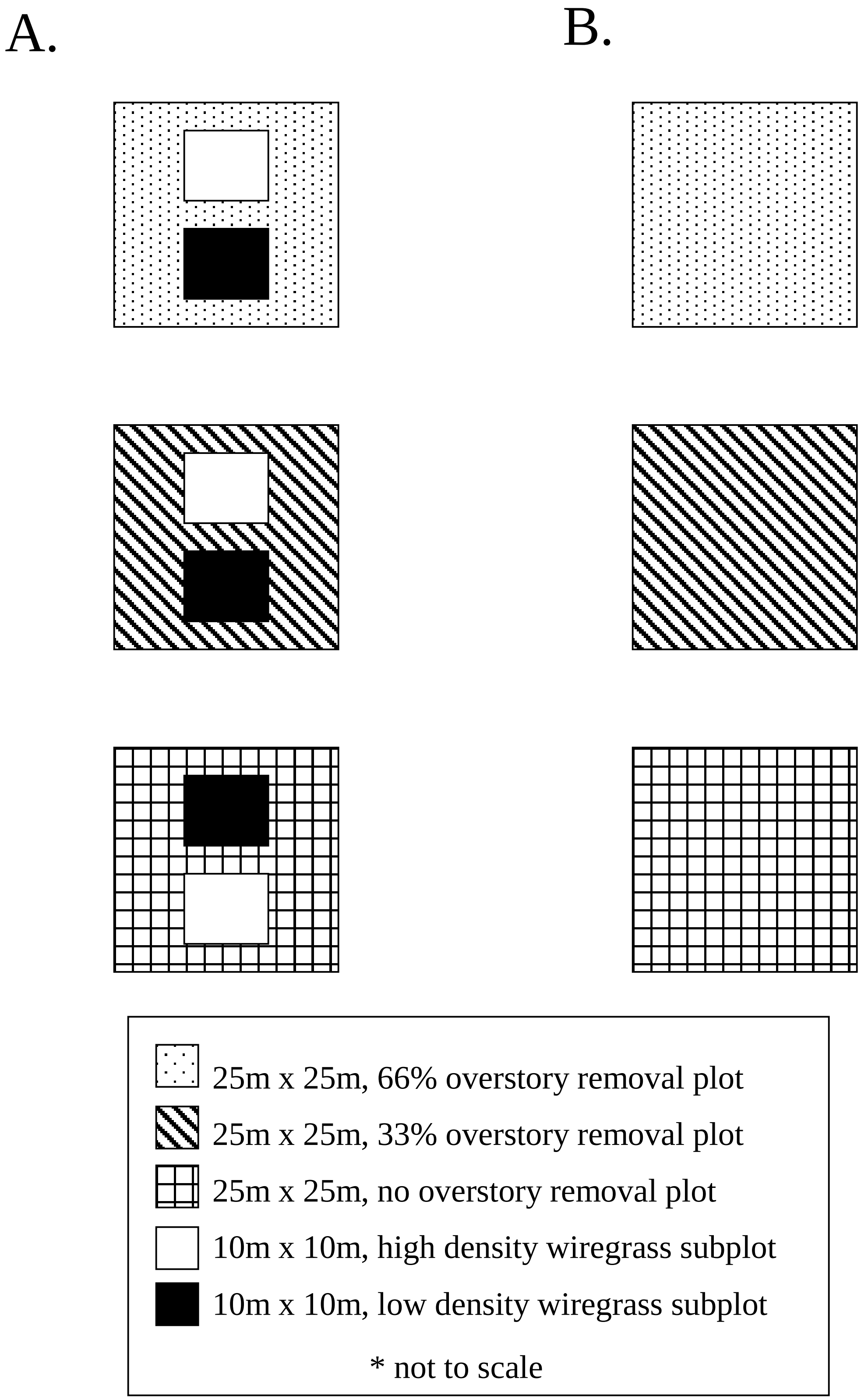

A.
B.
25m x 25m, 66% overstory removal plot
25m x 25m, 33% overstory removal plot
25m x 25m, no overstory removal plot
10m x 10m, high density wiregrass subplot
10m x 10m, low density wiregrass subplot
* not to scale

Fig. 2 Experimental plot layout of the old field experiment in the fallow margins of actively managed wildlife food plots (replicated 6 times).

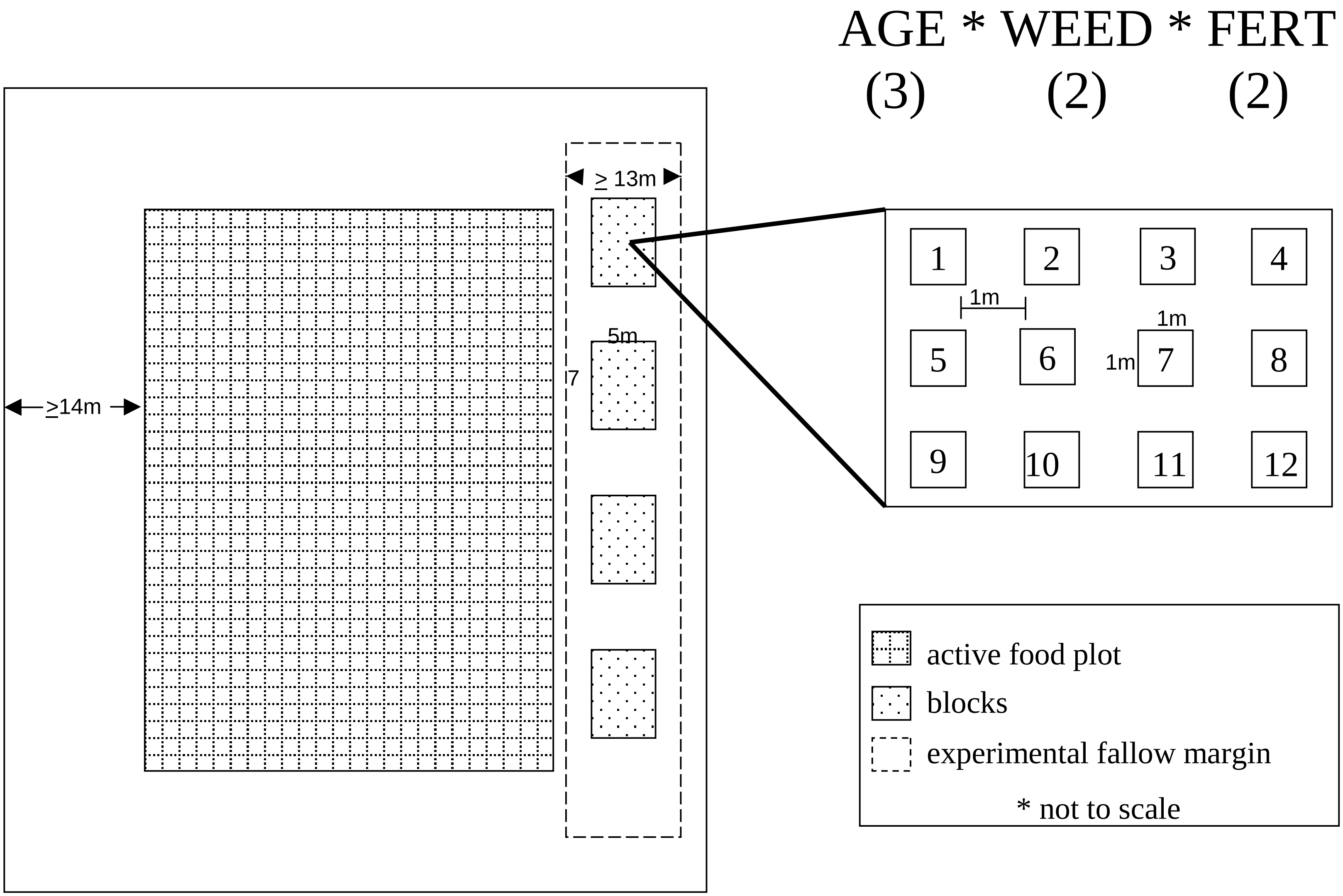

AGE * WEED * FERT
(3) (2) (2)
≥ 13m
5m
7
≥14m
1
2
3
4
1m
1m
5
6
1m
7
8
9
10
11
12
active food plot
blocks
experimental fallow margin
* not to scale

Fig. 3 Wiregrass seedling percent survival in the longleaf pine plantation experiment with wiregrass understory. Relationship of seedling survival at various ages (at time of planting) and competitive treatments (mean±SE). Treatments with dissimilar letters significantly differ within age class ($p<0.017$). Differences among age class means are indicated with asterisks (*) ($p<0.05$).

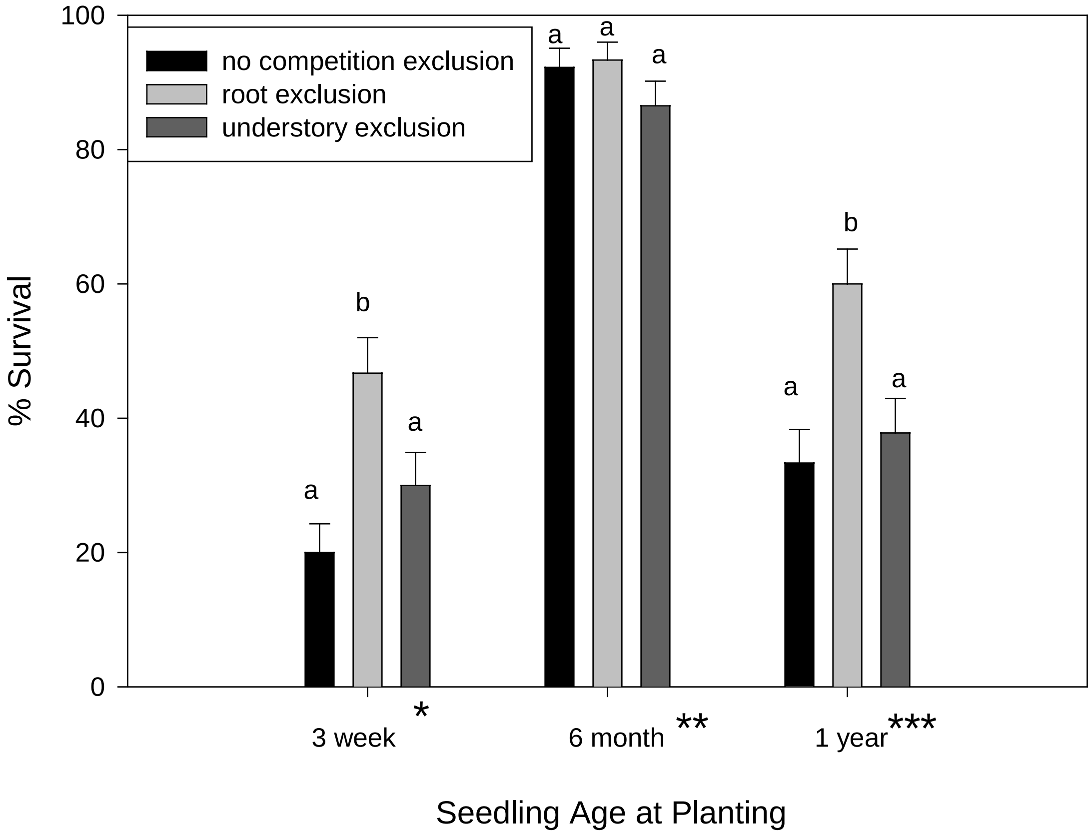

100
80
60
40
20
0
% Survival
no competition exclusion
root exclusion
understory exclusion
a
b
a
a
a
a
a
b
a
3 week
*
6 month
**
1 year
***
Seedling Age at Planting

Fig. 4 Wiregrass seedling percent survival in the longleaf pine plantation without wiregrass understory. Relationship of seedling survival at various ages (at time of planting) and competitive treatments (mean±SE). Treatments with dissimilar letters significantly differ within age class ($p<0.025$). Differences among age class means are indicated with asterisks (*) ($p<0.05$).

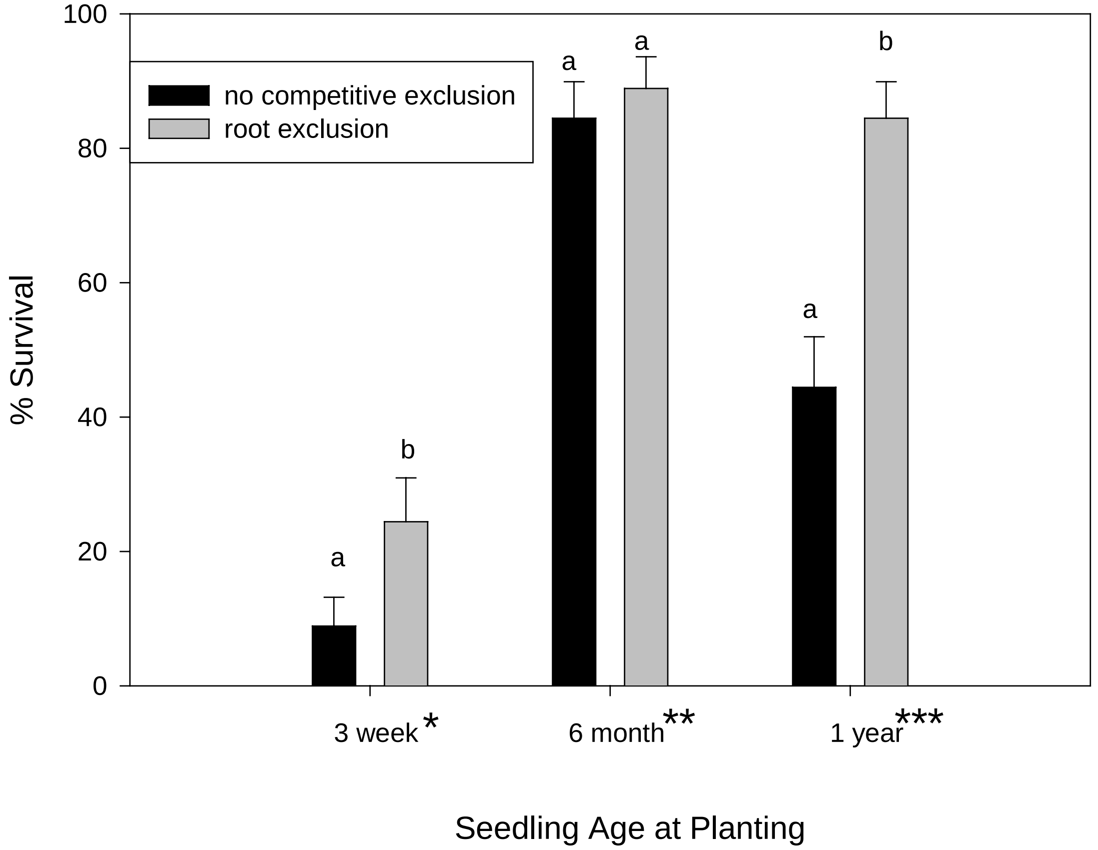

100
80
60
40
20
0
% Survival
no competitive exclusion
root exclusion
a
b
a
a
a
b
3 week *
6 month**
1 year***
Seedling Age at Planting

Fig. 5 Wiregrass seedling size (tiller number) in the longleaf pine plantation experiment with wiregrass understory. Relationship of seedling size at various ages (at time of planting) and competitive treatment (mean±SE). Treatments with dissimilar letters significantly differ ($p<0.017$). Differences among age class means are indicated with asterisks (*) ($p<0.05$).

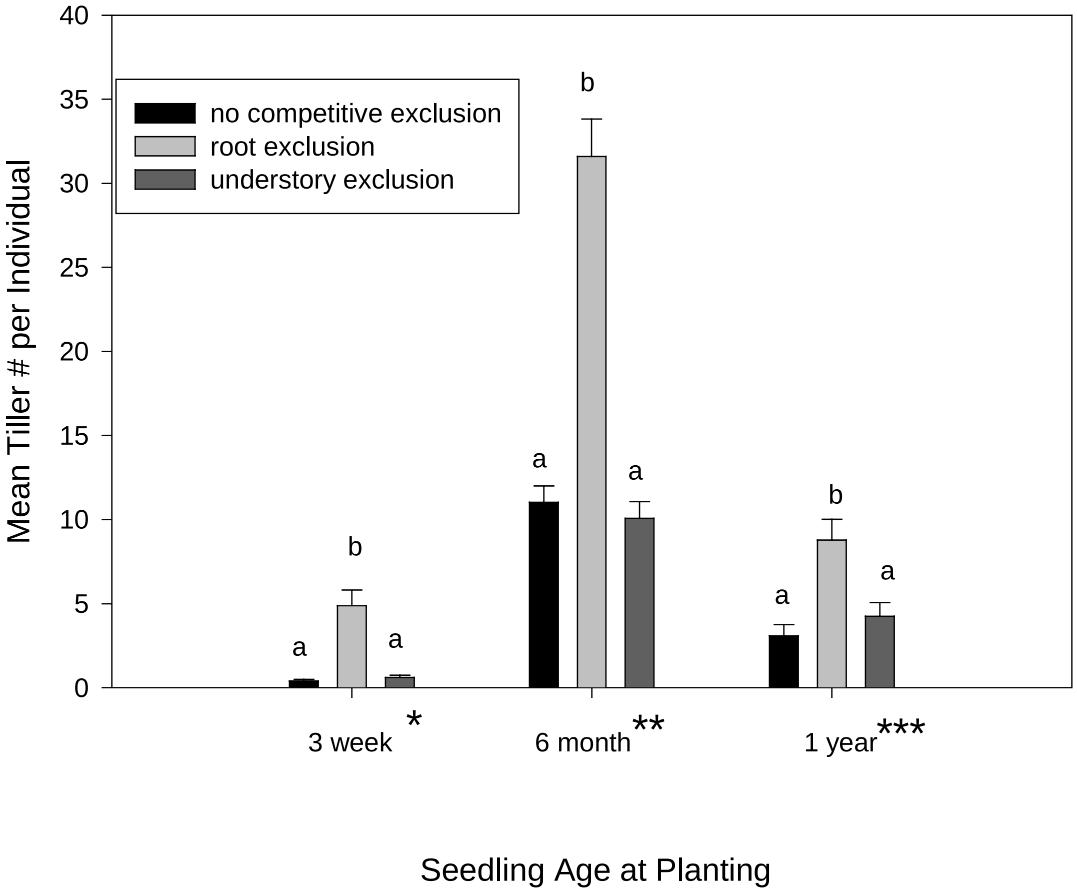

Mean Tiller # per Individual
0
5
10
15
20
25
30
35
40
no competitive exclusion
root exclusion
understory exclusion
a
b
a
a
b
a
a
b
a
3 week *
6 month**
1 year***
Seedling Age at Planting

Fig. 6 Wiregrass seedling size (tiller number) in the longleaf pine plantation experiment without wiregrass understory. Relationship of seedling size at various ages (at time of planting) and competitive treatments (mean±SE). Treatments with dissimilar letters significantly differ ($p<0.025$). Differences among age class means are indicated with asterisks (*) ($p<0.05$).

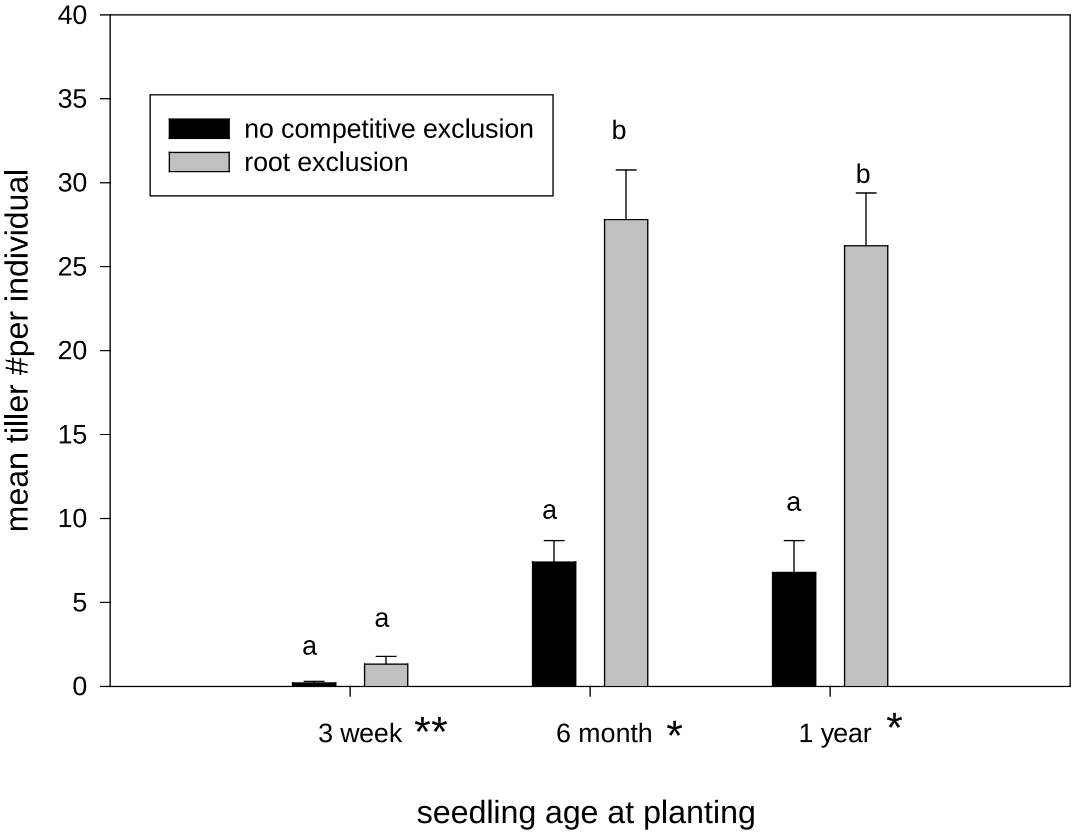

40
35
30
25
20
15
10
5
0
mean tiller #per individual
no competitive exclusion
root exclusion
a
a
a
b
a
b
3 week **
6 month *
1 year *
seedling age at planting

Fig. 7 Wiregrass seedling survival in the old field establishment experiment. Differences among age class means are indicated with an asterisk (*) ($p<0.05$). Differences in mean percent survival between weeding treatments (mean±SE) within age class are indicated by dissimilar letters ($p<0.025$).

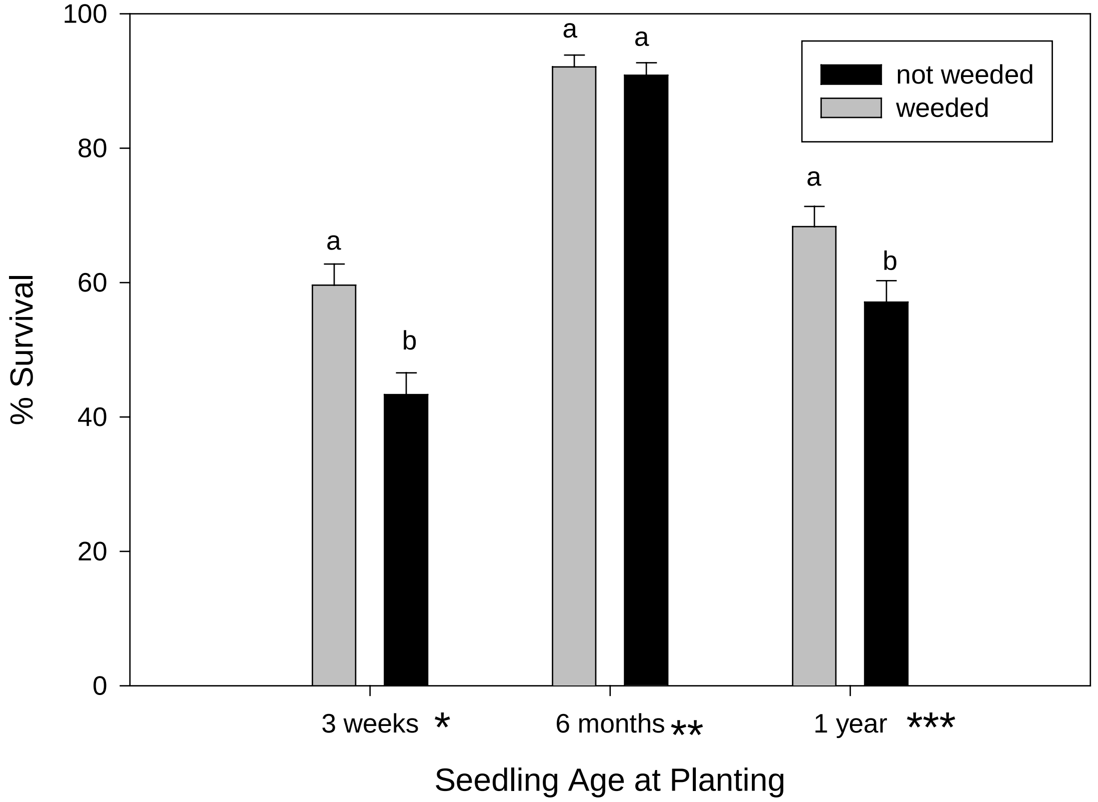
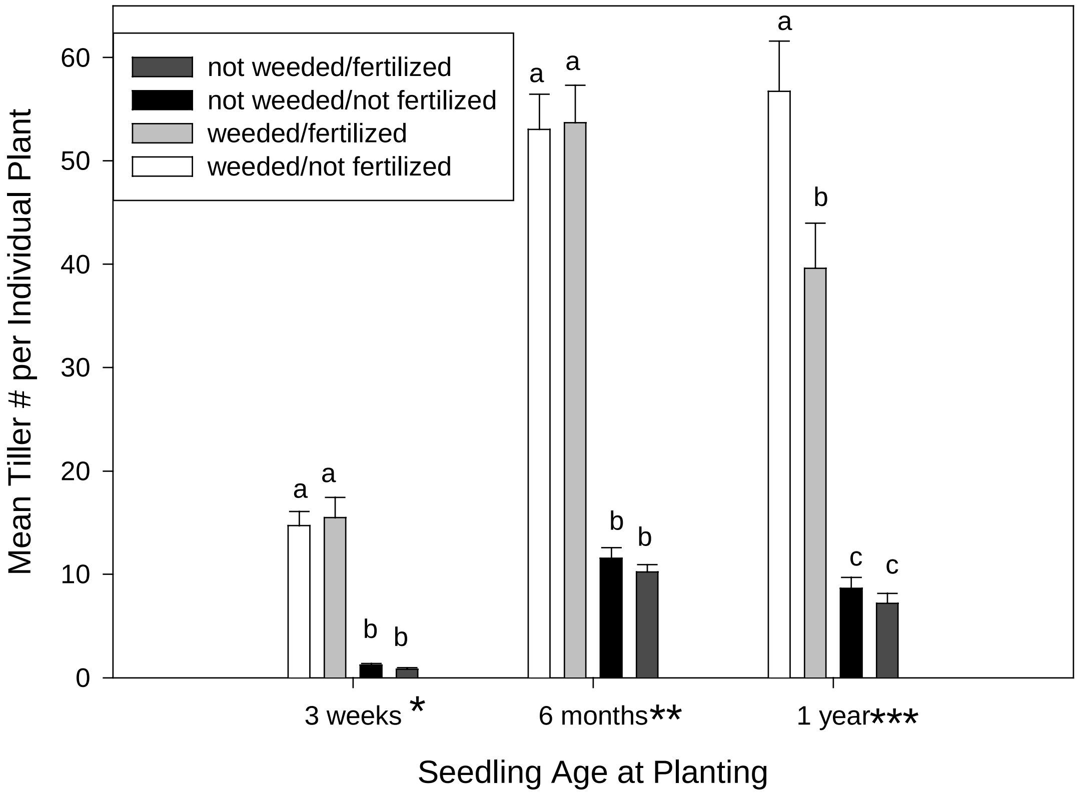

% Survival
100
80
60
40
20
0
a
a
a
b
a
b
a
not weeded
weeded
3 weeks *
6 months **
1 year ***
Seedling Age at Planting

Fig. 8 Wiregrass seedling size (tiller number) in the old field establishment experiment. Differences among age class means are indicated with an asterisk (*) ($p<0.05$). Differences among weeding/fertilizer combination mean tiller number per individual seedling (mean±SE) within age class are indicated by dissimilar letters ($p<0.01$).


Mean Tiller # per Individual Plant
0
10
20
30
40
50
60
not weeded/fertilized
not weeded/not fertilized
weeded/fertilized
weeded/not fertilized
a
a
b
b
a
a
b
b
a
b
c
c
3 weeks *
6 months**
1 year***
Seedling Age at Planting

CHAPTER 5: CONCLUSIONS

The once dominant longleaf pine-wiregrass ecosystems of the southeastern United States are now extremely rare. Because wiregrass (*Aristida beyrichiana*) is often considered a keystone species in these communities, recent restoration efforts have focused on its regeneration; however, little information is available on wiregrass population dynamics. In this study, wiregrass establishment and recruitment was assessed in several restoration situations including longleaf pine plantations and formerly cultivated fields.

Low canopy densities were shown to be necessary for successful wiregrass recruitment and establishment although wiregrass can persist in closed canopy situations. Prescribed burning in the first two years following seed germination resulted in higher seedling mortality than no-burn, particularly for small seedlings in the first summer. Weedy competition decreased wiregrass growth regardless of seedling age. However, seedling survival increased only for 3-week-old and 1-year-old individuals in the absence of weedy competition. Root competition resulted in smaller seedlings and lower survival regardless of seedling age; whereas, neighboring, aboveground wiregrass competition did not significantly affect seedling survival or growth. Furthermore, fertilizer additions did not influence wiregrass growth or survival, rather, it appears that water is limiting plant growth and survival in these systems.

These studies provide useful information to aid management and restoration efforts of wiregrass. First, the season and frequency of fire has a significant effect on seedling survival (chapter 3 this thesis). Therefore, the timing and frequency of prescribed burns should vary to allow for successful seeding and establishment events according to management objectives. Secondly, wiregrass can persist in dense canopy situations (pines and early successional communities) albeit with decreased growth and seedling recruitment. Hence, restoration opportunities may include areas where remnant patches of wiregrass persist in areas that have been long unburned as well as in old fields. In either case, open canopy conditions provide optimum circumstances for wiregrass growth, seedling recruitment and population expansion. Similarly, low adult wiregrass density does not affect the number of seedling recruits per adult to the extent of overstory density and further emphasizes the importance of open canopy conditions for vigorous wiregrass. Finally, fertilizer applications do not improve wiregrass growth or establishment. Thus, at least in dry years, fertilizer application is not recommended.

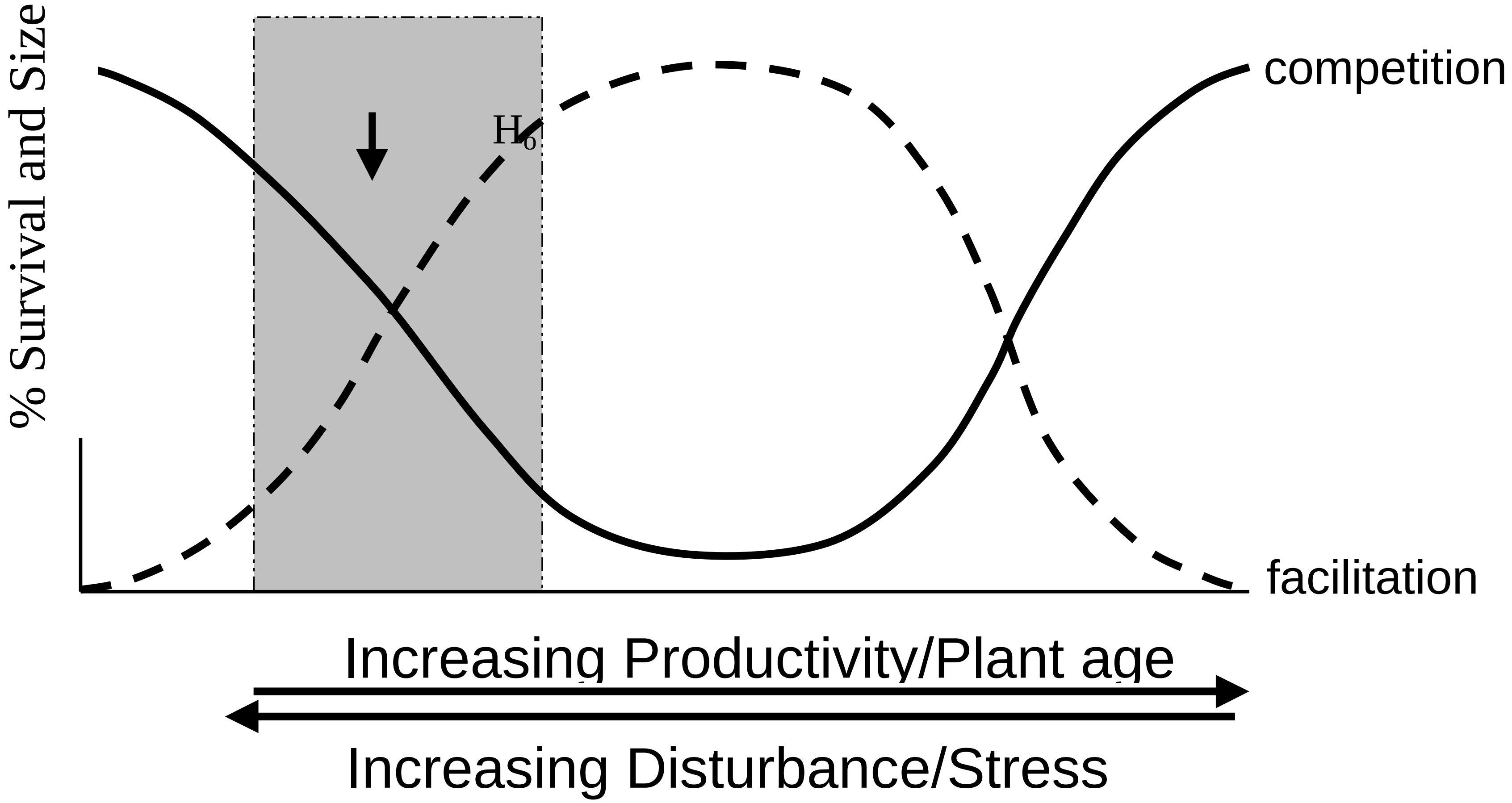
Conceptual model of interaction effects on wiregrass

Seedling establishment studies historically have focused on the impacts of competition. As a result, many community models incorporate competition as the major interaction affecting community structure and individual plant survival and growth (Grime 1979, Tilman 1982, Goldberg & Novoplansky 1997). Our study would seem to agree with the concept that negative interactions (competition) determine wiregrass establishment success. Facilitation was not observed, but should not be ruled out as a possibility. In view of recent studies suggesting the occurence of an integration and interplay of competition and facilitation in community structure (Hacker & Gaines 1997, Holmgren et al. 1997, Brooker & Callaghan 1998, Rebele 2000), it may be appropriate to consider the possibility of shifts in plant interactions with changes in productivity, disturbance, stress, and stage of plant development. Especially when considering the extreme drought conditions that occurred throughout this study and the inherent harshness of the environment, it is possible that earlier developmental stages (e.g. germination or emergence) or during years with average rainfall would allow for positive interactions to surface (Tielbourger and Kadmon 2000).

We propose a basic conceptual model illustrating how shifts in productivity, plant age, disturbance and stress levels might result in fluctuations and shifts between the relative strength (intensity) of both positive and negative interactions in wiregrass development (Figure 1). This model allows for competition and facilitation to occur simultaneously and in a wide range of habitats. We expected facilitation to play a role in wiregrass establishment given the severity of the habitat and the drought conditions (H_o on Figure 1). Although facilitation was not observed in this experiment, it should not be ruled out as a possible outcome of plant interactive effects on wiregrass development as it may be present, but not be apparent given the methods we used (Goldberg et al. 1999, Rebele 2000). It may be possible that facilitation occurs and is more common than previously expected, but additional methods of measurements are needed to capture positive effects.

Fig. 1 Conceptual model representing shifts in positive (facilitation) and negative (competition) plant interactions on wiregrass establishment using plant biomass and survival as measures of the intensity of the interactions with changing levels of productivity, plant age, disturbance, and stress. The gray box represents the range of interactions found in the longleaf and wiregrass communities. The arrow represents actual results. H_o indicates where we expected interactions to be significant for wiregrass establishment.

Conceptual Model of Interaction Effects on Wiregrass



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