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Restoring longleaf pine wiregrass ecosystems: Hexazinone application enhances effects of prescribed fire

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Abstract

A longleaf pine wiregrass ecosystem in the sandhills of north central Florida, upon which turkey oak gained dominance following a wildfire, was treated with applications of hexazinone (1.1 or 2.2 kg/ha) in May 1991. All applications successfully reduced competition from oaks in the overstory and understory (mortality >80%), resulting in progressive increases in the foliar cover of wiregrass, all graminoids and forbs through time. Broadcast application caused a decline in forb cover and species richness during the initial growing season, which recovered by the following year. The 2.2 kg/ha spot application resulted in an increase in species richness, while evenness declined with the continuing expansion of wiregrass. The entire site was then burned in June 1995 by prescribed fire, which caused a widespread decrease in the cover of oaks, shrubs, wiregrass, all graminoids and forbs and plant species richness. In the following year, forb cover increased and oak cover remained significantly lower on plots treated with the combination of hexazinone plus fire than on fire-only plots. The overall cover of forbs, graminoids, shrubs and longleaf pines continued to increase through time. Broadcast application initially exposed a greater number of understory plants to direct contact with herbicide, posing a higher mortality risk than may be acceptable in restoration efforts. Although recovery occurred in subsequent years, the lower selectivity of broadcast application makes it a less suitable restoration technique. Spot application of hexazinone was more selective in its effects upon the plant community. The 2.2 kg/ha spot application produced increases in the cover of wiregrass, all graminoids and forbs and the highest levels of species richness and diversity. The 2.2 kg/ha application rate was also most effective in controlling woody plant competition and is therefore recommended for restoring longleaf pine wiregrass ecosystems in sandhills and similar environments. Hexazinone application followed by prescribed fire accelerates the rate of ecosystem restoration over that achievable by using fire alone. The ecological benefits of controlling competition and rebalancing floristic composition rapidly achieved through this combination of treatments would likely require many cycles of prescribed fire, if used as an individual treatment, over a period of several decades.

Keywords: *Pinus palustris* Mill.; *Aristida beyrichiana* Trin. & Rupr.; *Quercus laevis* Walt.; Foliar cover; Plant species diversity; Sandhills; Herbicide

1. Introduction

Although once among the most extensive ecosystems in North America (Landers et al., 1995), occupying 37 million ha in the southern United States prior to settlement (Frost, 1993), longleaf pine (*Pinus*

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palustris) forests have undergone a steady decline to 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 <1.2 million ha. Area reductions continue for stands in every diameter class below 41 cm (Kelly and Bechtold, 1990), therefore most remaining longleaf pine forests are aging without replacement. The factors responsible for this decline include clearing land for agriculture (Ewel, 1990), conversion of longleaf pine forests to other coniferous species such as loblolly pine (*Pinus taeda*) and slash pine (*Pinus elliottii*) and interruption of natural fire regimes (Pyne, 1982; Wright and Bailey, 1982). Interruption of natural fire cycles may be the most ecologically significant cause for this decline, since the absence of frequent ground fires impedes the natural regeneration of longleaf pine and allows the invasion of longleaf pine sites by hardwood trees and more aggressive southern pines, including loblolly pine, slash pine and sand pine (*Pinus clausa*).

Throughout its natural range, extending along the Coastal Plain from Texas to Virginia and from central Florida to the Piedmont and mountains of northern Alabama and Georgia (Schwarz, 1907; Stout and Marion, 1993), longleaf pine occurs in forests, woodlands and savannas on a wide variety of sites, ranging from wet poorly-drained flatwoods to xeric sandhills and mountain ridges (Boyer, 1990a). Longleaf pine understories in the western Gulf Coastal Plain are principally bluestem grasses (*Andropogon* spp. and *Schizachyrium* spp.), while those in Florida and along the Atlantic Coastal Plain are dominated by wiregrass, *Aristida beyrichiana* from Florida to central South Carolina and *Aristida stricta* from central South Carolina through North Carolina (Peet, 1993). A characteristic feature of this ecosystem is an open, park-like stand structure (Harper, 1914; Laessle, 1942; Edmisten, 1963), containing few shrubs or hardwood trees, because longleaf pine and understory grasses facilitate the ignition and spread of growing season fires (Platt et al., 1988a; Noss, 1989; Landers, 1991; Robbins and Myers, 1992). 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 and (8) reducing fuel levels and the wildfire hazard (McKee, 1982; Wade and Lewis, 1987; Wade and Lundsford, 1990; Dickmann, 1993; Brennan and Herman, 1994).

The rich biological diversity in this ecosystem is maintained by a combination of disturbance events and site factors, including lightning strikes, tree mortality and animal interactions at local scales and tropical storms, soils and hydrologic regimes at broader scales. Such disturbances across site gradients provide large living trees, snags, coarse woody debris, forest openings and hardwood thickets that support numerous plants and animals adapted to this disturbance-prone, yet largely stable ecosystem. The high diversity of plant species ranks this as one of the most species-rich communities outside the tropics (Peet and Allard, 1993). Yet, with this ecosystem occupying <4% of its original range, habitat reduction has caused the increased rarity of 191 vascular plant taxa (Hardin and White, 1989; Walker, 1993) and several vertebrate species.

Recent concern over loss of this unique ecosystem (Means and Grow, 1985; Noss et al., 1995) has led to discussion concerning how the longleaf pine wiregrass ecosystem can be effectively restored. Since longleaf pine still occurs in isolated fragments over most of its natural range, it is reasonable to conclude that restoration of this ecosystem is possible (Landers et al., 1995). Success in this endeavor will depend on identifying 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 (Frost, 1990; Streng et al., 1993). Dormant season fire may also provide a restoration and maintenance benefit to this ecosystem when growing season fire cannot be employed (Brockway and Lewis, 1997). Natural regeneration methods employing a regime of frequent fire are compatible with maintenance of the longleaf pine wiregrass ecosystem (Boyer and White, 1990). Fire at intervals as frequent as 2–4 years may be beneficial in ecosystem restoration without need for measures to protect regeneration. Mechanical site preparation methods have also been proposed, but must be carefully applied to avoid adverse effects upon wiregrass (Clewell, 1989; Outcalt and Lewis, 1990; Outcalt, 1993). Herbicide application has also been suggested as a means of selectively reducing competing vegetation, favoring expansion of longleaf pine and wiregrass, minimizing physical disturbance of the soil and avoiding displacement of site nutrients (Wilkins et al., 1993a, b; Brockway et al., 1998).

A degraded longleaf pine wiregrass ecosystem, that had been invaded by scrub oaks following timber harvest and wildfire in the sandhills of north central Florida, was treated with hexazinone and burned 4 years later with prescribed fire. In measuring post-treatment changes in the foliar cover and species diversity of vascular plants over 7 years, the objectives of this study were to (1) evaluate hexazinone as a selective agent for controlling competition from invasive woody vegetation (primarily oaks), (2) measure the effects of hexazinone on non-target plant species (principally wiregrass, other grasses and forbs), (3) determine whether application of hexazinone can serve as a viable restoration treatment and (4) compare the effectiveness of hexazinone application followed by prescribed fire with that of prescribed fire alone for rebalancing interspecific competition and adjusting plant community structure when restoring longleaf pine wiregrass ecosystems in sandhills and similar environments.

2. Methods and materials

2.1. Study site

This experiment was conducted on the Lake George Ranger District of the Ocala National Forest in Marion County, north central Florida. The study site is located on Riverside Island (29°28′N, 81°50′W), one of the largest remaining longleaf pine wiregrass areas along the Mount Dora Ridge (Laessle, 1958). The climate is humid subtropical (Chen and Gerber, 1990). Annual precipitation is abundant, averaging 1300 mm, with more than half of this arriving during the June to September season (Aydelott, 1966). Average monthly temperatures range from 21 to 28°C for the April to October period and from 14 to 19°C for November to March (NOAA, 1930–1985).

The study area is approximately 50 m above sea level in a sandhills landscape with rolling topography, devoid of surface drainages and characterized by closed depressions. Surface slopes, ranging from nearly level (0–2%) to moderately inclined (up to 8%), are aeolian dunes which developed during periods of climate and sea level fluctuation in the Pleistocene (Kalisz and Stone, 1984). Surface deposits are comprised of sands 2–3 m thick overlying the stratified sand, gravel and kaolinitic clays of the Citronelle Formation (Laessle, 1958). Soils developed in parent materials devoid of easily weathered primary minerals and consist of quartz sand with small amounts of iron and titanium (Kalisz and Stone, 1984). Clay-sized particles are primarily quartz, kaolinite, hydroxy-aluminum interlayered minerals and gibbsite (Carlisle et al., 1978). Soils present on the site are excessively drained entisols and typically exhibit little if any profile development (Brown et al., 1990). The predominant soil is the Astatula series (Typic Quartzipsamments, hyperthermic) which is low in organic matter, nutrients and water holding capacity (Aydelott et al., 1975). This environment is commonly described as a ‘wet desert’ or ‘desert in the rain’ since, while precipitation is abundant, the soil can become extremely dry within 1 week without substantial rainfall (Outcalt, 1993).

Vegetation on this ‘high pine’ sandhills area was previously dominated by an overstory of longleaf pine, within a larger matrix of sand pine (Laessle, 1958; Myers, 1985, 1990; Myers and White, 1987). Evidence suggests that these have been the two principal ecosystems in this area for the past 5000 years (Watts, 1971; Watts and Hansen, 1988; Watts et al., 1992). However, the degraded nature of the study site was reflected in the relative absence of longleaf pine and predominance of turkey oak (*Quercus laevis*) with lesser amounts of sand pine, Chapman oak (*Quercus chapmanii*), sand live oak (*Quercus geminata*) and myrtle oak (*Quercus myrtifolia*). Associated understory shrubs included dwarf live oak (*Quercus minima*), saw-palmetto (*Serona repens*), scrub palmetto (*Sabal etonia*), rosemary (*Ceratiola ericoides*), crookedwood (*Lyonia ferruginea*), wax myrtle (*Myrica cerifera*), prickly pear (*Opuntia humifusa*), shiny blueberry (*Vaccinium myrsinites*), gopherapple (*Licania michauxii*), Adam's needle (*Yucca filamentosa*) and coontie (*Zamia pumila*). Wiregrass, Curtiss dropseed (*Sporobolus curtissii*), broomsedge bluestem (*Andropogon virginicus*), lopsided indiangrass (*Sorghastrum secundum*), panicgrass (*Panicum* spp.), sandgrass (*Triplasis* spp.) and yellow nutsedge (*Cyperus recurvata*) were among the prominent graminoids. Forbs commonly observed included partridge-pea (*Cassia chamaecrista*), treadsoftly (*Cnidosculos stimulosus*), doveweed (*Crotan argyranthemus*), buckwheat (*Eriogonum tomentosum*), dogfennel (*Eupatorium compositafolium*), milkpea (*Galactia* spp.), St. Johnswort (*Hypericum* spp.), wild indigo (*Indigofera caroliniana*), silverthread goldaster (*Pityopsis graminafolia*), wireweed (*Polygonella gracilis*), blackroot (*Pterocaulon virgatum*), dollarweed (*Rhynchosia* spp.), blue-eyed grass (*Sisyrinchium solstitiale*) and queens delight (*Stillingia sylvatica*).

2.2. Site history and experimental treatments

The study area was occupied by a second-growth longleaf pine forest that was harvested for timber and replanted with longleaf pine seedlings in 1971. During the winter of 1989, the young longleaf pine trees were killed by a lightning-ignited wildfire. Fuel and weather conditions resulted in extensive damage to tree crowns and boles. The numerous oaks present vigorously resprouted and, in the absence of a longleaf pine overstory, quickly gained dominance on this site.

In April 1991, a randomized complete block experimental design was established on the study site. Four experimental treatments were replicated in five blocks distributed across the 230 ha study area. Each 1 ha (100 m×100 m) block contained four 0.25 ha (50 m×50 m) plots. All treatments were one-time applications of hexazinone applied in May 1991 following initiation of plant growth. Treatments included (a) 1.1 kg a.i. hexazinone/ha applied as a granular formulation that was broadcast evenly upon the soil, (b) 1.1 kg a.i. hexazinone/ha applied as 2 ml of liquid that was sprayed in a 2 m×2 m spot-grid on the ground, (c) 2.2 kg a.i. hexazinone/ha applied as 2 ml of liquid that was sprayed in a 2 m×2 m spot-grid upon the soil and (d) control that received no hexazinone. Since liquid hexazinone applied at these rates may not give the desired level of oak reduction during dry periods, treatment was timed so that rainfall occurred within 2 weeks following application, to facilitate efficient uptake by the widely spreading root systems of woody plants. During February 1992, longleaf pine seedlings were planted by hand (2.4 m×2.4 m) on all plots to promote the eventual development of a longleaf pine overstory and recovery of the ecosystem. In June 1995, the entire study site (all plots) was burned with prescribed fire.

Hexazinone (3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5-triazine-2,4(1H,3H)-dione) is one of several herbicides registered for forestry use. [**Pesticide precautionary statement!** *Pesticides can be injurious to humans, domestic and wild animals and desirable plants if they are not handled or applied properly. Use all pesticides selectively and carefully. Follow recommended practices for the disposal of surplus pesticides and pesticide containers*.] It is a triazine herbicide that is absorbed from soil solution by plant roots and distributed through the transpirational stream to its site of action in the chloroplasts (Ashton and Crafts, 1973). There the compound binds to a specific protein and inhibits its ability to mediate electron transport in the Hill reaction (Van Rensen, 1989). This results in a build-up of triplet state chlorophyll which generates singlet oxygen (Dodge, 1982) that peroxidize cell membrane lipids and the affected plant dies from oxidative stress (Balke, 1987; Bartels, 1987). Some species can metabolize the compound before it reaches the chloroplasts (McNeil et al., 1984; Jensen and Kimball, 1990), thereby imparting some degree of tolerance. While blueberries are fairly tolerant (Zutter and Zedaker, 1988), oaks, sweetgum (*Liquidambar styraciflua*) and sumac (*Rhus* spp.) are quite susceptible (Michael, 1980, 1981; Neary et al., 1981; Griswold et al., 1984; Miller, 1984; Zutter and Zedaker, 1988). Hexazinone is highly soluble in water and potentially very mobile in subsurface solution (Neary et al., 1983; Bouchard et al., 1985). Following application of 1.68 kg a.i./ha, off-site movement is minimal and of low toxicity risk to adjacent aquatic ecosystems (Neary et al., 1983), with aquatic macroinvertebrates exhibiting no major changes in community composition (Mayack et al., 1982; Michael et al., 1999). Following application of 2 kg a.i./ha on sandy loam, off-site movement was 2–3% and <0.1% of that applied was returned to the forest floor through defoliation (Michael and Boyer, 1983; Bouchard et al., 1985; Michael, 1985). Persistence in forest soils is relatively brief, with half-lives of 1–6 months in silt loam, 4–6 weeks in clay and <4 weeks in loamy sand (Rhodes, 1980; Sung et al., 1981; Lavy et al., 1989; Michael et al., 1990, 1999).

2.3. Measurements

In May 1991, plant cover was measured on all study plots to ascertain the pre-treatment status of the plant community. Repeated post-treatment measurements were then completed in September 1991–1993 and 1995–1997 to assess the ecological changes resulting from hexazinone application and prescribed fire. Total foliar cover (vertical projection of canopy) of all plant species was measured by line-intercept method along two permanent 20 m line transects (oriented north and south) within each treatment plot. Identification and nomenclature for plant species were consistent with taxonomic authorities (Bell and Taylor, 1982; Wunderlin, 1982; Clewell, 1985; Kurz and Godfrey, 1986; Godfrey, 1988; Foote and Jones, 1989; Grimm and Kartesz, 1993; Hall, 1993).

Foliar cover data for each species were summarized as estimates for each plot and analyzed by treatment and change through time. Foliar cover data were then used as importance values to compute numerous diversity indices (Ludwig and Reynolds, 1988). Species richness (total number of species present) and evenness (how abundance is distributed among species) are the two principal components of diversity. Species richness was characterized on each plot by counting the number of species present (N_0). Evenness (approaching one when all species are of equal abundance and declining toward zero when few species dominate) was determined through calculation of the modified Hill ratio (E_5). Diversity indices combine species richness and evenness into a single numeric value. Species diversity was estimated on all plots using the Shannon diversity index (H').

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 hexazinone and/or fire treatments. For each dependent variable, a comparison of differences among experimental treatments and through the time sequence of repeated measurements was then undertaken. A repeated measures ANOVA, using initial conditions as covariates, was used to evaluate time and treatment effects and interactions (Hintze, 1995). Hexazinone plus fire treatment responses were compared to the fire-only treatment response using a set of three pairwise contrasts. The trend through time after treatment was analyzed using orthogonal polynomials. Statistical analysis of the time and treatment interaction 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 significant differences.

3. Results

3.1. Foliar cover changes

The few residual adult and numerous seedling longleaf pines were unaffected by either the hexazinone application or the prescribed fire treatment (Table 1). Significant increases in the foliar cover of longleaf pine were observed on all treatments, except the 1.1 kg/ha spot application, by 1993 and on all treatments by 1996. Longleaf pine cover progressively expanded on all plots, exceeding 15% on the 1.1 kg/ha broadcast and 2.2 kg/ha spot treatments where the most rapid recovery of this principal overstory component was observed. Following hexazinone application in 1991, the foliar cover of turkey oak declined significantly, with the 1.1 kg/ha spot treatment causing an 82% decrease, the 1.1 kg/ha broadcast treatment causing a 90% decline and the 2.2 kg/ha spot treatment resulting in a 93% decrease. These foliar cover reductions for turkey oak persisted through the 1997 growing season with no evidence of recovery. During the same interval, turkey oak on the fire-only plots continued to expand its dominance, more than doubling its foliar cover. In 1995, the prescribed fire treatment caused a significant decrease in turkey oak cover on the fire-only plots; however, this decline was short-lived as turkey oak quickly recovered in

Table 1
Foliar cover response to hexazinone application and prescribed fire (% cover)

Hexazinone (kg/ha)	0.0	1.1 broadcast	1.1 spot	2.2 spot	Adjusted mean[a]
Longleaf pine					
Spring 1991	1.4	2.0	1.4	1.0	
Fall 1991	1.0	3.0	1.8	1.8	1.9[c]
Fall 1992	1.8	4.5	1.8	4.8	3.2[c]
Fall 1993	10.5	7.9	1.7	6.5	6.7[c]
Fall 1995	10.0	8.9	3.9	8.0	7.7[c]
Fall 1996	10.1	12.1	5.8	14.1	10.5[c]
Fall 1997	12.9	17.4	8.9	15.4	13.6[c]
Adjusted mean[a]	7.7	7.3	4.2	9.8	
Turkey oak					
Spring 1991	5.5	6.2	12.2	13.6	
Fall 1991	5.6	0.6	2.2	0.9	2.3[c]
Fall 1992	5.0	1.0	1.1	1.7	2.2[c]
Fall 1993	10.4	1.6	1.3	2.4	4.0[c]
Fall 1995	7.4	1.4	1.5	1.0	2.8[c]
Fall 1996	9.0	1.7	1.9	3.2	4.0[c]
Fall 1997	12.0	1.3	1.8	2.6	4.4[c]
Adjusted mean	8.6	1.5[b]	1.4[b]	1.6[b]	
All oaks					
Spring 1991	5.6	6.2	12.5	14.0	
Fall 1991	5.7	0.6	2.3	2.1	2.7[c]
Fall 1992	5.1	1.0	1.1	1.8	2.3[c]
Fall 1993	10.6	1.6	1.9	3.6	4.4[c]
Fall 1995	7.4	1.4	1.7	1.2	2.9[c]
Fall 1996	9.1	1.7	2.3	4.4	4.4[c]
Fall 1997	12.2	1.3	2.3	4.3	5.0[c]
Adjusted mean	7.7	0.7[b]	2.4[b]	3.6[b]	
All shrubs					
Spring 1991	4.4	6.6	8.5	11.9	
Fall 1991	4.4	5.4	4.1	3.3	4.3[c]
Fall 1992	5.5	6.3	7.5	3.9	5.8[c]
Fall 1993	7.0	8.4	7.7	5.5	7.2[c]
Fall 1995	1.1	1.3	2.5	0.9	1.5[c]
Fall 1996	3.3	4.5	6.1	3.5	4.4[c]
Fall 1997	5.2	5.8	7.1	3.8	5.5[c]
Adjusted mean	7.1	6.2	5.3	0.3	
All woody plants					
Spring 1991	11.4	14.8	22.3	26.8	
Fall 1991	11.1	9.0	8.6	7.5	9.1[c]
Fall 1992	12.5	11.8	11.0	12.1	11.8[c]
Fall 1993	28.0	18.8	13.5	16.3	19.1[c]
Fall 1995	18.6	11.5	11.2	10.1	12.8[c]
Fall 1996	22.5	18.3	18.6	21.9	20.3[c]
Fall 1997	30.3	24.5	23.1	23.6	25.3[c]
Adjusted mean	15.5	13.0	16.7	20.5	
Wiregrass					
Spring 1991	54.9	48.5	44.0	36.1	
Fall 1991	64.7	58.6	56.3	56.1	58.9[c]

Table 1 (*Continued*)

Hexazinone (kg/ha)	0.0	1.1 broadcast	1.1 spot	2.2 spot	Adjusted mean[a]
Fall 1992	65.3	64.8	59.5	62.9	63.1[c]
Fall 1993	67.4	68.5	62.9	67.1	66.5[c]
Fall 1995	41.3	41.9	39.1	42.3	41.2[c]
Fall 1996	60.2	61.1	55.3	56.3	58.3[c]
Fall 1997	67.2	71.6	64.0	70.5	68.3[c]
Adjusted mean	64.7	62.1	55.4	55.2	
All graminoids					
Spring 1991	58.8	54.8	50.4	51.0	
Fall 1991	68.0	67.2	64.1	65.6	66.2[c]
Fall 1992	69.6	72.5	73.5	76.1	72.9[c]
Fall 1993	72.7	74.0	74.5	75.7	74.2[c]
Fall 1995	45.1	47.3	47.5	48.8	47.2[c]
Fall 1996	68.0	72.0	72.2	70.4	70.7[c]
Fall 1997	75.6	82.4	82.5	84.7	81.3[c]
Adjusted mean	63.7	68.7	70.9	71.7	
All forbs					
Spring 1991	4.5	7.2	5.0	3.0	
Fall 1991	7.3	3.2	8.5	5.3	6.1[c]
Fall 1992	9.3	12.8	10.0	9.1	10.3[c]
Fall 1993	7.4	14.8	10.8	10.1	10.8[c]
Fall 1995	3.4	3.7	3.2	3.0	3.4[c]
Fall 1996	11.6	20.3	10.9	16.1	14.7[c]
Fall 1997	7.8	14.7	12.4	15.0	12.5[c]
Adjusted mean	6.5	17.9[b]	9.6	4.5	

[a] Post-treatment mean adjusted by analysis of covariance.

[b] Significantly different from control (fire-only) plots, $p \leq 0.05$.

[c] Significant change through time from pre-treatment condition, $p \leq 0.05$.

1996 and continued its expansion through the 1997 growing season. A quite similar pattern was observed for all oak species combined. Hexazinone application significantly reduced the foliar cover of all oaks. On the fire-only plots, oak cover declined following prescribed burning, but then quickly recovered and, within 3 years, increased to levels exceeding the pre-treatment condition. The effect of hexazinone treatment on shrubs was less consistent, with only the 2.2 kg/ha application rate producing a significant decrease in shrub cover that lasted through the 1997 growing season. In 1995, prescribed fire caused a temporary significant decline in shrub cover on all plots. However in all cases, shrubs recovered rapidly during 1996 to pre-fire levels by 1997. Hexazinone application diminished the overall cover of woody plants from 1991 to 1993, by curtailing the rapid increase of oaks. Fire treatment in 1995 temporarily contributed to oak control on all plots. Although the foliar cover of woody plants recovered from prescribed burning by 1997, on hexazinone treated plots this resulted largely from the emergence of longleaf pine, while on fire-only plots it was due to the rapid expansion of oaks in combination with longleaf pine.

From 1991 to 1993, the foliar cover of wiregrass increased following hexazinone application at all rates (Table 1). Wiregrass cover expanded 23% on the fire-only plots, 41% on the 1.1 kg/ha broadcast treatment, 43% on the 1.1 kg/ha spot treated plots and 86% on the 2.2 kg/ha spot treatment. In 1995, prescribed fire caused significant decreases on all plots, but wiregrass recovered rapidly during 1996 to reach its greatest coverage in 1997. Although wiregrass cover increased over time more rapidly on hexazinone treated plots than on fire-only plots, when adjusted for initial conditions these differences were not significant and thus largely time driven ($p \leq 0.05$). While wiregrass cover in 1997 was nearly comparable among all treatments, ranging from 64 to nearly 72% foliar cover, the largest overall increase (95%) was observed for the 2.2 kg/ha application. The smallest increase in wiregrass cover occurred on the fire-only plots (22%) where expansion of oak canopies continued.

The foliar cover response pattern for all graminoids combined closely corresponds to that for wiregrass (Table 1). Significant linear increases in cover occurred over time; however, no significant differences among hexazinone treatments were noted. Following hexazinone application and prescribed fire treatment, graminoids expanded into available growing spaces adjacent to and beneath the skeletal crowns of dead trees and shrubs.

During the 1991 growing season, the 1.1 kg/ha broadcast application resulted in a significant (56%) decline in the foliar cover of forbs (Table 1). However, forb cover recovered during 1992 and was significantly greater than all other treatments by 1993. Forb cover was uniformly reduced on all plots to <4% by prescribed fire during 1995. Then in 1996, forb cover on the 1.1 kg/ha broadcast treatment once again became significantly greater than on all other treatments, exceeding 20% cover. By 1997, no significant differences among treatments were detectable. A significant trend of overall progressive increases in the foliar cover of forbs through time was observed on all treatments. Both the broadcast application of hexazinone and the prescribed fire treatment temporarily impeded forb expansion.

3.2. Plant diversity dynamics

A total of 95 plant species were counted on the Riverside Island study site. With few tree species present in this plant community, turkey oak dominated both overstory and understory prior to hexazinone application in 1991. Following application, no tree species was dominant in the overstory. By 1997, many of the longleaf pine seedlings planted during the winter of 1992 had emerged from their 'grass stage' and were positioned to eventually form the new overstory in the absence of substantial competition from the declining oaks. Although there was a moderate number of shrubs on the site, turkey oak sprouts initially dominated this layer. Following hexazinone application and fire treatment, the most prominent shrubs included rosemary, crookedwood, shiny blueberry and gopherapple. Among the variety of graminoids, *Aristida*, *Sporobolus* and *Andropogon* were most abundant, with yellow nutsedge, panic grass and sandgrass well represented on some portions of the site. Forbs were present in great variety, but typically persisted at low levels, approximating 5% cover, prior to treatment.

Species richness (N_0) was generally unaffected by hexazinone application rate (Table 2). However in 1991, the 1.1 kg/ha broadcast application caused a significant 28% decline in richness, from 18 to 13 species, during the initial post-treatment growing

Table 2
Plant species richness, diversity and evenness responses to hexazinone application and prescribed fire

Hexazinone (kg/ha)	0.0	1.1 broadcast	1.1 spot	2.2 spot
Number of species				
Spring 1991	15.0	18.2	16.0	17.0
Fall 1991	17.4	13.2[a,b]	19.6	17.6
Fall 1992	18.4	17.6	20.8	21.6
Fall 1993	17.8	18.2	20.4	21.2
Fall 1995	16.0	14.4[b]	17.2	16.6
Fall 1996	22.0[c]	21.6[c]	23.6[c]	24.8[c]
Fall 1997	20.6[c]	20.0[c]	20.8	25.0[c]
Shannon index				
Spring 1991	1.11	1.49	1.51	1.51
Fall 1991	1.03	0.99	1.29	1.20
Fall 1992	1.23	1.37	1.53	1.44
Fall 1993	1.33	1.39	1.47	1.43
Fall 1995	1.19	1.17	1.45	1.08
Fall 1996	1.55[c]	1.63	1.80	1.77[c]
Fall 1997	1.44[c]	1.51	1.76	1.66[c]
Modified Hill ratio				
Spring 1991	0.40	0.45	0.52	0.60
Fall 1991	0.39	0.46	0.41	0.39[b]
Fall 1992	0.38	0.44	0.42	0.40[b]
Fall 1993	0.47	0.46	0.43	0.39[b]
Fall 1995	0.56[c]	0.52	0.46	0.45[b]
Fall 1996	0.46	0.49	0.45	0.48[b]
Fall 1997	0.48	0.50	0.48	0.43[b]

[a] Significantly different from control (fire-only) plots, $p \leq 0.05$.

[b] Significant decrease through time from pre-treatment condition, $p \leq 0.05$.

[c] Significant increase through time from pre-treatment condition, $p \leq 0.05$.

season. By 1992, plant species richness fully recovered on the broadcast application plots and continued to increase on the spot treated plots, exceeding the 20 species present. In 1995, prescribed fire caused a decline in species richness on all plots, but this decrease was significant only for the 1.1 kg/ha broadcast application. By 1996, species richness recovered on all plots, reaching its highest values. In 1997, plots receiving the 2.2 kg/ha spot application followed by prescribed fire contained as many as 25 species, while those treated with fire-only typically supported about 20.

All hexazinone application rates resulted in non-significant declines in plant diversity during the first post-treatment growing season (Table 2). The largest of these was a decrease in the Shannon diversity index (H'), from 1.49 to 0.99, for the 1.1 kg/ha broadcast application. Alpha diversity declines for the spot applications were typically from 1.51 to 1.25. Diversity values on broadcast treated plots were comparable to those on untreated control plots, while those on spot treated plots were somewhat higher. During 1992 and 1993, species diversity recovered on all plots, approaching values averaging 1.40. In 1995, prescribed fire produced non-significant declines in diversity for all treatments, followed by abrupt increases in 1996 that continued through 1997. Plant diversity increases in 1996 and 1997 were significant only for the 2.2 kg/ha spot treatment and the fire-only treatment.

Only the 2.2 kg/ha spot application of hexazinone significantly affected plant species evenness during the first and all subsequent growing seasons through 1997 (Table 2). The high mortality rate among oaks and great increase in the cover of wiregrass associated with this treatment likely account for this sustained decrease in the modified Hill ratio (E_5) from 0.60 in 1991 to 0.43 by 1997. All other treatments appear to have little influence upon species evenness, except for the fire-only treatment. On these plots, plant species evenness significantly increased from the 1993 level of 0.47 to 0.56 in 1995 and then returned to a pre-fire level of 0.46 in 1996. This temporary increase appears related to a significant decline in shrub cover on fire-only plots during 1995, thus providing a brief season of greater equity in species distribution prior to the resumption of vigorous growth by woody plants in 1996.

4. Discussion

4.1. Effects on foliar cover

Neither hexazinone nor fire adversely affected the relatively rapid increase of longleaf pine. With exception of the 1.1 kg/ha spot application, longleaf pine cover was generally greater on plots treated with hexazinone plus fire than on the fire-only plots. Although studies elsewhere report that longleaf pine is subject to injury by growing-season fire (Boyer, 1990a, b), the progressive increase in longleaf pine cover on this study site suggests that such was not the case here. While not specifically measured, the growth losses attributed to prescribed fire treatment in earlier studies (Cary, 1932; Garren, 1943; Boyer, 1987, 1994; Landers et al., 1995) were not apparent on this site.

Hexazinone application on this xeric sandhills site greatly reduced the foliar cover of turkey oak and other oaks that had begun to dominate the longleaf pine wiregrass ecosystem. Similar results have been reported for higher-rate hexazinone applications ($\leq$6.8 kg/ha) on sandhills (Wilkins et al., 1993a) and lower-rate applications (0.3, 0.6 and 0.9 kg/ha) on well-drained uplands (Long and Flinchum, 1992). Initial turkey oak mortality rates, ranging from 82 to 93%, indicate that hexazinone application may be useful in selectively shifting the balance of competition for site resources to favor desirable plant species in the understory and overstory (Wilkins et al., 1993b; Brockway et al., 1998). Although shrub cover was initially decreased only by the spot applications, the overall early decline of woody plants appeared to have created opportunity for expansion of plants already occupying the site and liberated microsites where additional species might colonize.

While prescribed fire on the fire-only treatment did produce a pronounced decrease in oaks similar to that reported elsewhere (Rebertus et al., 1989a, b; Glitzenstein et al., 1995), the foliar cover of oaks rapidly increased in subsequent years, indicating that this brief decline would be short-lived. This result concurs with reports concerning the relatively minor effects of a single fire event in sandhills and similar environments (Abrahamson and Abrahamson, 1996a, b; Liu et al., 1997). Prescribed fire also caused a widespread decrease in shrub and woody plant cover, similar to that reported in previous studies (Moore et al., 1982;

Abrahamson and Hartnett, 1990; Haywood et al., 1995; Brockway and Lewis, 1997). However, the rapid recovery of these woody components indicates that the overall effect of fire by itself was ephemeral. Prescribed burning of hexazinone treated plots 4 years following application provided no additional benefit in oak control. This attests to the effectiveness of hexazinone application as a restoration technique for adjusting ecosystem composition and structure, which can then be maintained over the long-term with periodic prescribed fire.

The progressive expansion of wiregrass and all graminoids was unimpaired by either the hexazinone application rate or method, with an observable trend of steadily increasing cover through time. Although grass cover universally declined following the 1995 prescribed fire, recovery was rapid during the ensuing growing seasons, as wiregrass is known to respond relatively quickly to increased availability of site resources (Parrott, 1967). These results generally concur with earlier studies showing the beneficial effects of hexazinone application on wiregrass and other grasses (Bush et al., 1990; Outcalt, 1992, 1993, 1994a, 1995). Even though prescribed fire temporarily reduced graminoid cover, its overall benefit to grasses is well known (Garren, 1943; Moore et al., 1982; Wright and Bailey, 1982; Wade and Lewis, 1987; Landers et al., 1990; Outcalt, 1994b). Unlike less fire-tolerant plants, grasses typically (1) maintain substantial nutrient stores in extensive below ground root systems, (2) have their leaf meristems at least 4 cm below the ground surface and (3) produce and disseminate abundant reproductive bodies (Lemon, 1949). These characteristics allow them to rebound quickly following a fire and even expand their occupancy of the site. Repeated fires accentuate the prominence of grasses in the plant community (Lewis, 1964; Hilmon and Hughes, 1965; Stoin, 1979; Abrahamson and Hartnett, 1990; Waldrop et al., 1992; Brockway and Lewis, 1997).

Although hexazinone application rate did not influence the foliar cover of forbs, the application method produced a pronounced differential effect on these understory plants. During the first post-treatment growing season, broadcast application of hexazinone adversely affected forb cover, causing a 56% decline. The broadcast method distributes granules of hexazinone evenly upon the ground across the entire plot. This places nearly all plants growing on the plot in direct physical contact with hexazinone, thus a higher probability of assimilation and mortality (Brockway et al., 1998). However, forbs quickly recovered during the following year and were significantly greater here than on all other treatments by 1993, reaching nearly 15% cover. Thus, hexazinone applied by the broadcast method appears to initially depress and subsequently stimulate the growth of forbs. By contrast, the spot application method deposits a small dose of liquid on the soil surface in a 2 m×2 m grid pattern, thus creating numerous large interstitial zones that are free of hexazinone. As the crowns and root systems of forbs are typically not widely spreading, the probability of any individual plant being directly ‘hit’ by a spot is quite low, thus most understory species escaped the effects of this type of herbicide treatment. The overall danger to understory plants when using the spot application technique is lower, yet the mortality of targeted overstory species, because of their widely spreading root systems, is at least as great as that resulting from the broadcast application method (Brockway et al., 1998).

Although growing-season fire universally depressed forb cover in 1995 to <4%, forbs rapidly recovered during the next growing season, reaching levels as high as 15 and 20%. This dynamic trend generally concurs with other studies, which document an initial decrease in forbs immediately after prescribed fire (Haywood et al., 1995) followed by increases over time (Moore et al., 1982; Brockway and Lewis, 1997). Forbs are widely reported to benefit from recurrent fire in southern pine ecosystems (Hilmon and Hughes, 1965; Wright and Bailey, 1982; Lewis et al., 1988; Platt et al., 1988b; Abrahamson and Hartnett, 1990; Waldrop et al., 1992). Thus, while prescribed fire and herbicide application temporarily reduce forb cover in the short-term, these disturbances actually benefit forbs over the long-term by reducing competition from woody plants (principally oaks and shrubs) and providing microsites for colonization.

4.2. Influence on plant diversity

Hexazinone treatment caused significant decreases in plant species richness only on plots receiving the broadcast application. This initial decline in species richness was a result of the broadcast method bringing hexazinone into close physical contact with nearly all plants and can be largely attributed to decreases in the cover of turkey oak and several forbs. Richness then recovered in the following year to pre-treatment levels. The number of species on spot treated plots was unaffected by the less uniform distribution of hexazinone which impacted fewer understory plants here than on broadcast treated plots (Brockway et al., 1998). These findings concur with reports of plant species numbers being unchanged or slightly higher during the second and subsequent growing seasons following herbicide application (Blake et al., 1987). Species richness showed an overall linear increase through time for all treatments, until prescribed fire produced universal declines in the number of species during 1995. Of these, the only significant decrease was again noted on the broadcast treated plots. The recovery of richness following both hexazinone application and prescribed fire treatments was largely related to a resurgence of forb species during subsequent growing seasons. This positive response by forbs is unlike that reported on other xeric sandhills where higher hexazinone application rates resulted in declining herbaceous plant diversity (Wilkins et al., 1993b).

Nonsignificant decreases in plant species diversity were observed for all hexazinone treatments in the initial growing season after application, followed by recovery to pre-treatment levels during the next year. This response pattern is similar to that reported for single applications of herbicide used for site preparation, where initial depression of diversity is followed by recovery along a trajectory similar to that of an untreated site (Neary, 1991). While the reduction in diversity on the broadcast treated plots resulted from lower levels of species richness, the decline on the spot treated plots was largely attributed to decreases in evenness among plant species. Decreased plant species evenness resulted from the increasing dominance of wiregrass following the reduction of turkey oak. In 1995, prescribed fire produced minor declines in diversity and left evenness unaffected on all except the fire-only plots. On these, evenness was temporarily increased when shrubs were substantially reduced by fire, but returned to pre-treatment levels shortly thereafter. This short-lived increase in evenness indicated that the fewer remaining species were more equitably distributed across the site. Increases in species diversity during subsequent growing seasons were largely a product of increasing species richness, mostly from increasing forbs and grasses.

Sandhills have been characterized as ecosystems dominated by scrub vegetation of low species diversity, whose structure and function reflect adaptations for survival in an environment characterized by seasonal water deficits, periodic fires and low soil fertility (Snedaker and Lugo, 1972). However, the presence of 95 plant species on this site is typical of the high vascular plant diversity of longleaf pine ecosystems (Peet and Allard, 1993). Plant species diversity is largely determined by interspecific competition interacting with site productivity, microsite heterogeneity and disturbance regimes (Tilman, 1982). Hexazinone, by causing selective mortality among different groups of plants, altered the competitive relationships among species and thus influenced plant diversity dynamics. Herbaceous plant diversity is reported to initially increase and subsequently decline to predisturbance levels on sites disturbed by prescribed fire, tree harvest or site preparation (Swindel et al., 1984; Lewis et al., 1988). Fire typically creates a diverse understory with high numbers of grasses, legumes and forbs (Waldrop et al., 1992) 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 (Biswell and Lemon, 1943; Platt et al., 1988b; Landers et al., 1990; Streng et al., 1993; Outcalt, 1994b).

4.3. Restoring the ecosystem with hexazinone and fire

The close association of longleaf pine wiregrass ecosystems with periodic fire has been long recognized (Cary, 1932; Garren, 1943; Bruce, 1947; Komarek, 1968; Taylor, 1974; Veno, 1976; Christensen, 1981; Wright and Bailey, 1982; Abrahamson, 1984) and the need for frequent growing season fire to restore and sustain a wide range of resource values has been recently advocated (Noss, 1989; Rebertus et al., 1989b; Landers et al., 1990, 1995; Wade and Lundsford, 1990; Streng et al., 1993). 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). Indeed, the longleaf pine wiregrass ecosystem is ideally structured for transmuting a local disturbance (lightning) into a widespread disturbance (ground fires), thus creating conditions suitable for its own regeneration and perpetuation (Platt et al., 1988a). The pattern of diversity in this ecosystem is largely a product of such natural periodic disturbance.

Prescribed fire is perhaps the most frequently suggested restoration method, because periodic fire is an essential ecological process for maintaining longleaf pine wiregrass ecosystems. However, on degraded longleaf pine wiregrass sites, treatments such as selective herbicide application, planting seedlings or mechanical removal of competing vegetation may be required to achieve more prompt ecosystem restoration than could be obtained by using fire alone. Also, on sites where the fuels present are insufficient to carry a prescribed fire or too heavy to burn without risking destruction of desirable species or social constraints preclude the use of fire, hexazinone application may serve as a useful option. Hexazinone application provides the added benefit of time efficiency to longleaf pine wiregrass restoration efforts. In using fire alone, at least three biennial spring burns are required to significantly reduce oaks on sandhills sites (Glitzenstein et al., 1995). Many cycles of prescribed fire, over a period of several decades, may be required to attain an oak mortality rate >80% and a corresponding increase in desirable understory plants. A single low-rate hexazinone application achieves this objective in a very brief period, thereby greatly shortening the time required for ecological restoration. Longleaf pine wiregrass ecosystems thus restored can then be more quickly scheduled for subsequent maintenance treatments using prescribed fire at appropriate time intervals.

5. Conclusion

During the 7 years following treatment, single applications of hexazinone followed by prescribed fire produced substantial changes in a longleaf pine wiregrass ecosystem that had become dominated by turkey oak after a wildfire. All hexazinone applications caused significant declines in the foliar cover of turkey oak and other oaks in the first growing season that continued through the seventh year. The continuing expansion of longleaf pine cover, a prelude to development of the restored overstory, appeared unaffected by hexazinone application or prescribed burning. The resulting decrease in interspecific competition from oaks and shrubs produced progressive increases in the foliar cover of wiregrass, other graminoids and forb species through time. Significant increases in species richness were noted for all treatments by the fifth growing season, however, significant increases in plant diversity were observed only on plots receiving the 2.2 kg/ha spot application plus prescribed fire and those treated with fire-only. The sustained decrease in plant species evenness for the 2.2 kg/ha spot application plus prescribed fire treatment resulted from an early rapid decline in oaks followed by the continuing expansion of wiregrass. Prescribed fire caused a temporary decline in the cover of turkey oak, all oaks, shrubs, woody plants, wiregrass, all graminoids and forbs; however, each of these quickly recovered during the following growing season. Oaks dominated the fire-only plots prior to burning and continued their dominance following prescribed fire, with their foliar cover increasing rapidly over time.

Only on plots receiving the 1.1 kg/ha broadcast application were early short-term decreases in forb cover and species richness measured. Although these recovered in subsequent years, broadcast application seems to be a less desirable restoration method because hexazinone pellets are widely distributed on the soil, bringing the roots of nearly all understory plants into close proximity with herbicide. Therefore, the mortality risk to non-target plant species is higher. While both spot applications of hexazinone produced significant declines in oaks which led to increases in herbaceous plants, the 1.1 kg/ha treatment was not as effective in controlling competing shrubs. The 2.2 kg/ha spot treatment in combination with prescribed fire provided the highest degree of control for oaks and other competing woody vegetation and the greatest overall gains in wiregrass, all graminoids, forbs, species richness and plant diversity. A single prescribed fire treatment does not as effectively control competing oaks, shrubs and other woody plants. Within 7 years of treatment, areas receiving a 2.2 kg/ha spot application of hexazinone followed by prescribed fire were characterized by a prominent understory of wiregrass and a visibly emerging overstory of longleaf pine (Fig. 1), while those treated with fire-only were

Fig. 1. Scarce oak and prominent longleaf pine and wiregrass after sequence of hexazinone application followed by prescribed fire treatment.

Fig. 2. Continuing oak dominance following prescribed fire-only treatment.

still dominated by an expanding overstory of turkey oak (Fig. 2). Therefore, the 2.2 kg/ha spot application of hexazinone in combination with prescribed fire appears to be the most expedient treatment for restoration of degraded longleaf pine wiregrass ecosystems in xeric sandhills and similar environments. However, considering the wide array of site history, hydrology, soil and vegetation variables present throughout the greater longleaf pine wiregrass ecosystem, it seems inappropriate to identify a single universally applicable restoration prescription to cover all circumstances. For example, applications of liquid hexazinone are less reliable than granular formulations for oak control in areas prone to extended spring droughts and uncertain rainfall. Ultimately, the decision to use any one or a combination of physical, chemical and biological techniques to ecologically restore an ecosystem upon a specific site is best left to the land manager, who must consider social and economic imperatives in addition to ecological factors.

6. Commercial products disclaimer

The use of trade or firm names in this publication is for reader information and does not imply endorsement by the US Department of Agriculture of any product or service.

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