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Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem

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Abstract

A flatwoods longleaf pine wiregrass ecosystem, which regenerated naturally following wildfire in 1942, on the Coastal Plain of southern Georgia was treated over a period of four decades with prescribed fire at annual, biennial and triennial intervals during the winter dormant season. Burning caused substantial changes in the understory plant community, with significant reductions in the foliar cover of *Ilex glabra* in the shrub layer resulting in corresponding increases in the cover of *Vaccinium myrsinites*, *Sporobolus curtissii*, *Aristida stricta* and *Andropogon* spp. Understory plant species richness, diversity and evenness also increased as a result of periodic fire. Dormant-season burning decreased the cover of litter on the forest floor and significantly increased the standing biomass of *A. stricta*, *S. curtissii*, *Andropogon* spp., all other grasses and all forbs. Recurrent fire also prevented the development of a vigorous midstory, that impedes understory growth and poses a serious fire hazard to the stand. Overstory trees were largely unaffected by burning. Historical light grazing on the site produced no measurable effects on the plant community. Findings suggest that the biennial burning interval results in declines of *I. glabra* in the shrub layer and litter cover on the forest floor, leading to the largest increases in understory plant species richness and diversity and the biomass productivity of grasses and forbs. Although flatwoods plant communities evolved in environments characterized by growing-season fires of variable frequency, long-term application of dormant-season fire is also recommended as a useful option for sustaining resource values in this and similar longleaf pine wiregrass ecosystems. © 1997 Elsevier Science B.V.

Keywords: *Pinus palustris* Mill.; *Aristida stricta* Michx.; *Sporobolus curtissii* (Vasey) Small ex Scribn.; *Ilex glabra* (L) A. Gray; *Vaccinium myrsinites* Lam. flatwoods

1. Introduction

Longleaf pine (*Pinus palustris*) forests were at one time among the most extensive ecosystems in North America (Landers et al., 1995). These forests are estimated to have occupied over 37 million ha in the southeastern United States prior to European settlement (Frost, 1993). Since then, this ecosystem has suffered a progressive decline in occurrence to

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8 million ha in 1935 (Wahlenberg, 1946), 2 million ha by 1975 and 1.5 million ha in 1985 (Kelly and Bechtold, 1990), with current levels estimated at less than 1.2 million ha. A combination of factors appear to be responsible for the long-term decline of longleaf pine forests. Clearing land for crops and pasture account for major reductions, in that longleaf pine is a largely unsuccessful invader of open land when confronted with competition from more aggressive species. Conversion of longleaf pine forests to other southern pine species, such as loblolly pine (*Pinus taeda*) and slash pine (*Pinus elliottii*) has also contributed substantially to this decline. But perhaps most important could be the interruption of natural fire regimes, resulting from forest fire protection policies implemented during the 1920s, that impeded natural regeneration of longleaf pines and allowed invasion of longleaf sites by hardwood trees and more aggressive southern pines, including loblolly pine, slash pine and sand pine (*Pinus clausa*). Utilization of longleaf pine forests has been extensive since the colonial period (Croker, 1979). However, timber harvest in primary and second-growth forests appears compatible with sustaining the multiple values of longleaf pine forests, as long as suitable provision is made for timely pine regeneration by maintaining ecological processes such as fire (Landers et al., 1995). Unfortunately, declines are continuing in every diameter class below 41 cm, therefore most remaining longleaf pine forests appear to be aging without replacement.

Longleaf pine forests became established in northern Florida approximately 7800 years ago, during the warming trend following retreat of the last continental glacier (Watts et al., 1992), and during the ensuing 4000 years spread throughout the southeast (Delcourt and Delcourt, 1987). More recently, the natural range of longleaf pine consists of the area along the Gulf and Atlantic Coastal Plains from Texas to Virginia, extending well into central Florida and the Piedmont and mountains of northern Alabama and Georgia (Stout and Marion, 1993). Throughout its range, longleaf pine occurs in forests, woodlands and savannas on a wide variety of sites, ranging from wet poorly-drained flatwoods to xeric sandhills and rocky mountain ridges (Boyer, 1990b). In the western Gulf Coastal Plain, longleaf pine understories are commonly dominated by bluestem grasses (*Andropogon* spp.) and, from Florida eastward, longleaf pine is typically associated with wiregrass (*Aristida stricta*), a prominent bunchgrass. A distinguishing characteristic of these ecosystems is an open, park-like stand structure (Harper, 1914; Laessle, 1942, Edmisten, 1963), known commonly as "pine barrens" (Bartram, 1791). These ecosystems contain few shrubs or hardwood trees. because of the attributes of understory grasses that facilitate the ignition and spread of fire during the growing season (Landers, 1991).

Although potentially reaching ages of 500 years, few longleaf pine achieve their biological potential because the longleaf pine wiregrass ecosystem evolved in an environment influenced by catastrophic disturbances, such as damaging tropical storms and wildfires, and localized mortality from lightning strikes. The rich biological diversity in this ecosystem is maintained by a combination of disturbance events and site factors. Variation in lightning strikes, tree mortality and animal interactions at local scales and wind storms and hydrologic regimes at broader scales influence the landscape mosaic. Such disturbances across site gradients provide large living trees, snags, coarse woody debris, forest openings and hardwood thickets. Numerous organisms, including many species of plants, mammals, birds and reptiles are adapted to this disturbance-prone, yet largely stable ecosystem. The high diversity of understory plants per unit area makes these ecosystems among the most species-rich plant communities outside the tropics (Peet and Allard, 1993). Yet with this ecosystem now occupying only a fraction of its original extent, extreme habitat reduction has resulted in the increased rarity of 191 taxa of vascular plants (Hardin and White, 1989; Walker, 1993) and several wildlife species.

Recent concern expressed about loss of this unique ecosystem (Noss, 1989; Means and Grow, 1985; Noss et al., 1995) has stimulated discussion regarding how to effectively restore this important portion of the national heritage. Since longleaf pine still occurs over most of its natural range, albeit in isolated fragments, it is reasonable to conclude that restoration of this ecosystem is feasible. Success in such an endeavor will depend on identification of the ecological processes needed to create favorable conditions for a gradual expansion of longleaf pine and

wiregrass occupancy. The use of fire as an ecological process necessary for the maintenance of fire-dependent natural communities, especially growing-season fires where appropriate to promote diversity and stability, has been suggested (Noss, 1989; Frost, 1990; Streng et al., 1993; Noss et al., 1995). Mechanical site preparation methods have also been proposed, but must be carefully evaluated to avoid adverse effects upon wiregrass (Clewell, 1989; Outcalt and Lewis, 1990, Outcalt, 1993). Natural regeneration methods employing a regime of frequent fire are already compatible with maintenance of the longleaf pine wiregrass ecosystem (Boyer and White, 1990). In this ecosystem, longleaf pine and bunchgrasses function together as keystone species that facilitate but are resistant to fire, exhibit substantial longevity and demonstrate nutrient and water retention to a degree that reinforce their site dominance and minimize change in the plant community following disturbance (Landers et al., 1995). The benefits of periodic fire include: (1) maintaining the physiognomic character of longleaf pine wiregrass ecosystems through excluding invasive plants that are ill-adapted to fire; (2) preparing a seedbed favorable for the regeneration of longleaf pine seedlings; (3) reducing the density of understory vegetation, thus providing microsites for a variety of herbaceous plants; (4) releasing nutrients immobilized in accumulated phytomass for recycling to the infertile soil and subsequently more rapid uptake by plants; (5) improving forage for grazing; (6) enhancing wildlife habitat; (7) controlling harmful insects and pathogens; (8) reducing fuel levels and the wildfire hazard (McKee, 1982; Wade and Lewis, 1987; Wade and Lundsford, 1990; Dickmann, 1993; Brennan and Hermann, 1994). Fire at intervals as frequent as 2–4 years may provide such benefits in ecosystem restoration without need for measures to protect regeneration.

This long-term study examines the influence of fire frequency on and efficacy of prescribed burning during the dormant season for restoring and maintaining longleaf pine wiregrass ecosystems. Over a period of 40 years, a flatwoods longleaf pine wiregrass ecosystem on the southern Georgia Coastal Plain was treated with prescribed fire at annual, biennial and triennial intervals during the winter season. Forest floor and vascular plants in the understory and overstory were examined to: (1) assess the effects on forest stand structure; (2) evaluate the changes in foliar cover and species richness, diversity and evenness; (3) measure the amount of forest litter that has accumulated or mineralized; (4) quantify the growth of plant biomass, in response to the various fire treatments. Analysis of long-term trends should provide insights useful in developing fire regimes and related management strategies for successfully restoring and maintaining longleaf pine wiregrass ecosystems in similar environments.

2. Methods and materials

2.1. Study site

The prescribed fire study was conducted at the Alapaha Experimental Range of the Coastal Plain Experiment Station, a unit of the University of Georgia in Berrien County, south central Georgia (31°10′ N, 83°15′ W). The site is located in the transition between the Upper and Lower Atlantic Coastal Plain, approximately 88 m above sea level. Here the geologic parent materials consist of unconsolidated Tertiary and Quaternary sediments known as the Hazelhurst Terrace (Lemon, 1949). This nearly level (0–2% slope) coastal terrace consists of marine sands approximately 3 m in thickness (Halls et al., 1952), underlain by the Pleistocene Brandywine formation. The site is representative of coastal plain flatwoods ecosystems (Shepherd et al., 1953), in that minor variation in elevation results in noticeable differences in vegetation, soils and the water table.

Swampy lowlands, under water for extended portions of the year, occupy 36% of the site while poorly drained uplands, seldom covered by water, comprise the remaining 64% (McKee and Lewis, 1982). Soils present on the site are low in native fertility and of low porosity, hence drainage is quite slow. They include poorly drained Alapaha loamy sand (Arenic Paleaquult, loamy siliceous thermic), somewhat poorly drained Leefield loamy sand (Arenic Plinthoquic Paleudult, loamy siliceous thermic), moderately well drained Irvington loamy sand (Plinthic Fragiudult, fine–loamy siliceous thermic) and poorly drained Pelham loamy sand (Arenic Paleaquult, loamy siliceous thermic). These flat-

woods soils remain wet for extended periods throughout the year because of impeded drainage and abundant precipitation, approximately 1200 mm annually (Halls et al., 1956).

The climate is humid and mild with an average annual temperature of 15–22°C and an average frost-free period of 252 days. Herbaceous growth often continues for considerably longer periods, with some plants remaining green throughout the year (Halls et al., 1952). Forest vegetation in upland areas consists of an overstory of longleaf pine and slash pine associated with a shrub understory dominated by gallberry (*Ilex glabra*), with lesser amounts of saw-palmetto (*Serona repens*) and staggerbush (*Lyonia fruiticosa*). Herbaceous plants principally consist of wiregrass, Curtiss dropseed (*Sporobolus curtissii*), numerous bluestems, panic grass (*Panicum spp.*), toothachegrass (*Ctenium aromaticum*), lopsided Indiangrass (*Sorghastrum secundum*), carpetgrass (*Axonopus affinis*) and lovegrass (*Eragrostis refracta*). Additional plant species found in lowlands and along their margins include cypress (*Taxodium distichum*), black gum (*Nyssa sylvatica*), sweetbay (*Magnolia virginiana*), red maple (*Acer rubrum*), water tupelo (*Nyssa aquatica*), swamp cyrilla (*Cyrilia racemiflora*), buckwheat-tree (*Cliftonia monophylla*), summersweet clethra (*Clethra alnifolia*), red chokeberry (*Aronia arbutifolia*), bedstraw St. Johnswort (*Hypericum galioides*), myrtle dahoon (*Ilex myrtifolia*), wireleaf dropseed (*Sporobolus teretifolius*), plumegrass (*Erianthus spp.*), sedges (*Carex* spp.), rushes (*Juncus* spp.) and numerous forbs (Halls et al., 1956).

2.2. Site history and experimental treatments

The study area was occupied by a second-growth longleaf pine forest that was periodically burned prior to 1934. From 1934 to 1941, the site was completely protected from fire while naval stores were collected and all mature trees were harvested for timber. During the winter of 1942, most of the remaining trees were killed by a wildfire. Having been recently acquired in 1941 by the Georgia Agricultural Experiment Station, this site became the location for a long-term study on the effects of periodic fire on the longleaf pine wiregrass ecosystem begun by researchers from the University of Georgia, the USDA Agricultural Research Service and the USDA Forest Service.

In 1942, a completely randomized experimental design was established on the 160-ha study site. Four fire treatments were replicated twice, resulting in eight 20-ha rectangular plots, approximately 450 × 450 m. The fire treatments were all applied during the winter dormant season and included annual burning (once every year), biennial burning (once every 2 years), triennial burning (once every 3 years) and control (complete protection from fire). Burning treatments were conducted from 1942 to 1954 and then temporarily suspended from 1955 to 1964 to permit natural regeneration of pines. Biennial fire treatments were then continued on all treated plots from 1965 to 1982.

2.3. Field measurements

In September 1980 (39 years following study initiation), all vegetation, forest floor and soil components in this ecosystem were measured to assess the ecological changes that had occurred during this extended time period of fire treatment. The interval between the most recent fire on all burned plots and these measurements was 8 months. Overstory trees in each of the large treated plots were measured on six 32 × 32 m (0.1 ha) sampling subplots. On each subplot, all trees were tallied, each tree diameter at 1.4 m (dbh) was measured to the nearest cm, the total height of each tree (to a zero top) was measured to the nearest 0.3 m and total foliar cover (vertical projection of canopy) was ocularly estimated. Stand basal area was measured using a 10-factor wedge prism at 36 points within each larger treatment plot. Understory shrubs and tree seedlings in each of the large treated plots were measured on 12 sampling subplots, each 6.4 × 6.4 m (40 m^2). The total number of stems was tallied and the total foliar cover was estimated by eye. Understory cover of grasses, forbs and litter on the forest floor was estimated by eye on 36 sampling subplots, each 2 × 2 m (4 m^2), within each larger treatment plot. Identification and nomenclature for plant species were consistent with taxonomic authorities (Gleason, 1952; Hitchcock, 1971; Duncan and Foote, 1975; Wunderlin, 1982; Clewell, 1985; Kurz and Godfrey, 1986; Godfrey, 1988; Foote and Jones, 1989). Biomass of herbaceous understory

plants was measured on 36 sampling subplots, each 1×1 m ($1\,m^2$), within the larger treatment plots. Standing biomass of all herbaceous plants was destructively sampled by clipping at the groundline and placing the samples in paper bags. The mor humus of the forest floor and the mineral soils was also sampled on these plots. Methods for that portion of the study were previously reported (McKee and Lewis, 1982).

2.4. Laboratory analysis

Data for overstory trees were summarized for each treated plot and used to estimate the mean and variance for various forest stand structural attributes relative to fire treatment. All samples of herbaceous plants were sorted by species, dried to constant mass in a force draft oven at 75°C for 24 h and weighed. These data were then used to construct productivity estimates for understory herbs relative to fire treatment. Data on the foliar cover of each species were summarized as estimates for each treated plot and analyzed by fire treatment. Foliar cover data were used as importance values to compute numerous diversity indices (Ludwig and Reynolds, 1988). Diversity indices include: (1) number of species present, N_0; (2) Margalef species richness, R_1; (3) Menhinick species richness, R_2; (4) Simpson's diversity index, λ; (5) Shannon's diversity index, H'; (6) abundant species, N_1; (7) very abundant species, N_2; (8) Pielou's evenness index, E_1; (9) Sheldon's evenness index, E_2; (10) Heip's evenness index, E_3; (11) Hill's evenness index, E_4; (12) the modified Hill's ratio, E_5.

All data for dependent variables were summarized as estimates of the mean for each experimental plot. Each plot mean was then used to estimate the mean and variance for each of the four fire treatments. For each dependent variable, a comparison of differences among experimental treatments was then undertaken. Statistical analysis for scalar variables was completed using a general linear models analysis of variance and covariance (GLM-ANOVA) program, which computes the F-ratio and conducts Fisher's LSD test (Hintze, 1987). Statistical analysis for computed diversity indices was completed using the bootstrap technique PROC MULTTEST in SAS (Efron and Tibshirani, 1993; Westfall and Young, 1993; SAS Institute, 1996). Adjusted P-values, which maintain a constant Type I error across the full range of comparisons, were used to determine significant differences among means (10 000 bootstrap iterations were used). A probability level of 0.05 was used to discern all significant differences.

The initial experimental design split each sampling subplot into a half that was ungrazed and a half lightly grazed by domestic cattle. Analysis of the data from these grazed and ungrazed subplots indicated that no significant difference exists between these two groups for estimates of the mean and variance. Therefore, data from these split subplots were pooled and estimates of the mean and variance reported here for each dependent variable reflect these combined data in the computation.

3. Results and discussion

3.1. Overstory structure and growth

Four decades following initiation of the fire study, the overstories on all experimental plots were dominated by mature longleaf pine. The unburned control plots, however, differed substantially from the fire-treated plots in having a well developed midstory and numerous mature slash pine in the overstory. This midstory was primarily composed of shrubs and hardwood trees that exceeded 2 m in height and intercepted appreciable quantities of fallen pine needles. As such, this midstory constitutes a potentially hazardous fuel ladder, that increases the likelihood of catastrophic stand-replacement fire in the event of a nearby lightning strike. The inferred fire frequency in the longleaf pine flatwoods ecosystem is estimated as one fire every 2–4 years (Landers et al., 1990). Therefore, under pre-settlement fire regimes, such forest stand conditions would have been extremely rare, perhaps occurring only on small landscape units such as small, well protected islands and peninsulas that were relatively free of frequent wildfire.

Although the prescribed fire treatments prevented development of a midstory, numerous immature slash pine were present on fire-treated plots. These slash pine (approximately 20 years old) date back to the period between 1955 and 1964, when prescribed burning was temporarily suspended. Parent trees pre-

sent in low numbers on more poorly drained soils, were very likely the progenitors of these invasive slash pines. Most young southern pines with ground level diameters (GLDs) less than 3.8 cm are typically killed by prescribed fire (Wade, 1993). The absence of recurrent fire during this period allowed slash pine to become established in the stand long enough to reach the age beyond which they were sufficiently fire resistant to persist. While recurrent fire maintains the longleaf pine flatwoods as a stable non-successional ecosystem, alteration of fire frequency or seasonality can cause successional shifts to a variety of vegetation types (Abrahamson and Hartnett, 1990).

The presence of a well developed midstory in the unburned control plots and the invasion of the stand by slash pine during the period of prescribed fire suspension were anticipated. Numerous accounts in the literature described the need for repeated fire to either exclude or control aggressive southern pines, hardwoods and shrubs in longleaf pine ecosystems (Garren, 1943; Wright and Bailey, 1982; Platt et al., 1988; Abrahamson and Hartnett, 1990; Boyer, 1990a; Streng et al., 1993; Glitzenstein et al., 1995). It is thought that with the total absence of fire, the longleaf pine forest would completely disappear (Landers et al., 1990), though such a complete demise would require several hundred years for such a long-lived conifer. Yet if one's view of the forest includes the understory as well as the overstory, functional loss of the longleaf pine wiregrass ecosystem could occur quite rapidly, long before the collapse of the last longleaf pine tree. Thus remains the need to examine the role that ecological processes such as fire play in maintaining the long-term sustainability of the entire forest ecosystem (Landers et al., 1990).

No significant differences could be discerned among the fire treatments for the various characteristics measured in the forest overstory (Table 1). Overall, tree height and diameter were remarkably similar among treatments. However, greater variability was noted for tree density and basal area, and thus no significant differences were apparent in tree volume growth. Fire appears to have somewhat depressed volume production in the overstory pines. However, greater numbers of pine trees were present on the control plots than on the fire treated plots prior to suspension of burning in 1955. This initial differential is most likely responsible for the apparent difference in volume.

Table 1
Response of overstory trees to fire treatments

	Control	Triennial	Biennial	Annual
Density (trees ha^{-1})	1034	668	1061	879
Height (m)	14.7	15.3	13.8	14.8
Diameter (cm at 1.4 m)	14.6	15.9	13.9	19.9
Basal Area (m^2 ha^{-1})	23.3	16.4	14.6	14.5
Volume (m^3 ha^{-1})	241.5	158.7	140.5	135.4

No significant differences were detected among treatments at the 0.05 level.

Growth reductions for burned longleaf pine forests have been noted elsewhere (Cary, 1932; Garren, 1943; Boyer, 1994; Landers et al., 1995). Although prescribed fire caused no adverse effect on the growth of coastal plain loblolly pine (Waldrop et al., 1992), substantial mortality for longleaf pine (Boyer, 1990a) and red pine (Van Wagner, 1970) has been reported. Adverse effects of fire on pine forest overstories are related to high fire intensities which produce crown scorch, cambial injury and root mortality (Dickmann, 1993). It is not surprising, however. that prescribed ground fires during the winter dormant season have had little impact on the overstory at this site. Such fires were expected to have the greatest effect on understory vegetation within the immediate reach of flames.

3.2. Foliar cover of understory plants

Most categories of vascular and non-vascular plants did not significantly respond to the fire treatments (Table 2). As a group, only graminoids appeared to be affected by periodic burning during the

Table 2
Response of understory plant groups to fire treatments (percent foliar cover)

	Control	Triennial	Biennial	Annual
Tree seedlings	3.3a	4.0a	1.4a	3.2a
Shrubs	68.4a	61.2a	55.2a	69.5a
Vines	1.0a	4.8a	1.3a	1.0a
Graminoids	1.5a	21.4b	39.Ob	23.4b
Forbs	8.4a	7.0a	12.9a	5.3a
Ferns and mosses	2.5a	0.8a	0.8a	0.3a

Means in same row followed by different letters are significantly different at the 0.05 level.

dormant season. Grasses in the unburned control plots persist at very low levels of less than 2% total cover, while grasses in all of the fire-treated plots exceed a total cover of 20%, with the biennial fire treatment approaching 40% foliar cover. Biennial burning in this longleaf pine wiregrass ecosystem increased the overall foliar cover of grasses by 2500% over that present in the unburned control areas.

This overall response pattern to fire concurs with earlier observations, where grasses were the principal beneficiaries of periodic fire (Garren, 1943; Wright and Bailey, 1982; Landers et al., 1990; Abrahamson and Hartnett, 1990; Waldrop et al., 1992). Unlike less fire tolerant plants, grasses typically: (1) maintain substantial nutrient stores in extensive belowground root systems; (2) have their leaf meristems at least 4 cm below the ground surface; (3) can produce abundant production and dissemination of reproductive bodies (Lemon, 1949). These characteristics allow them to rebound quickly following a surface fire and even expand their occupancy of the site. Typically, repeated burns serve to accentuate the prominence of grasses in the plant community. Forbs are also reported to benefit from recurrent fire in southern pine ecosystems (Lewis et al., 1988; Abrahamson and Hartnett, 1990; Waldrop et al., 1992). However, the persistence of a vigorous shrub layer, on fire treated as well as on control plots, appears to have diminished the overall response of forbs.

Foliar cover of certain shrub and grass species appears to be significantly influenced by fire treatment (Fig. 1). Unburned control plots have a well developed shrub layer dominated by gallberry, with 50% cover. Dwarf huckleberry (*Gaylussacia dumosa*), the next most common shrub, occurs nearer the ground with about 12% cover, followed by shiny blueberry (*Vaccinium myrsinites*) at approximately 2% cover. Individual grasses persist on unburned plots at extremely low levels, likely owing to competition from the vigorous shrub layer (Garren, 1943; Lemon, 1949; Halls et al., 1952; Halls et al., 1956) and smothering by the accumulated forest litter. According to earlier studies, as overstory canopy cover reaches 50% and shrub cover approaches 15%, an order of magnitude decline in the growth of grass is observed in this ecosystem (Halls et al., 1956). The abundant cover of gallberry alone is sufficient to suppress herbaceous plants in the understory.

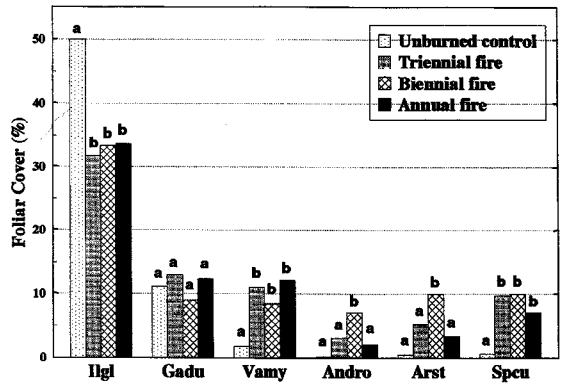

Fig. 1. Foliar cover response of major understory plants to fire treatments: Ilgl = *Ilex glabra*, Gadu = *Gaylussacia dumosa*, Vamy = *Vaccinium myrsinites*, Andro = *Andropogon* spp., Arst = *Aristida stricta*, Spcu = *Sporobolus curtissii* (means for the same species corresponding to different letters are significantly different at the 0.05 level).

On all fire treatments, gallberry is significantly reduced to less than 35% foliar cover, a reduction of approximately 33% relative to the control. Correspondingly, increases of up to 12% foliar cover for *V. myrsinites* and up to 10% foliar cover for *S. curtissii* are observed. These gains represent respective increases of approximately 500% and 1000% when compared with controls. *G. dumosa* appears to be the only prominent shrub not significantly changed by the fire treatments. This sharply contrasts with large increases in huckleberry and blueberry under Coastal Plain loblolly pine, which sprouted prolifically after fire (Waldrop et al., 1992). On the biennially burned plots, the greatest overall increases in the foliar cover of grasses occurred. *Andropogon* spp. increased by over 3000% up to 8% foliar cover, *A. stricta* expanded by nearly 2000% up to 10% foliar cover and *S. curtissii* increased by over 1300% up to 10% foliar cover. Relative to controls, these represent substantial gains for the major grasses in this ecosystem.

Photographic records indicate the understory was originally dominated by grasses with very few shrubs present (Fig. 2a). While all fire treatments initially prevented or slowed development of the shrub layer (Fig. 2b), shrub cover increased substantially during the period when burning was suspended. Resumption of fire treatments caused significant reductions in

gallberry (Fig. 2c), as contrasted with the well developed shrub layer on unburned plots (Fig. 2d).

Fire treatments did not significantly alter overstory canopy structure but did decrease cover of the dominant shrub, gallberry. It is therefore likely that gallberry acts as a major inhibitor of herbaceous plants in the understory. In causing the 33% decline in gallberry, fire has created opportunity for expansion of plants already occupying the site and liberated microsites where additional species might colonize subsequent to successful dispersal and germination. If this hypothesis is correct, it should be supported by an analysis of plant species diversity data, comparing the unburned and burned treatments.

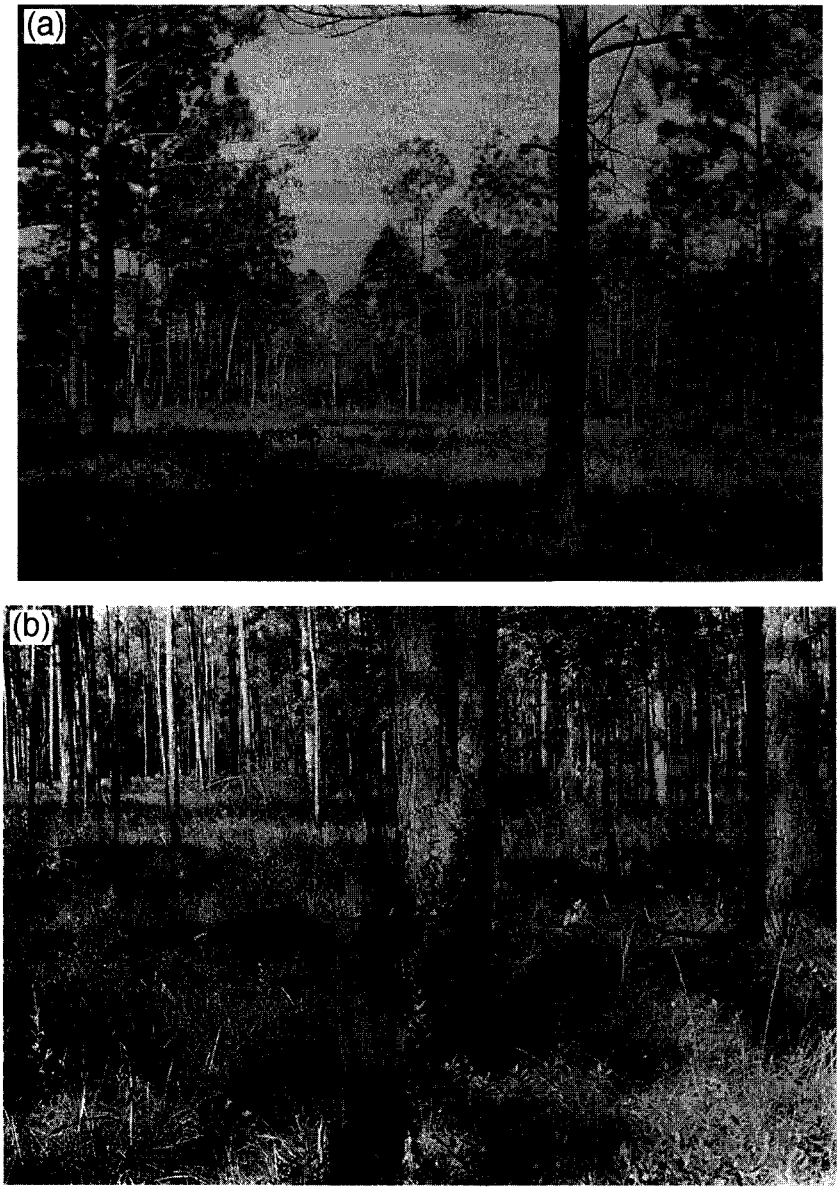

Fig. 2. Alapaha study site: (a) understory originally dominated by grasses; (b) initial fire treatments inhibited shrubs; (c) resumed fire treatments reduced gallberry; (d) well developed shrub layer on unburned control plots.

3.3. Overall species richness

A total of 87 vascular plant species were found on subplots where measurements were taken within the larger treatment plots (Table 3). Since the measurement subplots are located primarily in and near the upland portions of the study site, this species listing is not exhaustive. Numerous other species, especially those preferring the wetter habitats, should be added to this list to insure comprehensiveness. However, even this number of species is firm testimony to the high vascular plant diversity in longleaf pine ecosystems (Peet and Allard, 1993). Few tree species are present in this plant community and only two, longleaf pine and slash pine, appear to be prominent. Although there is a moderate number of shrubs, only gallberry appears dominant in the understory. The variety of grasses is obvious, however only a few

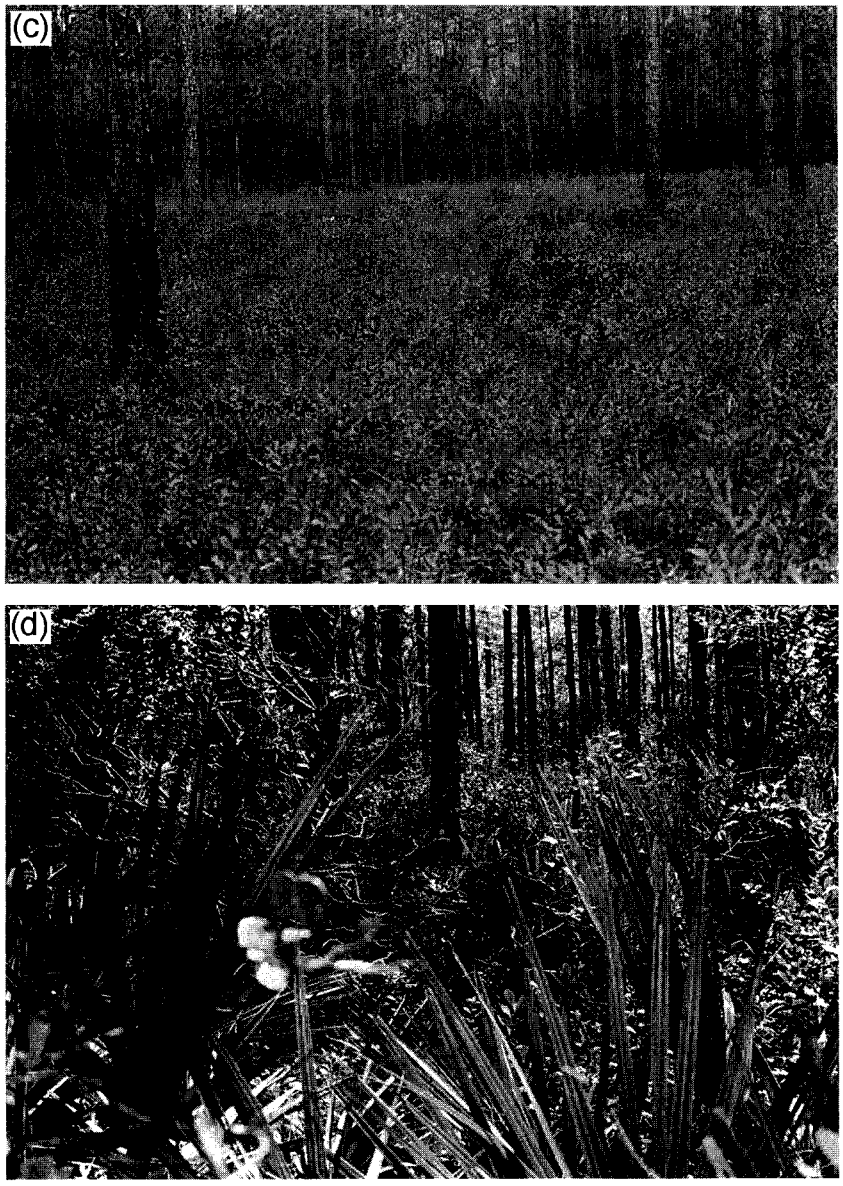

Fig. 2 (continued).

Table 3
Vascular plants present on the Alapaha, Georgia study site

Scientific name	Common name
Trees	
Acer rubrum	Red maple
Nyssa sylvatica	Black tupelo
Pinus palustris	Longleaf pine
Pinus elliottii	Slash pine
Prunus virginiana	Common chokecherry
Quercus spp.	Oaks
Shrubs	
Gaylussacia dumosa	Dwarf huckleberry
Ilex glabra	Gallberry
Ilex myrtifolia	Myrtle dahoon
Kalmia hirsuta	Wicky
Lyonia fruiticosa	Staggerbush
Lyonia lucida	Fetterbush
Lyonia mariana	Staggerbush
Myrica cerifera	Wax myrtle
Persea borbonia	Redbay
Quercus pumila	Running oak
Rhus copallina	Winged sumac
Sapindus spp.	Soapberries
Serona repens	Saw-palmetto
Vaccinium corymbosum	Highbush blueberry
Vaccinium myrsinites	Shiny blueberry
Xolisma ambigua	Staggerbush
Xolisma caroliniana	Staggerbush
Vines	
Rubus cunefolius	Sand blackberry
Smilax laurifolia	Catbrier
Toxicodendron radicans	Poison ivy
Vitis spp.	Grapes
Graminoids	
Andropogon tener	Slender bluestem
Andropogon ternarius	Splitbeard bluestem
Andropogon virginicus	Broomsedge bluestem
Aristida lanosa	Threeawn
Aristida purpurescens	Arrowfeather threeawn
Aristida stricta	Wiregrass, pineland threeawn
Aristida virgata	Threeawn
Axonopus affinis	Common carpetgrass
Carex spp.	Sedges
Ctenium aromaticum	Toothachegrass
Cyperus ovularis	Globe flatsedge
Dactyloctenium aegyptium	Crowfootgrass
Eragrostis refracta	Lovegrass
Muhlenbergia expansa	Cutover muhly
Panicum spp.	Panic grasses
Panicum virgatum	Switchgrass
Paspalum floridanum	Florida paspalum
Schizachyrium scoparium	Little bluestem
Sorghastrum secundum	Lopsided indiangrass
Sporobolus curtissii	Curtiss dropseed
Sporobolus floridanus	Florida dropseed

Table 3 (continued)

Scientific name	Common name
Forbs – legumes	
Baptisia tinctoria	Yellow wild indigo
Cassia chamaecrista	Partridgepea
Cassia nictatans	Wild sensitive plant
Desmodium ciliare	Littleleaf tickclover
Lespedeza capitata	Bush clover
Rhynchosia plumosa	Rhynchosia
Rhynchosia reniformis	Dollarleaf rhynchosia
Tephrosia virginiana	Goat's-rue
Forbs – composites	
Bigelowia nudata	Bigelowia
Elephantopus elatus	Florida elephant's-foot
Erigeron pusillus	Small fleabane
Erigeron vernus	Fleabane
Eupatorium spp.	Dogfennels
Helianthus radula	Rayless sunflower
Liatris spp.	Gayfeathers
Solidago spp.	Goldenrods
Forbs – general	
Asclepias spp.	Milkweeds
Carphephorus odoratissimus	Vanilla plant
Chrysopsis aspera	Goldaster
Chrysopsis graminifolia	Grassleaf goldaster
Eriocaulon spp.	Pipeworts
Eriocaulon lineare	Pipewort
Gelsemium sempervirens	Yellow jessamine
Hypericum crux-andraea	St. Johnswort
Iris spp.	Iris
Lachnocaulon anceps	Bog-buttons, hatpin
Lycopodium spp.	Clubmosses
Pteridium aquilinum	Brackenfern
Pterocaulon virgatum	Blackroot
Rhexia lutea	Meadow beauty
Rhexia mariana	Pale meadow beauty
Richardia scabra	Florida pusley
Sabatia brevifolia	White sabatia
Sarracenia spp.	Pitcherplants
Sarracenia flava	Trumpet pitcherplant
Scutellaria spp.	Skullcaps
Seymeria cassioides	Seymeria
Symplocus tinctoria	Sweetleaf
Tragia urens	Waxyleaf noseburn
Total Plant Species = 87	

such as *Andropogon, Aristida* and *Sporobolus* appear to be abundant. Forbs seem to be present in great variety, but they typically persist at generally low levels whether this forest ecosystem is burned or not. This lack of response to fire by forbs is quite unlike that reported beneath burned coastal plain

loblolly pine forests (Waldrop et al., 1992) and may in part be a result of the high residual cover of gallberry and other competing shrubs on fire treated plots.

3.4. Species diversity of understory plants

The understories of all fire-treated plots contained significantly higher numbers of vascular plant species than did the unburned controls (Table 4). Species richness (N_0) for the biennial fire treatment was highest, with 39 species present, followed by the annual fire treatment, which supported 34 species, and the triennial fire treatment, which resulted in 31 species. Only 17 plant species were typically found in the understories of the unburned control plots, probably a result of the singular dominance of gallberry shrubs. Computations for the Margalef richness (R_1) and Menhinick richness (R_2) indices closely correspond to these trends, as do the indices for abundant species (N_1) and very abundant species (N_2).

Plant species diversity was significantly greater on all fire treated plots than on the unburned control areas (Table 4). The Shannon diversity index (H') was highest, at 2.54, in the biennially burned understories, followed by the annually burned plots, at 2.30, and the triennially burned areas, at 2.23. The Shannon index in the unburned control plots averaged a mere 1.47. The Simpson diversity index (λ), a reciprocal computation, showed an overall similar trend.

Table 4
Response of understory plant species diversity to fire treatments

	Control	Triennial	Biennial	Annual
Number of species, N_0	17.5a	31.3b	39.3b	34.0b
Margalef richness, R_1	3.7a	6.6ab	8.2b	7.2b
Menhinick richness, R_2	1.9a	3.lab	3.8b	3.4ab
Simpson diversity, λ	0.38a	0.17b	0.13b	0.16b
Shannon diversity, H'	1.47a	2.23b	2.54b	2.30b
Abundant species, N_1	4.4a	9.4b	13.2b	10.0b
Very abundant species, N_2	2.7a	6.3ab	8.8b	6.4ab
Pielou evenness, E_1	0.52a	0.65b	0.69b	0.65b
Sheldon evenness, E_2	0.26a	0.30a	0.33a	0.30a
Heip evenness, E_3	0.21a	0.28a	0.31a	0.28a
Hill evenness, E_4	0.62a	0.67a	0.65a	0.64a
Modified Hill evenness, E_5	0.50a	0.62a	0.62a	0.59a

Means in same row followed by different letters are significantly different at the 0.05 level.

The results for evenness in distribution among plant species is somewhat less clear. Pielou's evenness index (E_1) is significantly higher on all fire treated plots than on the unburned control (Table 4). This index ranges from 0.65 to 0.69 on the burned plots, as contrasted with an average of only 0.52 on the unburned plots. Computations for the other evenness indices (Sheldon, E_2; Heip, E_3; Hill, E_4; Modified Hill, E_5) indicate a similar trend. However, the differences among fire treatments and control are not significant.

Winter burning typically creates a diverse understory with high numbers of grasses, legumes and forbs (Moore et al., 1982; Waldrop et al., 1992). Fire may accomplish this by reducing the shrub layer (Abrahamson and Hartnett, 1990), clearing microsites for herbaceous colonization and expansion (Moore et al., 1982) and stimulating the production and dissemination of reproductive propagules (Landers et al., 1990). However, seed production by important understory species, such as wiregrass, is thought to be primarily stimulated by burning during the growing season (Biswell and Lemon, 1943; Streng et al., 1993). On this site, winter burning reduced the cover of gallberry in the shrub layer and created opportunity for colonization of the fire-treated plots by a greater number of plant species, as indicated by higher levels of species richness. This increase in species richness from 17 species on the unburned plots to 39 on biennial fire treatment plots represents a 129% gain through burning. The disparity among species diversity indices reinforces this trend, with the biennial fire treatment exhibiting a Shannon index of 2.54, which is 73% greater than the index of 1.47 computed for the unburned control. Also, evenness values generally indicate that plant species are more equitably distributed across the fire-treated plots than on the unburned control plots where fewer species, principally gallberry, dominate the flora.

3.5. Forest floor

Fire treatment resulted in a significant decline in litter cover on the forest floor (Fig. 3). Control plots

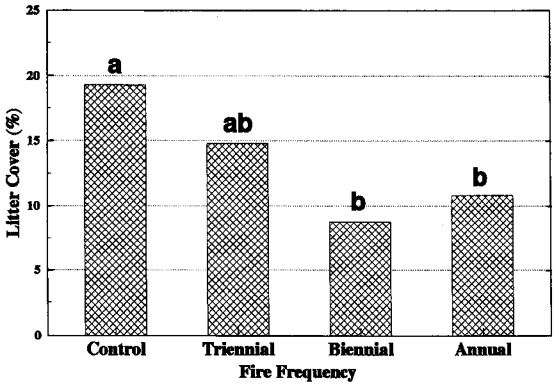

Fig. 3. Litter cover response of forest floor to fire treatments (means corresponding to different letters are significantly different at the 0.05 level).

had the highest litter cover, averaging 19% after nearly four decades of complete protection from fire. Litter cover of 15% on triennially burned plots was not significantly less than controls. However, litter cover of 9% on biennially burned plots and 11% on annually burned plots was significantly less than on control plots. Forest litter in control plots frequently accumulated to a thickness of 15–25 cm, typically smothering understory herbaceous plants. Reduction of this thick litter layer by prescribed fire, very likely contributed to the increased abundance of understory herbs found on fire treated plots. Substantial (though unquantified) amounts of forest litter, primarily pine needles, were observed to be intercepted by the well developed midstory present on control plots. This intercepted material was suspended above the forest floor, and thus could have ultimately contributed to even higher average estimates of litter cover on the forest floor of controls.

This trend corresponds to findings concerning decay and mineralization rates of forest floor phytomass reported earlier (McKee, 1982; McKee and Lewis, 1982; Brockway and Lewis, 1993). Soil nutrient limitations, principally nitrogen, in longleaf pine ecosystems typically result in litter which is slow to decompose (Christensen, 1993). Despite associated nutrient losses such as nitrogen volatilization, fire consumes much aboveground biomass and litter, appreciably increasing the rate of nutrient turnover (Abrahamson and Hartnett, 1990). Increased nutrient cycling rates for phosphorus and cations (Gholz et al., 1985) raise soil pH and stimulate nitrogen fixation (Gholz and Fisher, 1984). Thus, forest floor reduction by fire releases immobilized nutrients to the mineral soil for more rapid assimilation in the production of plant biomass following each prescribed burn.

3.6. Productivity of herbaceous understory plants

Standing biomass of herbaceous understory plants was significantly higher on all fire treated plots than on the control areas (Fig. 4). The largest standing biomass of 602 kg ha^{-1} was measured on the biennial fire treatment. *Andropogon* spp. accounted for the greatest proportion of this biomass with 171 kg ha^{-1}, followed by *S. curtissii* at 169 kg ha^{-1}, all forbs at 98 kg ha^{-1}, *A. stricta* at 87 kg ha^{-1} and all other grasses at 77 kg ha^{-1}. The standing biomass for the triennial fire treatment totaled 284 kg ha^{-1}. *S. curtissii* was the largest contributor with 131 kg ha^{-1}, followed by *A. stricta* at 68 kg ha^{-1}, all forbs at 33 kg ha^{-1}, *Andropogon* spp. at 30 kg ha^{-1} and all other grasses at 22 kg/ha. Standing biomass observed on the annual fire treatment totaled 217 kg ha^{-1}. *S. curtissii* accounted for the largest share of this with 86 kg ha^{-1}, followed by all other grasses at 43 kg ha^{-1}, *Andropogon* spp. at 34 kg ha^{-1}, *A. stricta* at 27 kg ha^{-1} and all forbs at 27 kg ha^{-1}. The smallest standing biomass occurred on the control plots with a total of 15 kg ha^{-1}. All forbs constituted the largest proportion of that with

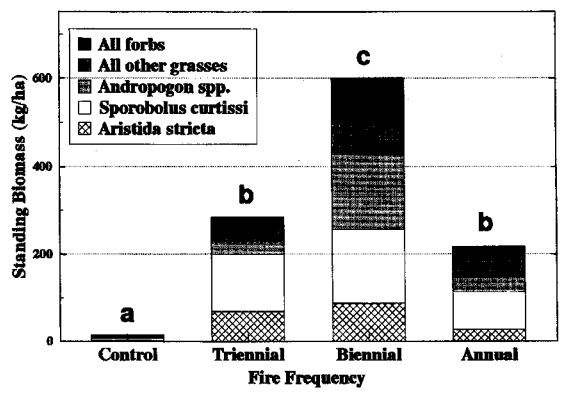

Fig. 4. Productivity response of herbaceous understory plants to fire treatments (means corresponding to different letters are significantly different at the 0.05 level).

8 kg ha^{-1}, followed by *S. curtissii* at 5 kg ha^{-1}, *A. stricta* at 2 kg ha^{-1} and all other grasses with less than 1 kg ha^{-1}. While occurring at low levels in the foliar cover subplots of the control, *Andropogon* spp. did not appear on the plant biomass sample subplots. Although grasses appeared to be the greatest overall beneficiaries of recurrent fire treatments, the productivity of forbs also improved by burning.

This pattern of recurrent fire improving the productivity of grasses and forbs is consistent with earlier reports in the literature (Lewis, 1964; Hilmon and Hughes, 1965; Stoin, 1979; Moore et al., 1982; Wright and Bailey, 1982; Abrahamson and Hartnett, 1990; Waldrop et al., 1992). Longleaf pine wiregrass ecosystems periodically treated with fire are known to produce two to four times more herbaceous biomass than those left unburned (Hilmon and Hughes, 1965). Herbaceous growth typically begins sooner in the spring on fire-treated areas because of warmer soil temperatures (Garren, 1943). Beneath the sparse tree canopy in longleaf pine forests that are periodically burned, herbaceous production typically averages 2245 kg ha^{-1} (Carter and Hughes, 1974), but may approach 3930 kg ha^{-1} (Hilmon and Hughes, 1965; Lewis and Hart, 1972), depending on canopy cover (Halls et al., 1952, 1956).

Unlike the higher values reported beneath sparse tree canopies, herbaceous production beneath the well developed tree canopy on the Alapaha site was 15 kg ha^{-1} in the control plots, 217 kg ha^{-1} on the annual burning treatment, 284 kg ha^{-1} for the triennial fire treatment and 602 kg ha^{-1} on the biennial burning treatment. The herbaceous standing biomass for the biennial fire treatment represents a 3900% increase over that present on the control plots and is quite typical of frequently burned mature longleaf pine ecosystems. Thus, while gallberry retained high residual cover (greater than 30%) in the shrub layer, individual gains of 5000% for *A. stricta*, 3400% for *S. curtissii* and 1100% for all forbs are indicative of a substantial benefit to the ecosystem from winter dormant season prescribed fire on a biennial cycle.

3.7. Restoring and sustaining the ecosystem with fire

The close association of longleaf pine wiregrass ecosystems with periodic fire has been long recognized (Garren, 1943; Wright and Bailey, 1982; Abrahamson and Hartnett, 1990) and a need for frequent burning to restore and sustain a wide range of resource values has been recently advocated (Noss, 1989; Frost, 1993, Streng et al., 1993; Landers et al., 1995). This ecosystem occupies a portion of the Southeast that is highly prone to lightning with a high potential for wildfire ignition (Paul et al., 1968; Paul and Waters, 1978; Goodman and Christian, 1993). Indeed, the longleaf pine wiregrass ecosystem has been described as ideally structured for the purpose of transmuting a localized disturbance (lightning) into a widespread disturbance (ground fires), thus providing conditions suitable for its own regeneration and perpetuation (Platt et al., 1988). Since European settlement, active fire suppression policies have decreased the number of fires that have been allowed to burn and landscape fragmentation has decreased the area burned by each fire event (Christensen, 1981). The decrease in fire frequency and extent of area burned has contributed to the serious decline of this ecosystem. Continued fire exclusion will increasingly jeopardize the native flora and fauna and contribute to their replacement by less desirable plants and animals (Brenner and Wade, 1992).

Recurrent fire is therefore understood to be an ecological process essential for restoring and maintaining the longleaf pine wiregrass ecosystem. However, some disagreement exists concerning the season and frequency of fire best suited to achieve such management objectives. It is commonly believed that the summer growing season was the time of greatest likelihood for fire during the pre-human period (Abrahamson and Hartnett, 1990; Christensen, 1993). Good evidence suggests that summer fires are of greater value in sustaining this ecosystem, through better control of invasive plants (Hilmon and Hughes, 1965; Wright and Bailey, 1982; Glitzenstein et al., 1995) and improved production of seed by wiregrass and associated understory herbs (Noss, 1989; Streng et al., 1993). However, a substantial change brought to this ecosystem by humans was introduction of burning during the winter dormant season (Christensen, 1993). For many years, summer growing season burns were thought to be harmful and actively discouraged (Garren, 1943; Wright and Bailey, 1982). Evidence does suggest that high intensity fires may cause as much mortality among desirable longleaf pines as undesirable hardwoods (Boyer, 1990a).

Thus, depending on existing ecosystem conditions and the desired outcome, winter dormant-season burning remains a useful management option.

Fire frequency appears somewhat less controversial with historic intervals estimated at one fire every 2–4 years (Landers et al., 1990). Although some managers may utilize a fire-return interval as long as 5–7 years in this ecosystem, findings in this study suggest that biennial prescribed burning during the winter dormant season is also beneficial to plant species diversity and productivity. Unfortunately, the original experimental design, conceived in 1942, did not include summer growing-season fire so that a long-term comparative evaluation of seasonal effects could be undertaken. Nonetheless, both winter and summer burning, as judged by results reported elsewhere, appear to be useful in maintaining longleaf pine wiregrass ecosystems. The difference between the two seasons may be largely the degree of effect and speed with which results are achieved, with summer burning producing more dramatic and rapid results. Considering the wide array of site history, hydrology, soil and vegetation variables in longleaf pine wiregrass ecosystems ranging from those in very poor to excellent condition, it seems inappropriate to identify a single universally applicable restoration and maintenance prescription to cover all circumstances. The decision to burn as well as the selection of fire season and return interval is best left to the land manager, who must consider social and economic imperatives in addition to ecological factors.

4. Conclusion

Periodic winter dormant-season prescribed fire caused substantial changes in the understory of a longleaf pine wiregrass ecosystem, after nearly four decades. Significant reduction in the foliar cover of gallberry in the shrub layer resulted in corresponding increases in the cover of blueberry, Curtiss dropseed, wiregrass and bluestem grasses. Understory plant species richness, diversity and evenness also increased as a result of fire. Winter burning decreased the cover of litter on the forest floor and significantly increased the standing biomass of wiregrass, Curtiss dropseed, bluestem grasses, all other grasses and all forbs. Recurrent fire also prevented the development of a vigorous midstory that impedes understory growth and poses a serious fire hazard to the stand. Overstory trees were largely unaffected by burning. Historical light grazing on the site produced no measurable effects on the plant community.

Prescribed burning in natural stands is known to increase the abundance and productivity of herbaceous plants. while having little effect on woody species (Lewis et al., 1988). In that sense, prescribed fire is not appreciably different from natural disturbance regimes and causes little alteration in flatwoods ecosystems (Abrahamson and Hartnett, 1990). Although shrub density is increased through prolific resprouting on many flatwoods sites periodically burned during the dormant season, such fire does prevent establishment of a midstory layer and maintains conditions sufficiently open for the continued existence of most herbaceous plants (Outcalt and Outcalt, 1994). Prescribed burning with a frequency of one fire every 2–3 years is known to prevent site invasion by aggressive southern pines (Bruce, 1947; Langdon and Bennett, 1976) and reduce potentially hazardous fuels (Sackett, 1975). Our findings suggest that the biennial burning interval results in declines of gallberry in the shrub layer and litter cover on the forest floor, leading to the greatest increases in understory plant species richness and diversity and the biomass productivity of grasses and forbs. Although growing-season fires more closely mimic natural disturbance regimes and afford better control of woody plants, not all longleaf pine forests can or will be burned during the summer season. Thus we recommend long-term application of dormant-season fire as another useful option for sustaining resource values in this and similar longleaf pine wiregrass ecosystems.

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