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Longleaf pine and oak responses to hardwood reduction techniques in fire-suppressed sandhills in northwest Florida

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Abstract

Restoring fire-suppressed longleaf pine (*Pinus palustris* Mill.) sandhill communities often includes reducing hardwood structure before re-establishing maintenance fire regimes. Using a randomized complete block design, we compared the effects of three hardwood reduction techniques (spring burning, application of the ULW® form of the herbicide hexazinone, and midstory chainsaw felling/girdling) and a no-treatment control on oak and longleaf pine densities in fire-suppressed sandhills at Eglin Air Force Base, FL. Treatments were applied in the spring and summer of 1995. Felling/girdling and herbicide plots were also burned for fuel reduction from March to April in 1997. Frequently burned, high-quality sandhill plots were sampled to establish reference conditions. Pre-treatment diameter distributions of oaks followed a negative-exponential curve in all treatments, but were flat with low tree densities in reference plots. Oak densities were significantly reduced in the herbicide and felling/girdling plots in 1995. Compared to the controls, growing season fire topkilled up to 20% more hardwoods among smaller trees in 1995, but this value increased to approximately 50% after 1996. In all years, the greatest reduction of oak juvenile density (<1.4 m high) was caused by herbicide application. Control plots contained significantly fewer oak juveniles than the burn and felling/girdling plots. Reference plots contained the lowest and most variable oak juvenile densities. Size distributions of longleaf pine across all plots were bimodal with modes at 0–4.9 and 25–29.9 cm in diameter. The highest mode was at 0–4.9 cm in treatment plots and at 25–29.9 cm in reference plots. Only fire quantitatively changed the distributions by the attrition of the smallest trees >1.4 m high in all years. Fire caused approximately 50% decreases in longleaf pine juvenile (<1.4 m high) density in 1995 and 1997. By 1997, median juvenile densities converged to 5–6 stems/200 m^2 in all treatments, including the control. Juvenile densities were slightly higher and more variable in reference plots than in treatments. In 1997, fuel reduction burns in the herbicide and felling/girdling plots decreased densities of recently germinated longleaf pines to <5 seedlings/20 m^2, a 90% decrease compared to 1996 densities. Seedling densities dropped by approximately 50% in control and burn plots, although these sites received no manipulations after 1995. Seedling densities only decreased by 22% in reference plots (205 seedlings/20 m^2 in 1996), which did experience some fires.

Keywords: Longleaf pine sandhills; Hardwood reduction; Fire; Hexazinone; Chainsaw felling/girdling; Northwest Florida

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1. Introduction

Longleaf pine (*Pinus palustris* Mill.) forests were once dominant across much of the southeastern Coastal Plain (Frost, 1993; Landers et al., 1995; Plunkett and Hall, 1995). Fires occurring historically every 1–10 years maintained an open overstory of longleaf pine, topkilled many of the hardwoods, such as turkey oak (*Quercus laevis* Walt.), which subsequently resprouted, stimulated flowering and seed production of several of the herbaceous species, created an ideal seedbed for recruitment of longleaf pine seedlings and herbaceous species, and constrained the distributions of fire-intolerant species (Myers, 1990). Lightning and early human activities established this fire regime, which was seasonally biased toward the growing season months of April–July (Robbins and Myers, 1992).

During this century, the acreage of longleaf pine communities has decreased by over 98% (Landers et al., 1995). Additionally, prolonged fire suppression in most remaining sites has resulted in hardwood encroachment to levels that threatened the recruitment of longleaf pine and herbaceous plants, and the viability of many federal- and state-listed endangered species. Returning fire to fire-suppressed sandhills is necessary to reverse degradation. However, the accumulation of woody fuels and fuel ladders represents a fire hazard to both the longleaf pine canopy and juveniles (Robbins and Myers, 1992), and the reduced flammability of fuel requires more dangerous burn parameters for ignition success. Moreover, fire is not expected to topkill larger oaks (Waldrop et al., 1992; Streng et al., 1993), and topkilled oaks generally resprout in densities that would far exceed pre-burn levels in the absence of frequent fires (Waldrop et al., 1992). Therefore, restoration and management goals may require that other methods be coupled with fire to kill larger hardwoods while preserving the longleaf pine component.

In this study, we experimentally compared the initial effects of three hardwood reduction techniques on the densities of different diameter classes of longleaf pine and oaks in fire-suppressed, longleaf pine-dominated sandhills. The treatments were: growing season burn; application of the ULW® form of the herbicide hexazinone; midstory mechanical felling/girdling; a no-treatment control. Sandhill communities that received treatments were also contrasted to frequently burned longleaf pine-dominated sandhills, which were not part of the experimental design but are considered here as reference sites.

2. Methods and materials

2.1. Study area

Eglin Air Force Base (EAFB) occupies approximately 145 000 ha in the southern portions of Walton, Okaloosa, and Santa Rosa counties in the western Florida Panhandle. The climate is temperate with mild winters and hot, humid summers. Winters tend to be somewhat milder near the coast compared to the inland regions (Chen and Gerber, 1990). The mean annual temperature is 18.3°C, with approximately 275 freeze-free days per year. Thunderstorms and lightning strikes are frequent during the summer months. Mean annual precipitation is 158 cm per year (DoD-Air Force, 1995). Monthly precipitation levels peak slightly during late spring and early summer months and decrease during the winter months. Snow accumulation is rare. Tropical storms are frequent along the Gulf Coast of Florida and neighboring states. Between 1871 and 1985, 115 tropical storms and hurricanes made landfall within 110 km of EAFB (NOAA, 1994).

The terrain is level to gently rolling with occasional areas of steep slopes down to ravines. Elevation ranges from 0 to 100 m above sea level, and the landscape generally slopes to the southwest toward the Gulf of Mexico. Throughout most EAFB sandhills, Lakeland is the common surficial soil (Overing et al., 1995). This series is a rapidly permeable and strongly acidic sandy soil with nearly level to steep slopes. The Lakeland soil series may be several to as much as 10 m in depth with little to no soil development in the horizons. Generally, the Lakeland series is composed of medium to fine sand and contains 5–10% silt and clay (Overing et al., 1995).

2.2. Experimental design

2.2.1. Restoration blocks

We compared the initial effects of three hardwood reduction techniques and control (fire-suppression) on

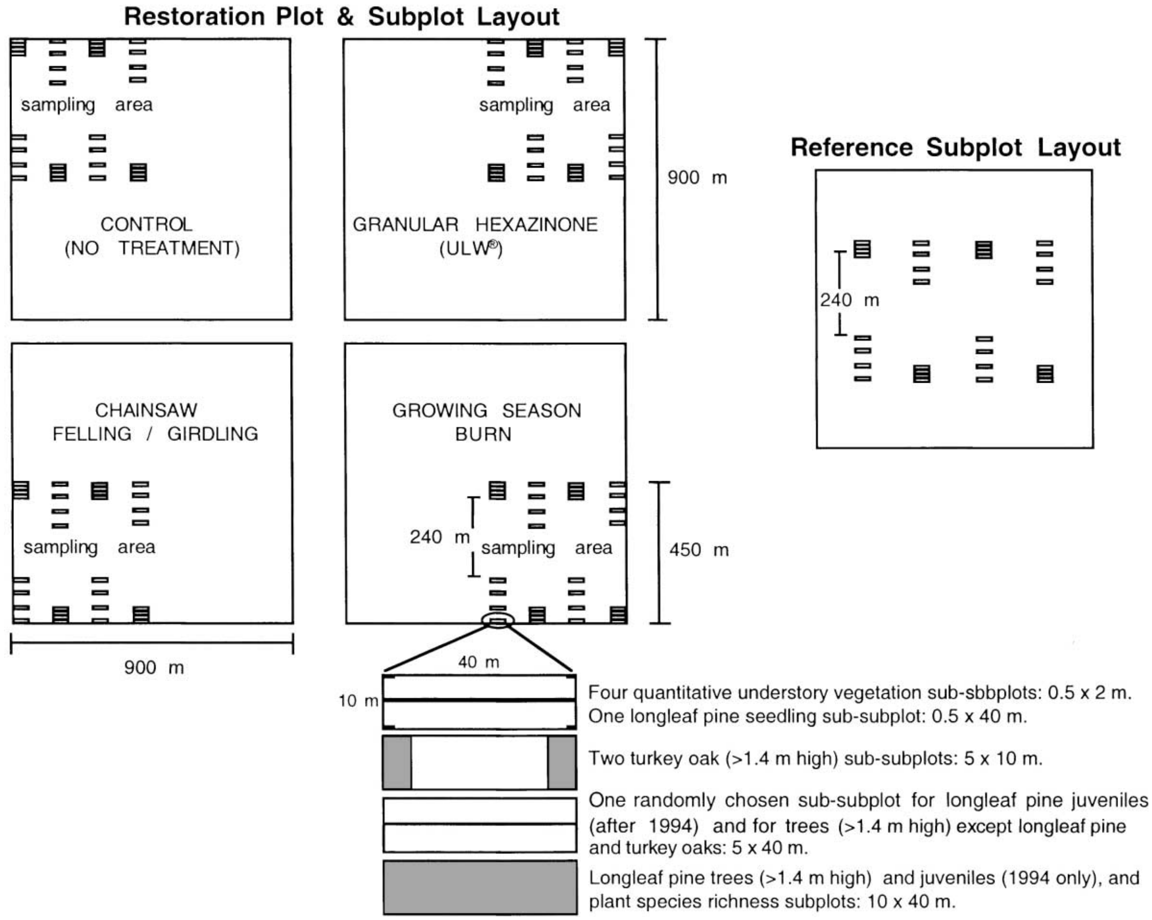

Fig. 1. Sample layout of four 81 ha in one of six restoration blocks and in one of six reference plots. Spatial randomization of 10 and 50 m subplot groups varied per plot.

longleaf pine and oak densities in fire-suppressed, longleaf pine-dominated sandhills. Treatments were growing season fire, application of the ULW® form of the herbicide hexazinone (1.68 kg active ingredient/ha), and chainsaw felling/girdling. One replicate of each treatment (including the control) was randomly assigned to a 81 ha plot in one of six blocks in a randomized complete block design (Fig. 1) (Steel and Torrie, 1980). We choose this plot size as a management compromise between the average minimum burn size and the maximum average size for a single herbicide application in 1994. All blocks were situated in the northern third of EAFB (see map in Rodgers and Provencher, 1999). The two most distant blocks were separated by 60 km on a west to east axis, although some were adjacent to one another. Two blocks were located in the eastern third of EAFB, whereas the remaining four blocks were in the western third. The four plots within a block were generally adjacent to one another with their inner corners never more than 2 km apart. All plots were selected if they were located in areas larger than 81 ha that contained a high density of relatively large diameter hardwood trees, had been fire-suppressed for several decades, and were adjacent to three other such sites. Plots had a relatively sparse herbaceous understory and a thick litter of hardwood leaves interspersed with bare ground.

Following pre-treatment sampling from spring 1994 to spring 1995, plots were burned in April–June 1995.

ULW® was applied by leaf-blower in early May, but the herbicide only became active in mid-May following sufficient precipitation. Felling/girdling operations occurred between June and late August in the 20 ha sampling area of each plot. The majority of the remaining 61 ha portion of the plots was completed by August, but felling/girdling operations persisted until November in two plots. Herbicide and felling/girdling plots were burned for fuel reduction from early March to late April 1997. We understand that burning confounds the purity of the initial treatments but it is a standard practice to burn herbicide and felling plots two dormant seasons after initial treatment at EAFB. The plots burned in 1995 did not receive fire in 1997, because EAFB managers cannot afford to burn sandhills that have not received fire for three or more years. We worked with EAFB to purposely emulate management practices as much as possible, while providing insights into unintended restoration effects on the understory applied at a large scale.

In each 81 ha plot, all subplots and sampling stations were located in the 20 ha corner farthest from the neighboring plots of the block in order to minimize confounding edge effects (Fig. 1). Each plot contained 32, 10×40 m^2 subplots (Fig. 1); any sampling unit within a subplot was referred to as a sub-subplot.

2.2.2. Reference blocks

Three pairs of 81 ha frequently burned, *P. palustris* dominated sandhill plots were established to represent objective goals for the restoration of fire-suppressed plots. All reference plots were on the western side of EAFB (see map in Rodgers and Provencher, 1999). Reference plots were not part of the restoration effort described above, but are a critical research component because they provide a benchmark for vegetation recovery in removal plots. Reference plots were chosen on the basis of the following criteria, which together should approximate the original condition of sandhills: an uneven age distribution of *P. palustris*; presence of old-growth *P. palustris*; abundance of understory species interspersed with bare ground; low midstory cover; presence of active red-cockaded woodpecker (*Picoides borealis*Vieillot) clusters, a federally endangered and characteristic species; a history of frequent growing season fires (Myers, 1990). In addition, plots had to be within a square area larger than 81 ha. Although we did not know this at the time of plot establishment, historical photos revealed that these areas had been spared from logging prior to 1950, although selective thinning may have occurred later in some sections of the plots. Furthermore, the establishment of bombing ranges in the area in the 1960s and 1970s re-established a regular fire regime sustained by live ammunition. Further description of the pre-treatment vegetation of these plots is included in Rodgers and Provencher (1999).

Each reference plot contained the same number of subplots as the restoration plots (Fig. 1). However, the positioning of the subplots within reference and removal plots differed. Groups of four subplots were placed in four parallel lines in the plot centers instead of the corners used in restoration plots (Fig. 1). Management unit boundaries, rather than interactions among treatments, were the edges we hoped to avoid with this design. For the duration of the restoration study, reference plots were under a “let burn” management policy. All six plots burned once and four plots burned at least twice during the study period.

2.3. Data collection and sampling

Pre-treatment tree densities, DBH, and height were collected from 1 November 1994 until 1 April 1995. Groundcover oak seedling densities were counted as part of the groundcover vegetation sampling from 8 July to 30 October 1994. The first post-treatment tree sampling period spanned from December 1995 until March 1996. The first late summer/fall post-treatment sampling of oak seedlings began immediately after treatment application and was completed by October 1995. Although longleaf pine juveniles and seedlings and oak seedlings were counted in the second year post-treatment, trees <1.4 m high were not sampled for DBH or height during fall 1996 and winter 1997. Third and fourth years post-treatment sampling closely matched the first year’s schedule.

Based on preliminary analyses, we sub-sampled each 10×40 m^2 subplot to facilitate collection of tree density, height, and DBH data. The area sampled was determined by evaluating variance components for dominant species in successively smaller units. Height and DBH of all longleaf pine within each 10×40 m^2 subplot were measured (Fig. 1). *P. palustris* juveniles (<1.4 m high) were counted from August to November

1994 and from December 1995 to March 1998 within a pre-determined, random longitudinal half of the 10×40 m^2 area (200 m^2) (Fig. 1). (Hereafter, we use the term *juvenile* to describe individuals that range from the grass stage to <1.4 m height and that established prior to the fall 1996 mast year. *Seedlings* are those individuals that originated from the 1996 crop and that were recognizable by their blue–green color and a limited number of needles.) From 1996 to 1997, *P. palustris* seedlings were counted from December to March in a central rectangle measuring 0.5×40 m^2. In 1998, naturally regenerated seedlings were no longer distinguished from planted juveniles and were counted in the 5×40 m^2 sub-subplot.

Turkey oaks were sampled within two 5×10 m^2 areas each situated at one end of each 10×40 m^2 subplot (Fig. 1). All other tree species were sampled in a randomly selected longitudinal half (i.e., 5×40 m^2) of each 10×40 m^2 subplot (Fig. 1). Individual stems of groundcover oak seedlings (including tree species <1.4 m high) were counted in the four 0.5×2 m^2 corner sub-subplots during the summer/fall vegetation sampling (Fig. 1).

2.3.1. Soil homogeneity

As a cautionary measure, we purged from our dataset reference subplots that were not representative of the sandhill restoration subplots. We were not aware initially of this issue because soil conservation maps indicated normal sandhill soils (i.e., mostly Lakeland series interspersed with Troup series) and soil texture analysis was conducted 3 years after plot establishment. We used canonical correspondence analysis (Kenkal and Orlóci, 1986; Ter Braak, 1986) and non-metric multidimensional scaling (Kruskall, 1964; Kenkal and Orlóci, 1986) on grain size and percent total silt and clay to identify these subplots as outliers (Provencher et al., 1998, 1999). Percent total silt and clay was not a good predictor of subplot ordination. A simple ranking of subplots by percent total silt and clay most clearly identified mesic subplots associated with underground sources of water or proximity to creeks and depressions. All reference subplots with >8% total silt and clay were discarded, affecting only plots A-78 west and east (Provencher et al., 1999). Interestingly, the removal of these reference subplots had no discernable effect on the variables presented here.

2.4. Statistical analyses

We tested restoration treatment effects with a randomized complete block analysis of (co)variance (two-way ANOVA, ANCOVA) (Steel and Torrie, 1980) for selected tree species variables in restoration plots. ANOVA was used for longleaf pine seedlings, because pre-treatment data did not exist (seedlings originated from the 1996 mast crop). Because of the availability of pre-treatment data for tree diameter distributions, and longleaf pine and oak juvenile density, we tested the effect of pre-treatment data on post-treatment data using ANCOVA, using covariate analysis to adjust post-treatment data and to account for differences among treatments that existed prior to treatment application. The adjusted plot averages were the values used in the figures, except in tree diameter distribution figures, because of a management need to observe actual pre- and post-treatment values. (Thus, figures show the median of plot averages.) We first tested treatment effects by ANCOVA in order to generate contrasts per diameter class. There was a potential problem with univariate tests and the value of significance probabilities, however, if significant correlation among classes was present. Shading and root competition may cause a correlation among diameter classes. Any correlation would violate the assumption of independent tests when several diameter classes are tested as independent variables, hence the need for multivariate methods. The univariate probabilities should be viewed as a measure of relative treatment strength. Therefore, multivariate analysis of covariance (MANCOVA) was used to test restoration effects on longleaf pine and oak size density distributions (only the four smallest 5 cm diameter classes had sufficient densities to allow testing).

Keeping within the maximum number of allowable independent contrasts for three degrees of freedom (Sokal and Rohlf, 1981), we contrasted the following treatments: control versus spring burn (C vs. B), burn versus the ULW® herbicide (B vs. U), and ULW® herbicide versus felling/girdling (U vs. F). In the first contrast, we were testing whether maintaining fire suppression (control) was as efficient as burning. Burning is the management default at EAFB, because it is the least expensive management tool and because chronic fires characterize the maintenance condition of sandhills. We compared burning to the herbicide to contrast techniques that differ greatly in cost (herbicide was eight times more expensive than burning) and in the amount of oak resprouting and topkill mortality they cause. Burning should result in approximately 50% topkill and resprouting (Glitzenstein et al., 1995), while ULW® should practically eliminate oaks. We also expected approximately 50% mortality to fire among smaller longleaf pines (2–5 cm DBH class), including juveniles <1.4 m high (Boyer, 1990; Streng et al., 1993), because of their thinner bark and exposed terminal shoots. In addition, a large fraction (>90%) of longleaf pine seedlings from the 1996 mast year were expected to be killed by fuel reduction burns in 1997 (Grace and Platt, 1995). Herbicide application was compared to felling/girdling to discriminate between equally expensive methods that differ in oak resprouting: resprouting is stimulated by felling oaks whereas the herbicide prevents it (Brockway et al., 1998).

We conducted ANCOVA using a computer randomization test (Edgington, 1987) to process a large number of variables and to handle non-normal distributions. The randomization procedure is distribution-free, but still depends on homogeneous variances among treatments. The computer test created a random distribution of the treatment variance through random permutations among treatments of the original data (i.e., the null hypothesis was that the observations can belong to any treatment within a block) and determined if the observed treatment variance from the original unpermutated data was greater than or equal to $1-\alpha$ ($\alpha=0.05$, critical significance probability) of the random values (i.e., if it was in the 5% tail of the distribution). Each permutation consisted of randomly assigning the original observations among the four treatments within blocks, but not among blocks (Edgington, 1987), thus preserving the structure of the randomized complete block design. The null hypothesis of no difference among restoration treatments was rejected with a significance probability that was equal to $1-$(relative rank of the original treatment variance in the distribution) (Edgington, 1987). The three independent contrasts were performed with the same set of permutations and methods, but we used the t statistic with standard errors for two adjusted means calculated from ANCOVA to compare means (Steel and Torrie, 1980). We permutated the original data 10 000 times to create a random distribution for each variable. We partitioned sum of squares following the ANCOVA formulas in Steel and Torrie (1980) and Cochran and Cox (1957). The effect of pre-treatment data on post-treatment values (covariate effect) was determined directly from the F-ratio calculated with the original data and from published statistical tables, not the result of permutations.

Logarithmic transformations were applied to all variables because they showed significant and positive mean–variance relationships (Sokal and Rohlf, 1981). MANCOVA was executed with the software STATISTICA (1994). For simplicity and ease of reading, we have termed the tests of restoration treatments in the statistical tables as "restoration". We refer to the multivariate effect of restoration treatments as "multivariate restoration effect" in the text.

3. Results

3.1. Oak size distributions

Pre-treatment oak size distributions followed a negative-exponential curve in all restoration treatments (Fig. 2). The size distribution in reference plots was practically flat in all years, with low tree densities in all diameter classes, although densities somewhat decreased with increasing size (Fig. 2). The data for 1997 were not presented in Fig. 2 because they were largely redundant with those of 1998.

In 1995, multivariate restoration effects and pre-treatment effects on the four smallest diameter classes were highly significant (Table 1). Univariate tests show that densities in the five smallest diameter classes were significantly reduced by >60% in herbicide and by >90% in felling/girdling plots, although these percentages varied with diameter classes (Fig. 2). The negative effect of felling/girdling on densities was significantly greater than that of the herbicide application only for the smallest oaks. Burning resulted in significantly more topkill than the control treatment for trees in the 0–4.9 and 15–19.9 cm classes. In both cases, topkill was less than 20% based on medians compared to pre-treatment densities. Burning topkilled significantly fewer oaks than herbicide treatments (Table 1).

The multivariate restoration effect persisted in 1997 (data not shown in Fig. 2) and 1998, but the

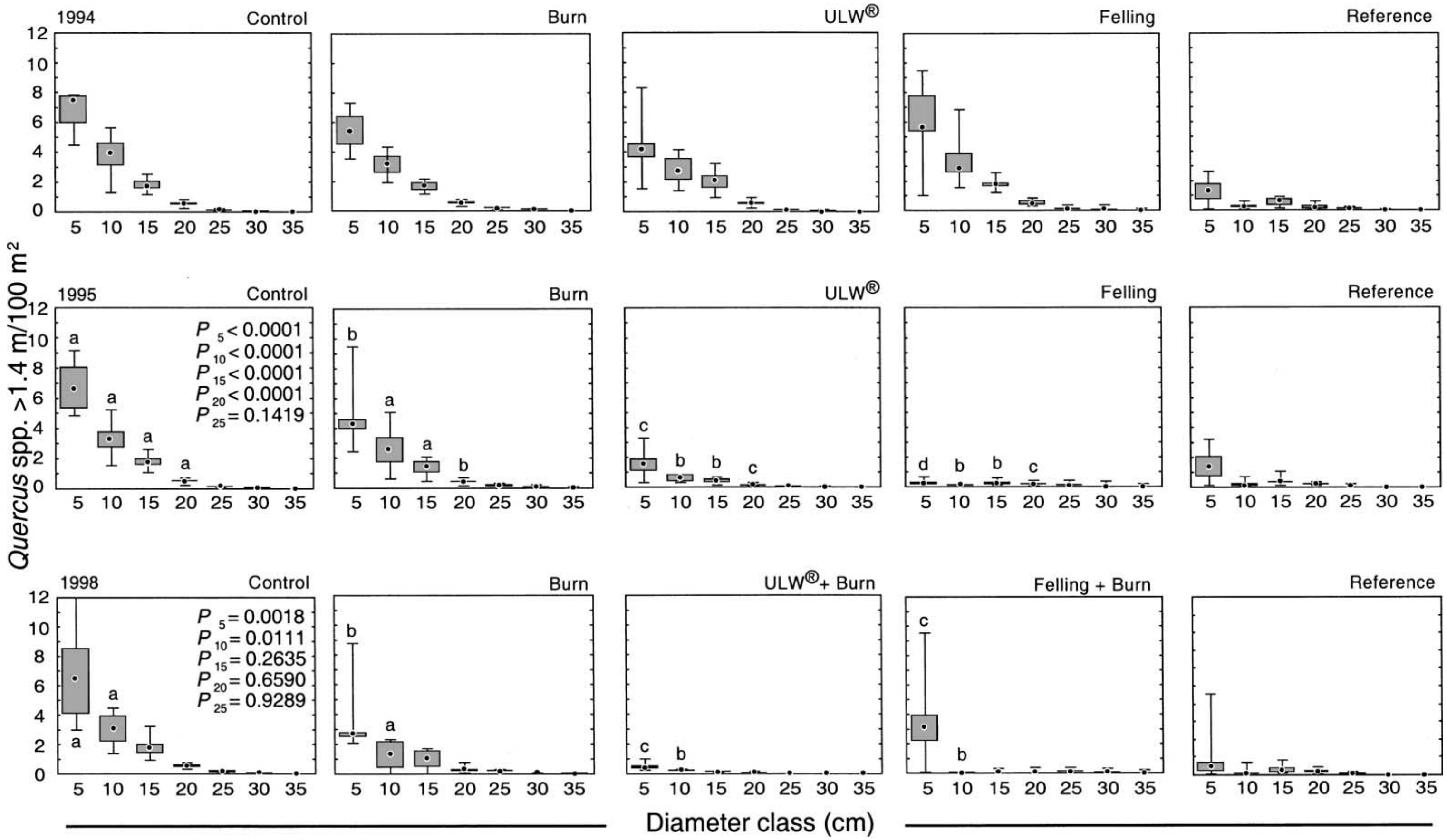

Fig. 2. Pre- (1994) and post-treatment (1995, 1998) densities of all oak species per 5 cm diameter class in restoration and reference plots. Trees were not sampled in 1996 and 1997 data were not presented due to their redundancy with 1998 results. Other hardwoods not presented. Significance probability is the univariate test of the effects of the four restoration treatments for the more abundant diameter classes, which do not include the reference plots. Lowercase letters associated with error bars code for the three following independent contrasts among treatments (not among diameter classes): C vs. B, B vs. U, and U vs. F. Different letters indicate significantly different adjacent means. Legend: B=burn; C=control; F=felling/girdling; R=reference; U=ULW® herbicide. Calculations and tests followed Steel and Torrie (1980). Center of box represents the median, upper and lower edges of box are 25 and 75% quartiles, respectively, and error bars represent the minimum and maximum plot averages. Sample size=6.

Table 1
Multivariate tests. Two-way MANCOVA for tests of restoration treatments and pre-treatment effects on densities of oaks by 5 cm diameter class from 1995 to 1998 in mixed hardwood and longleaf pine forests at Eglin Air Force Base, Florida. Restoration treatments are growing season burn, application of ULW® herbicide, hand felling and girdling of hardwoods and sand pine, and no-treatment control. The experimental design is a randomized complete block, split-plot design, but only the block design at the whole plot level is presented here. The covariate was the pre-treatment data from the fall 1994. The error term is the mean square of the interaction of the block and restoration effects. MANCOVA was performed with STATISTICA (1994). Tree sizes were log(X+1)-transformed to stabilize variances

Year	Source	Wilks' λ	d.f.	P
1995	Pre-treatment	0.0218	16, 25	0.0011
	Restoration	0.0027	12, 21	<0.00001
1997	Pre-treatment	0.0778	16, 25	0.0524
	Restoration	0.0282	12, 21	0.0006
1998	Pre-treatment	0.0830	16, 25	0.0620
	Restoration	0.0147	12, 21	0.00006

Table 2
Multivariate tests. Two-way MANCOVA for tests of restoration treatments and pre-treatment effects on densities of longleaf pine by 5 cm diameter class from 1995 to 1997 in mixed hardwood and longleaf pine forests at Eglin Air Force Base, Florida. Restoration treatments are growing season burn, application of ULW® herbicide, hand felling and girdling of hardwoods and sand pine, and no-treatment control. The experimental design is a randomized complete block, split-plot design, but only the block design at the whole plot level is presented here. The covariate was the pre-treatment data from the fall 1994. The error term is the mean square of the interaction of the block and restoration effects. MANCOVA was performed with STATISTICA (1994). Tree sizes were log(X+1)-transformed to stabilize variances

Year	Source	Wilks' λ	d.f.	P
1995	Pre-treatment	0.0001	16, 25	<0.00001
	Restoration	0.1540	12, 21	0.1071
1997	Pre-treatment	0.0012	16, 25	<0.00001
	Restoration	0.0909	12, 21	0.0249
1998	Pre-treatment	0.0021	16, 25	<0.00001
	Restoration	0.0582	12, 21	0.0064

pre-treatment effect was marginally significant (P=0.0524 in 1997 and P=0.0620 in 1998, Table 1). Oak densities were approximately 50% smaller for the 0–4.9, 5–9.9, and 10–14.9 cm DBH classes in 1998 compared to 1994, which indicates a delayed mortality response by oaks to burning (Fig. 2). (This effect had occurred by 1997.) Densities were significantly lower in these diameter classes in burn plots compared to control plots, but not in the 20–24.9 cm class (Fig. 2). There was no significant univariate difference between herbicide and felling/girdling plots after fuel reduction burns (Table 1). These burns, however, may have reduced resprout densities in the 0–4.9 cm class of the felling/girdling plots (Fig. 2). Large numbers of resprouts were observed in the field prior to fuel reduction burns. In herbicide plots, densities of all DBH classes remained low.

3.2. Longleaf pine size distributions

Size distributions of longleaf pine were similar among restoration treatments in the pre-treatment phase. Distributions were bimodal with peaks at 0–4.9 and at 25–29.9 cm (Fig. 3). The highest variability was also observed at these modes. The highest mode was at 0–4.9 cm in all treatment plots, but at 25–29.9 cm in reference plots (Fig. 3). Again, data from 1997 were not shown as they were redundant with the results for 1998.

The qualitative shapes of distributions and position of modes remained the same for all years post-treatment (Fig. 3). Highly significant pre-treatment effects from MANCOVA support this observation (Table 2). Only fire quantitatively changed the distributions by the attrition of the smallest trees; however, this difference was not significant in the MANCOVA in 1995 (Table 2). The only significant univariate test for trees 0–4.9 cm confirmed the negative effect of fire (Fig. 3).

Dormant season fuel reduction burns applied in herbicide and felling/girdling plots during 1997 once again decreased longleaf pine densities in the two smallest diameter classes in 1998 (Fig. 3). The MANCOVA restoration effect was significant in 1997 and 1998 (Table 2), and significant univariate restoration effects extended from the 0–4.9 cm to the 20–24.9 cm class (Fig. 3). Although fire following herbicide application was significantly less harmful to trees than growing season fire applied in 1995, we could not directly test the same relationship for felling/girdling plots (Fig. 3). The contrasts suggest that felling/girdling is more harmful to these diameter classes than

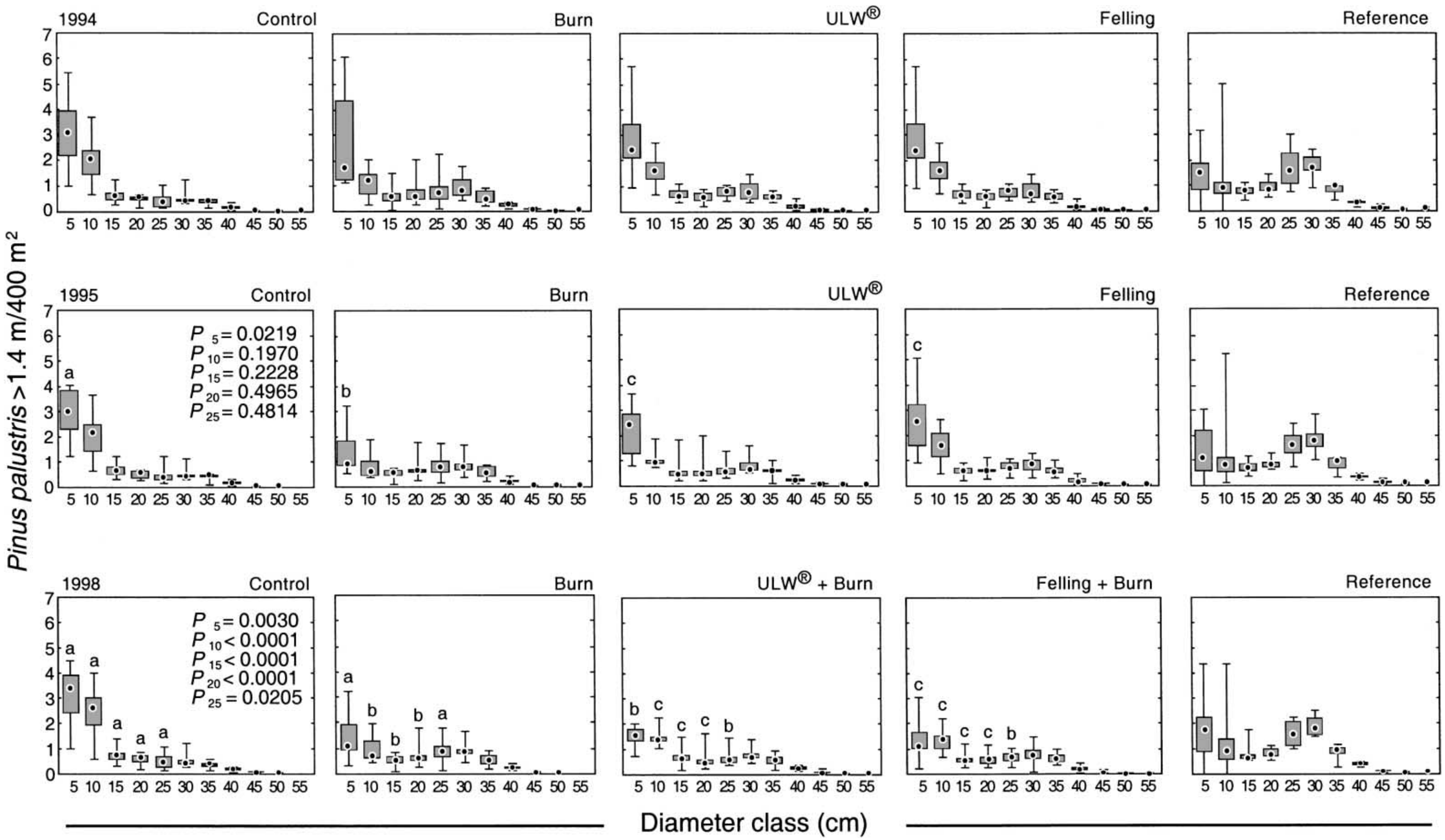

Fig. 3. Pre- (1994) and post-treatment (1995. 1998) densities of longleaf pines per 5 cm diameter class in restoration and reference plots. Trees were not sampled in 1996 and 1997 data were not presented due to their redundancy with 1998 results. Other hardwoods not presented. Significance probability is the univariate test of the effects of the four restoration treatments for the more abundant diameter classes, which do not include the reference plots. Lowercase letters associated with error bars code for the three following independent contrasts among treatments (not among diameter classes): C vs. B, B vs. U, and U vs. F. Different letters indicate significantly different adjacent means. Calculations and tests followed Steel and Torrie (1980). Center of box represents the median, upper and lower edges of box are 25 and 75% quartiles, respectively, and error bars represent the minimum and maximum plot averages. Sample size=6.

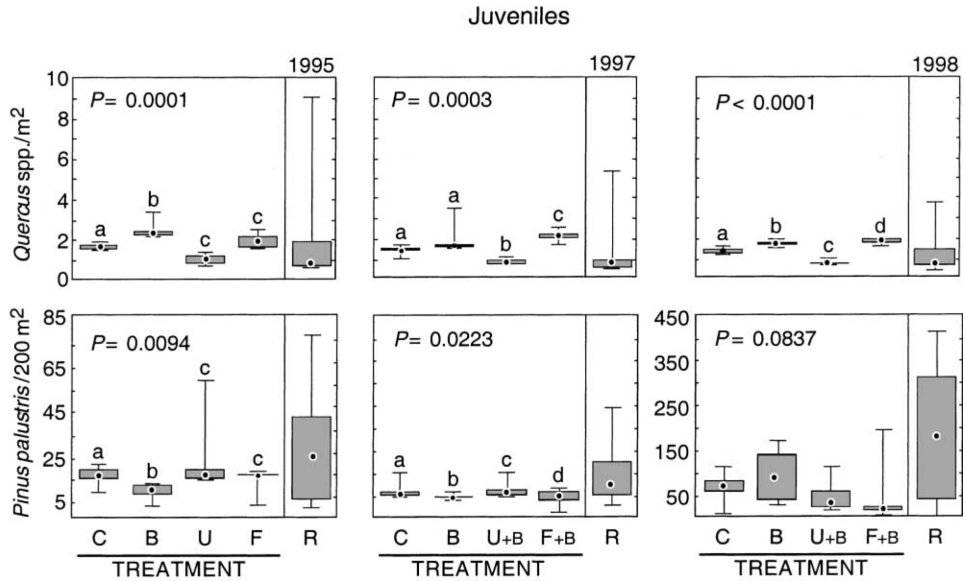

Fig. 4. Densities of all oak <1.4 m height and longleaf pine <1.4 m height in restoration and reference plots post-treatment (1995, 1997–1998). The 1996 data were not presented due to their redundancy with 1995 results. Oak and longleaf pine juvenile densities were adjusted for restoration treatments only and were estimated from pre-treatment values using ANCOVA. Longleaf pine juvenile densities did not include seedlings germinated in 1996, except in 1998 when we stopped differentiating between juveniles and seedlings. Fuel reduction burns were applied in 1997. Center of box represents the median, upper and lower edges of box are the 25 and 75% quartiles, respectively, and error bars represent the minimum and maximum plot averages. Significance probability is the test of the effects of the four restoration treatments, which do not include the R plots. Lowercase letters associated with error bars code for the three following independent contrasts: C vs. B, B vs. U, and U vs. F. Different letters indicate significantly different means.

herbicide application when both treatments were followed by fuel reduction fire.

3.3. Oak juveniles

In 1995, control plots contained significantly fewer oak juveniles than the burn plots, both had significantly more juveniles than the herbicide plots (Fig. 4). (The results from 1996 are practically identical to those of 1995 and therefore not shown in Fig. 4.) Reference plots contained the lowest and most variable median juvenile densities. The general pattern of densities persisted in 1997 and 1998, but with minor differences. Densities were not significantly different between control and burn plots in 1997 (Fig. 4). Also, felling/girdling plots contained significantly more juveniles than the herbicide plots, and perhaps, the other plots (Fig. 4). In 1998, all contrasts were significant, with burn having more juveniles than control and herbicide plots, and felling/girdling plots having slightly greater values than herbicide plots (P=0.0548, Fig. 4).

3.4. Longleaf pine juveniles

The adjusted densities of longleaf pine juveniles among treatments in all years post-treatment again reflect the critical role of fire. (Again, the results from 1996 are not shown in Fig. 4.) In 1995, growing season fire significantly decreased median density by approximately 50% to a value of 9 juveniles/200 m^2 compared to other treatments (Fig. 4). Longleaf pine juveniles were unaffected by other treatments. Median juvenile densities were slightly higher and substantially more variable in reference plots than in treatments (Fig. 4). Following fuel reduction burns in herbicide and felling/girdling plots in 1997, median adjusted density decreased to approximately 5–6 juveniles/200 m^2 in all plots, including the control. Slight treatment differences were significant because of very low variability: control and herbicide plots contained significantly more juveniles than burn and felling/girdling plots (Fig. 4). In 1998, densities of juveniles did not significantly differ among treatments. The lack

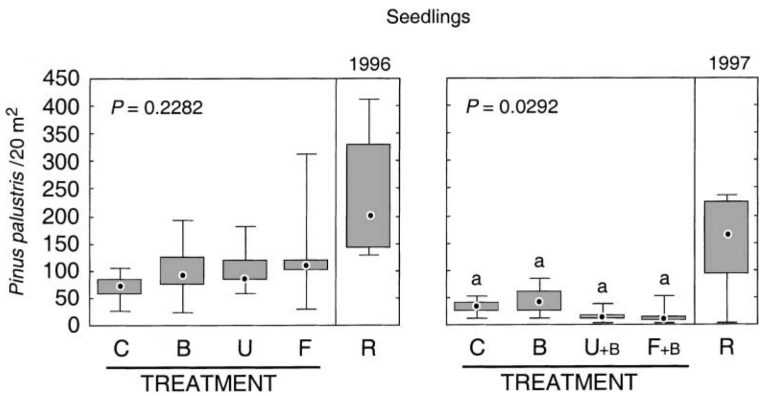

Fig. 5. Densities of longleaf pine seedlings (germinated in 1996) in restoration and reference plots post-treatment from the winters 1996–1997 and 1997–1998, respectively. Fuel reduction burns were applied in 1997. Pine densities were not adjusted. Center of box represents the median, upper and lower edges of box are the 25 and 75% quartiles, respectively, and error bars represent the minimum and maximum plot averages. Significance probability is the test of the effects of the four restoration treatments, which do not include the R plots. Lowercase letters associated with error bars code for the three following independent contrasts: C vs. B, B vs. U, and U vs. F. Different letters indicate significantly different means.

of significance may be an artifact of lumping the juveniles and seedlings together during the 1998 sampling (note the different scale of the *y*-axis). As expected, the seedlings swamped the number of juveniles.

3.5. Longleaf pine seedlings

Median seedling densities did not differ among treatments in 1996 (Fig. 5). Densities ranged between approximately 75 (control) and 105 seedlings/20 m^2 (felling/girdling) in treatment plots (approximately 37 000–50 000/ha). Reference plot densities were approximately 205 seedlings/20 m^2 (approximately 100 000/ha). Fuel reduction burns in 1997 decreased median densities by 95% to <5 seedlings/20 m^2 in herbicide and felling/girdling plots. Seedling densities dropped by approximately 50% in control and burn plots, which were not manipulated after 1995. Seedling densities decreased by only 22% in reference plots, which did experience some fires.

4. Discussion

4.1. Oak size distributions

We found that felling/girdling and herbicide application were most effective at topkilling oaks, as was expected. Neary et al. (1981), McLemore (1983), and Brockway et al. (1998) reported hardwood mortality values due to ULW®of 83–96%, 72–86%, and 83%, respectively. These mortality values were dependent on soils, hardwood composition, and application rates. In a recent study of hexazinone at EAFB, Berish (1996) found only 53% oak mortality caused by ULW® and 40% for Pronone® 1 year after treatment. We found a mortality value of 78% for turkey oak density 1 year post-treatment in ULW® plots, whereas the mortality of sand live oak (*Quercus geminata* Small.) density was 55% (Provencher et al., 1998). The higher density of sand live oak in Berish's (1996) plots compared to those reported here may explain the lower mortality values.

Growing season burning topkilled only 20% of all oaks 1 year post-treatment, but an unanticipated delayed mortality of approximately 50% for trees <15 cm DBH was observed in 1997. We believe that the first-year topkill mortality reported here was low because fire intensity was low in one or more growing season burns. The severe drought in August and September 1997 (NOAA, 1997) and several hurricanes may have killed already stressed trees belonging to the three smaller diameter classes, therefore causing delayed mortality. Oak topkill mortality caused by fire is usually stronger for the smallest diameter classes (Waldrop et al., 1992; Rebertus et al., 1993), but does not generally exceed 58% for all diameter classes combined (Rebertus et al., 1989a,b; Glitzenstein et al., 1995). Because most published experimental studies (Waldrop et al., 1992; Glitzenstein et al., 1995) of fire effects on hardwoods in the southeastern US involve repeated burns, we could not find data on delayed hardwood mortality following a single burn.

Both burning and felling oaks necessitate follow-up repeated growing season fires to control hardwood resprouting. Hardwood resprout densities can reach levels exceeding those found in the pre-burn state and control plots (Waldrop et al., 1992). Without chronic fire, we would likely observe such encroachment given the increasing densities of resprouts (0–4.9 cm) observed in felling/girdling plots after fuel reduction burns.

4.2. Longleaf pine size distributions

Bimodality in longleaf pine size distributions was also reported at the Wade Tract of southern Georgia (Platt et al., 1988) and at the Escambia Experimental Forest of southern Alabama (Boyer, 1990; Farrar, 1993). Their highest mode was for the smallest diameter classes, which we also reported for fire-suppressed stands. Platt et al. (1988) and Farrar (1993) detected a second mode for trees 40–49.9 cm in diameter, whereas we detected a second mode at 25–29.9 cm, which was dominant only in reference plots. The Wade Tract and the Escambia Experimental Forest are frequently burned forests. Therefore, these forests should be compared to our reference plots. The smaller mode at 25–29.9 cm compared to 40–49.9 cm found elsewhere could be explained by the very low productivity of sandhill soils on EAFB (Provencher et al., 1998). Nearly all trees measured here are found on Lakeland soils containing no more than 8% total silt and clay, whereas the more productive soils (>8% total silt and clay) underlying the Wade Tract (Red Hills) are a mosaic of loamy sands (e.g., Faceville, Fuquay, Grady, Lucy, Norfolk, Orangeburg) (Calhoun, 1979) and those at the Escambia Experimental Forest belong to the Troup series (Walker and Carlisle, 1960). We noted that the Wade Tract supports several trees >55 cm DBH (Platt et al., 1988), which are exceptionally rare at EAFB even among stands with trees older than 300 years. Therefore, trees at EAFB may just be smaller in diameter. This statement, however, assumes that the cause of these modes at intermediate diameter classes is the same regionally. We do not know that this is the case, but a past record mast year (Maki, 1952; Boyer, 1986) may explain the bimodal longleaf pine size distributions. Platt et al. (1988), however, proposed that bimodality may be indicative of major but unknown catastrophic events. This hypothesis was suggested because theoretical analyses showed that the age and size distributions of longleaf pine at the Wade Tract were unstable, probably due to strongly disruptive abiotic factors (Platt et al., 1988).

The other discrepancy between our reference plots and both the Wade Tract and the Escambia Experimental Forest was the lower number of longleaf pines in the smallest diameter classes at EAFB. These low densities increased the similarity between any burned restoration plot and the reference plots. Fire alone, therefore, can cause this pattern on EAFB. We caution, however, that the large variability among reference plots in these smaller size classes may mask other patterns, such as past silvicultural practices. The frequent maintenance fires in vegetation dominated by wiregrass (*Aristida beyrichiana*; formerly *A. stricta* Mich. in Florida (Peet, 1993)) at the Wade Tract and by bluestems at the Escambia Forest may be less harmful to saplings than the heavier fuel-driven fires experienced at EAFB. Provencher et al. (1998, 2001) showed that groundcover woody vegetation (<1.4 m tall) is more abundant than herbaceous vegetation at EAFB, and wiregrass is practically absent from most of the plots examined here. Heat generated by the combustion of mixed woody and herbaceous fuels may be more harmful to longleaf pine saplings than heat generated from the rapid combustion of wiregrass and herbaceous material.

The greater sensitivity of smaller diameter classes of longleaf pines to fire that we observed has also been reported by Streng et al. (1993) at St. Marks Wildlife Refuge, Florida, over a period of 7 years involving repeated burn treatments. In sandhill communities elsewhere in northwest Florida, longleaf pine mortality was 37% for trees of 2–4.9 cm DBH, 27% for trees 5–9.9 cm DBH, and <8% for all larger trees (Streng et al., 1993; Glitzenstein et al., 1995). Boyer (1990) reported greater longleaf pine mortality for the smallest (2.54 cm DBH class: 53%) and largest trees (56 cm DBH class: 25%) after July and August burns. Boyer (1990) observed that these burns caused greater damage to longleaf pines than to hardwoods after the first prescribed burn. At EAFB, the large amount of woody debris from felling hardwoods would be the most likely cause of more lethal fires for pines <10 cm diameter in felling/girdling plots compared to herbicide plots.

4.3. Oak and longleaf pine juveniles

Juvenile oaks and longleaf pines showed opposite responses to fire. Oak juvenile densities generally increased after a burn or a felling operation, due to resprouting (Waldrop et al., 1992; Rebertus et al., 1993). As expected, the only method that decreased oak juvenile densities in the short term was herbicide application. The percent mortality of juvenile longleaf pine in burn plots was consistent with values reported in the literature (Boyer, 1985, 1990; Grace and Platt, 1995). Other treatments, prior to fuel reduction burns, had no effect on longleaf pine juveniles, which we expected since hexazinone is not toxic to pines (McLemore, 1983; Griswold, 1984) and felling/girdling does not directly affect juveniles unless felled trees crush them. The important message was that longleaf pine juvenile densities converged to 5–6 individuals/200 m^2 (in 1997 only, because seedlings were not distinguished from juveniles in 1998) regardless of management action, including maintaining fire-suppression.

4.4. Longleaf pine seedlings

Pre-grass stage seedling densities as high as 24 000/ha were reduced to 2 600/ha within 2 years of growing season fire at the Wade Tract in southern Georgia (Grace and Platt, 1995), representing an 89% decrease. We observed a 95% mortality from dormant-season fuel reduction burns. These results are consistent with the well-known high, fire-caused mortality in longleaf pine seedlings during their first year (Wahlenberg, 1946). In the absence of fire, however, background mortality was estimated at 50% from control and growing season burn plots (not burned after 1995). We suggest that competition with hardwoods or the inability of pine seedling roots to contact mineral soil because of thick litter may inflict this level of mortality on seedlings. We counted many seedlings growing entirely within leaf litter a few months after germination. Interestingly, mortality in reference plots was 22%, despite seedlings having been exposed to prescribed burns and wildfires. We suspect, following field visits, that fires probably killed more seedlings at the Wade Tract because groundcover there is more dense and continuous than in EAFB's reference plots. Graminoid cover is only 14% on average (Provencher et al., 1998) and litter is patchy within EAFB reference plots. Fine fuels are thus probably not sufficiently continuous for fire to reach everywhere on EAFB. Importantly, these findings suggest that there is a strong incentive for land managers to at least restore the groundcover of sandhills to a reference condition in time to reduce the attrition rate of seedlings from the next mast crop.

5. Management implications

- Longleaf pine seedling and juvenile mortality should not constrain management, because the repeated attrition of individuals by fire and other factors reduced them equally. Moreover, longleaf pines reproduce many times during their long life span (Wahlenberg, 1946) and produce thousand more seedlings that can ever grow to merchantable size.
- We recommended that managers using repeated prescribed fire to achieve maintenance condition as this will reduce the hardwood midstory regardless of droughts and hurricanes. Fire will expose mineral soil needed for longleaf pine seedling establishment and survival.
- Managers who need to rapidly remove the hardwood midstory due to endangered species mandates, e.g., may consider herbicides and mechanical methods, but at a potential cost to restoration of the vegetation and insects (Provencher et al., 1999, 2001).
- If the greater financial cost of herbicide and mechanical hardwood reduction techniques is not a constraint to managers, the choice between these alternatives should be based on whether hardwood resprouting following felling and the detrimental effects of herbicides on the rest of the community are serious problems. Managers should choose felling/girdling because repeated prescribed burns, the default management technique at EAFB, will control resprouting and benefit other sandhill species.

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