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Restoring longleaf pine wiregrass ecosystems: plant cover, diversity and biomass following low-rate hexazinone application on Florida sandhills

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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 low-rate (1.1 or 2.2 kg/ha) applications of the herbicide hexazinone during the 1991 growing season. All applications successfully reduced oak in the overstory and understory, mortality ranging from 83 to 93%. The declining competition from oaks was associated with progressive increases in foliar cover of wiregrass, all graminoids and forbs over time. Plant species diversity declined in the initial year, but recovered by the second growing season. Species richness increased overall, while evenness declined with the continuing expansion of wiregrass. Initial increases in the standing biomass of wiregrass did not persist beyond the second growing season. The broadcast application method exposed a greater number of understory plants to contact with hexazinone, resulting in initial declines in forb cover, species richness and diversity. Although recovery was noted in subsequent years, because of lower selectivity this broadcast application method is not recommended as a restoration technique. Spot application of liquid hexazinone was generally more selective in its effect upon the plant community. The 1.1 and 2.2 kg/ha application rates, while producing an initial year reduction in diversity and evenness, resulted in increases in the cover of all graminoids and forbs and the highest species richness. While both application rates are useful, the 2.2 kg/ha application is most effective in controlling woody plant competition and stimulating increases in wiregrass and is therefore recommended for restoring xeric sandhills and similar longleaf pine wiregrass ecosystems. © 1998 Elsevier Science B.V.

Keywords: *Pinus palustris* Mill.; *Aristida stricta* Michx.; *Quercus laevis* Walt.; *Sporobolus curtissii* (Vasey) Small ex. Scribn.; *Andropogon virginicus* L.; Herbicide

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1. Introduction

Longleaf pine (*Pinus palustris*) forests became established in northern Florida about 7800 yr ago (Watts et al., 1992) and during the ensuing 4000 yr spread throughout the southeast (Delcourt and Delcourt, 1987). The native range of longleaf pine encompasses an 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, 1990). In the western Gulf Coastal Plain, longleaf pine understories are commonly dominated by bluestem grasses (*Andropogon* spp. and *Schizachyrium* spp.) and, from Florida eastward, longleaf pine is typically associated with wiregrass (*Aristida stricta*), otherwise known as pineland threeawn, 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). The plant communities contain few shrubs or hardwood trees, because of the attributes of understory grasses that facilitates the ignition and spread of fire during the growing season (Landers, 1991). In these ecosystems, longleaf pine and bunchgrasses function together as keystone species that facilitate but are resistant to fire (Platt et al., 1988; Noss, 1989). They 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).

Longleaf pines rarely achieve their biological potential of 500 yr, because the longleaf pine wiregrass ecosystem evolved in an environment influenced by catastrophic disturbance, such as damaging tropical storms. Lightning is an important agent in individual tree mortality and the creation of small scale disturbance in longleaf pine stands (Komarek, 1968; Taylor, 1974). 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, soils 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 resulting high diversity of understory plants per unit area makes this one of the most species-rich plant communities outside the tropics (Peet and Allard, 1993).

Longleaf pine forests were at one time among the most extensive ecosystems in North America (Landers et al., 1995). These forests occupied over 37 million ha in the southeastern United States prior to European settlement (Frost, 1993). Since then, this ecosystem has undergone a progressive decline in occurrence 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 less than 1.2 million ha. Several factors are responsible for this long-term decline, including clearing land for crops and pasture (Ewel, 1990) and conversion of longleaf pine forests to other southern pines such as loblolly pine (*Pinus taeda*) and slash pine (*Pinus elliottii*). Another major factor contributing to this decline has been interruption of natural fire regimes, resulting from forest fire protection policies implemented during the 1920s. This interruption 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*). Area reductions are continuing for stands in every diameter class below 41 cm (Kelly and Bechtold, 1990), therefore, most remaining longleaf pine forests appear to be aging without replacement. With this ecosystem now occupying only about 4% of its original extent, habitat reduction has resulted in the increased rarity of 191 taxa of vascular plants (Hardin and White, 1989; Walker, 1993) and several terrestrial vertebrate species.

Concern about loss of these unique forests (Means and Grow, 1985; Noss et al., 1995) has stimulated discussion regarding how to effectively restore the longleaf pine wiregrass ecosystem. 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 (Landers et al., 1995). 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 (Frost, 1990; Streng et al., 1993). Natural regeneration methods employing a regime of frequent fire are compatible with maintenance of the longleaf pine wiregrass ecosystem (Boyer and White, 1990). 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; Outcalt and Brockway, 1993; Brockway and Outcalt, 1994).

Longleaf pine wiregrass ecosystems in xeric sandhills, commonly referred to as 'high pine land,' grow on deep coarse textured soils with limited available water and nutrients (Kalisz and Stone, 1984; Myers, 1990). In central Florida, much of this type has been converted to citrus groves (Myers and White, 1987; Ewel, 1990), and elsewhere, pine cutting has left much of the area occupied by turkey oak (*Quercus laevis*) and related scrub oaks (Bums and Hebb, 1972; Myers and White, 1987). Harvest of longleaf pine timber and fire suppression have also encouraged invasion by sand pine and associated scrub oaks (Myers, 1990). The sandhills component of the longleaf pine wiregrass ecosystem is regarded by many as an endangered community (Means and Grow, 1985). The remaining longleaf pine wiregrass sites in the sandhills typically occur as 'pine islands' (Rawlings, 1933; Laessle, 1958) surrounded by a landscape dominated by sand pine forests or lands converted to agriculture and urban development (Kalisz and Stone, 1984; Myers, 1990). Many of these islands contain degraded longleaf pine wiregrass lands currently occupied by oaks and could benefit substantially from restoration treatments.

A degraded longleaf pine wiregrass ecosystem, that had been invaded by turkey oak and scrub oaks following timber harvest and wildfire in the sandhills of north central Florida, was treated with low-rates of hexazinone. In measuring the post-treatment changes in vascular plant cover, diversity and productivity over several 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) Quantify differential effects resulting from the methods of hexazinone application, and (4) Determine whether low-rate application of hexazinone can serve as a viable treatment for 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 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°C to 28°C for the April to October period and from 14°C to 19°C for November to March (NOAA, 1930–1985).

The study area is approximately 49 m above sea level in a sandhill landscape with rolling topography, devoid of surface drainages and characterized by closed depressions. Surface slopes at the study site range from nearly level (0 to 2%) to moderately inclined (up to 8%). The surface geology is underlain by a bedrock of Ocala Limestone, a relatively pure calcium carbonate deposit dating to the Eocene, approximately 40,000,000 yr old (Brooks, 1972). This limestone, also known as the Crystal River Forma-

tion, is largely responsible for the karst nature of the locale, forming numerous sinkholes and large springs (Brown et al., 1990). Above this limestone is the Citronelle Formation (Laessle, 1958), which occurs continuously throughout the central ridge of Florida over a distance of 240 km (Pirkle et al., 1963). The Citronelle Formation is composed of sand and gravel intermixed with clay (Brooks, 1972). Over this formation are aeolian dunes which developed during periods of climate and sea level fluctuation in the Pleistocene (Kalisz and Stone, 1984). Lands higher than 30 m above mean sea level remained above the ocean surface during the entire Pleistocene (Ah and Brooks, 1965).

Surface deposits are dominated by sands 2 to 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 inter-layered 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). The terms 'wet desert' and 'desert in the rain' are commonly used to describe this environment since, while precipitation is abundant, this soil can become extremely dry within one 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 and White, 1987; Myers, 1990). Evidence suggests that these have been the two principal ecosystems in this locale for the past 5000 yr (Watts, 1971; Watts and Hansen, 1988). However, the degraded nature of the study site was reflected in the absence of longleaf pine and predominance of turkey oak 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 indiagrass (*Sorghastrum secundum*), panic grass (*Panicum* spp.), sandgrass (*Triplasis* spp.) and yellow nutsedge (*Cyperus recurvata*) were among the prominent graminoids. Forbs commonly observed included partridge-pea (*Cassia chamaecrista*), treadssoftly (*Cnidoscopus stimulosus*), doveweed (*Crotan argyranthemus*), buckwheat (*Eriogonum tomentosum*), dogfennel (*Eupatorium compositifolium*), milkpea (*Galactia* spp.), St. Johnswort (*Hypericum* spp.), wild indigo (*Indigofera caroliniana*), silverthread goldaster (*Pityopsis graminifolia*), 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. The numerous oaks present vigorously resprouted and, in the absence of a longleaf pine overstory, quickly gained dominance on this site. It was soon obvious that this longleaf pine site would be lost to rapidly growing turkey oak.

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 a 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 a liquid that was sprayed in a 2 m X 2 m spot-grid upon the soil and (d) control that received no hexazinone. Since liquid hexazinone applied at these low rates may not give the desired level of oak reduction during dry periods, treatment was timed so that rainfall occurred within two weeks following application, to facilitate efficient uptake by the widely spreading root systems of woody plants. In February 1992, longleaf pine seedlings were planted by hand on the site to promote the eventual development of a longleaf pine overstory and recovery of the ecosystem.

Hexazinone [3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5-triazine-2,4(1*H*,3*H*)-dione] is one of several herbicides currently registered for forestry use in the United States and is commercially available as Velpar ULW™, Velpar L™ (E.I. Du Pont De Nemours) and Pronone 10G™ (Pro-Serve). Recommended application rates for site preparation range from 2.0 to 6.7 kg hexazinone/ha (E.I. Du Pont De Nemours). Rates used in our study are quite low and similar to those used to restore understory plants elsewhere in xeric sandhills (Wilkins et al., 1993b). These are characterized as trial rates for selective uses (Beste, 1983).

Hexazinone 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, the Hill reaction (Van Rensen, 1989). This results in a build-up of triplet state chlorophyll which generates singlet oxygen (Dodge, 1982). Singlet oxygen peroxidizes cell membrane lipids and the affected plant dies from oxidative stress (Balke, 1987; Bartels, 1987). Some species have greater abilities to metabolize the compound before it reaches the site of action (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 to hexazinone (Neary et al., 1981; Gniswold et al., 1984; Miller, 1984; Zutter and Zedaker, 1988).

Hexazinone is highly soluble in water (33,000 ppmw at 25°C) and is potentially very mobile in

subsurface solution (Neary et al., 1983; Bouchard et al., 1985). Following applications of 1.68 kg a.i./ha, off-site movement of hexazinone has been observed to be minimal and of low toxicity risk to adjacent aquatic ecosystems (Neary et al., 1983). Aquatic macroinvertebrates did not exhibit major changes in community composition (Mayack et al., 1982). Following hexazinone applications of 2 kg/ha on sandy loam sites in Arkansas, off-site movement was 2–3% and < 0.1% of that applied was returned to the forest floor upon oak defoliation (Bouchard et al., 1985). Persistence in forest soils is relatively short-lived (Lavy et al., 1989). Half-lives of hexazinone in silt loam soils in Delaware, Illinois and Mississippi have been reported at 1, 2 and 6 months, respectively (Rhodes, 1980). In Alabama, half-lives were 4–6 weeks in clay soil and < 4 weeks in loamy sand (Sung et al., 1981).

2.3. Measurements

In May 1991, plant cover and biomass were measured on all plots to assess the pretreatment status of the plant community. Repeated post-treatment measurements were then completed in September 1991, 1992 and 1993 to ascertain the ecological changes resulting from hexazinone application. 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 (Fernald, 1950; Gleason, 1952; Hitchcock, 1971; Duncan and Foote, 1975; Bell and Taylor, 1982; Wunderlin, 1982; Clewell, 1985; Kurz and Godfrey, 1986; Godfrey, 1988; Foote and Jones, 1989; Grimm and Kartesz, 1993; Hall, 1993). Wiregrass biomass was measured on two randomly selected 1 m X 1 m (1 m²) sampling subplots within the larger treatment plots. The standing biomass of all wiregrass was destructively sampled by clipping at the groundline and placing samples in paper bags.

All wiregrass samples were sorted into living (green) and nonliving (brown) components, dried to a constant mass in a force draft oven at 85°C for 24 h and weighed. These data were then used to construct productivity estimates for wiregrass relative to

hexazinone treatment. Data on the foliar cover of each species were summarized as estimates for each plot and analyzed by hexazinone treatment and change over time. Foliar cover data were 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 is frequently characterized by the number of species present (N_0), abundant species (N_1), very abundant species (N_2), Margalef species richness (R_1) and Menhinick species richness (R_2). Evenness (approaching one when all species are of equal abundance and declining toward zero when few species dominate) can be described by the evenness index of Pielou (E_1), evenness index of Sheldon (E_2), evenness index of Heip (E_3), evenness index of Hill (E_4) and the modified ratio of Hill (E_5). Diversity indices combine species richness and evenness components into a single numeric value. The most commonly used indices of diversity are the diversity index of Shannon (H') and the diversity index of Simpson (A).

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 hexazinone treatments. For each dependent variable, a comparison of differences among experimental treatments and over 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. Treated responses were compared to the untreated response using a set of three pairwise contrasts. The trend over time after treatment was analyzed using orthogonal polynomials. Because initial conditions were not significantly correlated to the post-treatment response of woody plants, an analysis of the time and treatment interaction was substituted for the analysis of covariance. 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). Except otherwise noted, a probability level of 0.05 was used to discern significant differences reported.

3. Results

3.1. Foliar cover changes

The foliar cover of turkey oak declined dramatically during the 1991 growing season following hexazinone treatment (Fig. 1). The broadcast and liquid spot 1.1 kg/ha applications caused an average 83% decrease in turkey oak cover and the liquid spot 2.2 kg/ha treatment resulted in a 92% decline (Table 1). These foliar cover reductions for turkey oak persisted throughout the 1992 and 1993 growing seasons without evidence of any significant recovery relative to the control. During this same period, turkey oak on control plots continued to extend its dominance, doubling its foliar cover. A similar pattern was noted for all oak species combined. Hexazinone application significantly reduced the foliar cover of all oaks, while their cover essentially doubled on untreated plots. The effects of hexazinone treatment on shrubs were less pronounced. Only the 2.2 kg/ha application rate caused a significant decline in shrub cover. Overall woody plant cover on the control plots increased by 175% between 1991 and 1993. All hexazinone application rates appear to have curtailed the rapid ascent of oaks. However, only the liquid spot 1.1 and 2.2 kg/ha treatments resulted in significant reductions of total woody plant cover 2 yr after application.

Foliar cover of wiregrass increased following hexazinone application at all rates (Table 1). While wiregrass cover on control plots expanded only 18% during the 1991 growing season, increases in wiregrass cover on liquid spot treatment plots ranged from 29 to 58%. Although wiregrass cover increased over time more rapidly on hexazinone treated plots than on untreated plots, when adjusted for initial conditions these differences were not significant and thus, largely time driven ($p < 0.05$). The 20% increase on broadcast plots was not significant when compared with controls.

During the 1992 and 1993 growing seasons, wiregrass cover continued to expand, showing increases



Fig. 1. Contrast in overstory oak cover between hexazinone treated area (foreground) and untreated control area (background) two growing seasons following treatment.

for all hexazinone treatments. While wiregrass cover was nearly comparable on all applications, ranging from 60 to nearly 70% foliar cover, the largest overall increase (89%) and only significant increase ($p = 0.09$) was observed for the 2.2 kg/ha treatment. By the second and third growing seasons, wiregrass on plots receiving the broadcast 1.1 kg/ha treatment expanded to coverage comparable to that found on the other treatments. The smallest increase in wiregrass cover was noted on control plots where oak canopies continued to expand.

The foliar cover response pattern for all graminoids combined corresponds to that of wiregrass (Table 1). Significant linear increases in cover occurred over time; however, there were no significant differences among hexazinone treatments. Following application, grasses expanded into growing spaces adjacent to and beneath the skeletal crowns of dead trees and shrubs. Significant increases through time in the foliar cover of forbs were observed, but no significant differences among hexazinone treatments were noted. During the 1991 growing season, the broadcast 1.1 kg/ha application caused a 56% decline in forb cover. However, during the 1992 and

1993 growing seasons, forb cover recovered on this treatment to the highest overall levels, approaching 15%. The liquid spot 1.1 and 2.2 kg/ha treatments resulted in progressive increases in forb cover during all three growing seasons, eventually exceeding 10%.

3.2. Plant diversity dynamics

A total of 87 plant species were found on the Riverside Island study plots (Table 2). With few tree species present in this plant community, turkey oak dominated both overstory and understory prior to hexazinone application. Following treatment, no tree species was dominant in the overstory. Longleaf pine seedlings planted during the winter of 1992 appeared 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 dominated this layer prior to hexazinone application. Following treatment, the most prominent shrubs were rosemary, crookedwood, shiny blueberry and gopherapple. The variety of graminoids was obvious; however, only a few such as *Andropogon*, *Aristida* and *Sporobolus*

Table 1
Foliar cover response to hexazinone application (% cover)

Hexarmone (kg/ha)	0.0	11 broadcast	1.1 spot	2.2 spot	Adjusted Mean ^a
<i>Turkey oak</i>					
Spring 1991	5.5	6.2	12.2	13.6	
Fall 1991	5.6	0.6	2.2	0.9	3.3 ^b
Fall 1992	5.0	1.0	1.1	1.7	3.2 ^d
Fall 1993	10.4	1.6	1.3	2.4	4.9 ^d
Adjusted Mean ^a	10.8	1.1 ^b	1.6 ^b	1.7 ^b	
<i>All oaks</i>					
Spring 1991	5.6	6.2	12.5	14.0	
Fall 1991	5.7	0.6	2.3	2.1	3.7 ^d
Fall 1992	5.1	1.0	1.1	1.8	3.3 ^d
Fall 1993	10.6	1.6	1.9	3.6	5.5 ^d
Adjusted Mean	11.3	1.1 ^b	1.8 ^b	2.5 ^b	
<i>All shrubs</i>					
Spring 1991	4.4	6.6	8.5	11.9	
Fall 1991	4.4	5.4	4.1	3.3	5.0 ^d
Fall 1992	5.5	6.3	7.5	3.9	6.4 ^b
Fall 1993	7.0	8.4	7.7	5.5	7.8 ^d
Adjusted Mean	8.7	7.5	6.0	3.4 ^b	
<i>All woody plants</i>					
Spring 1991	11.4	14.8	22.3	26.8	
Fall 1991	11.1	9.0	8.6	7.5 ^b	
Fall 1992	12.5	11.8	11.0	12.1 ^b	
Fall 1993	28.0	18.8	13.5 ^b	16.3 ^c	
<i>Wiregrass</i>					
Spring 1991	54.9	48.5	44.0	36.1	
Fall 1991	64.7	58.6	56.3	56.1	58.9 ^d
Fall 1992	65.3	64.8	59.5	62.9	63.1 ^d
Fall 1993	67.4	68.5	62.9	67.1	66.5 ^d
Adjusted Mean	57.8	61.7	61.2	70.7 ^c	
<i>All graminoids</i>					
Spring 1991	58.8	54.8	50.4	51.0	
Fall 1991	68.0	67.2	64.1	65.6	65.8 ^d
Fall 1992	69.6	72.5	73.5	76.1	72.5 ^d
Fall 1993	72.7	74.0	74.5	75.1	73.8 ^d
Adjusted Mean	65.6	70.1	74.5	72.7	
<i>All forbs</i>					
Spring 1991	4.5	7.2	5.0	3.0	
Fall 1991	7.3	3.2	8.5	5.3	6.1 ^d
Fall 1992	9.3	12.8	10.0	9.1	10.3 ^d
Fall 1993	7.4	14.8	10.8	10.1	10.8 ^d
Adjusted Mean	8.6	7.7	9.6	10.3	

^aPost-treatment mean adjusted by analysis of covariance.

^bSignificantly different from untreated control plots, $p \leq 0.05$.

^cSignificantly different from untreated control plots, $p \leq 0.10$.

^dSignificant linear change through time following application, $p \leq 0.05$.

Table 2
Plant species present on the Riverside Island study site. Ocala NF

	Scientific name	Common name
Trees	<i>Pinus clausa</i>	sand pine
	<i>Pinus palustris</i>	longleaf pine
	<i>Quercus chapmanii</i>	Chapman oak
	<i>Quercus geminata</i>	sand live oak
	<i>Quercus laevis</i>	turkey oak
	<i>Quercus myrtifolia</i>	myrtle oak
Shrubs	<i>Asimina incarna</i>	pawpaw, polecat bush
	<i>Asimina obovatum</i>	flag pawpaw
	<i>Baccharis halimifolia</i>	groundsel tree
	<i>Ceratiola ericoides</i>	rosemary
	<i>Garberia fruticosa</i>	garberia
	<i>Licania michauxii</i>	gopherapple
	<i>Lyonia ferruginea</i>	crookedwood
	<i>Myrica cerifera</i>	wax myrtle
	<i>Opuntia humifusa</i>	prickly pear
	<i>Quercus minima</i>	dwarf live oak
	<i>Sabal etonia</i>	scrub palmetto
	<i>Serona repens</i>	saw-palmetto
	<i>Smilax auriculata</i>	greenbrier, catbrier
	<i>Smilax bona-nox</i>	greenbrier, catbrier
	<i>Vaccinium my-sinites</i>	shiny blueberry
	<i>Vaccinium darrowii</i>	groundbush blueberry
	<i>Yucca filamentosa</i>	Adam's needle
<i>Zamia pumila</i>	coontie	
Graminoids	<i>Andropogon floridanus</i>	Florida bluestem
	<i>Andropogon gyrans</i>	bluestem
	<i>Andropogon tracyi</i>	Tracy's bluestem
	<i>Andropogon virginicus</i>	broomsedge bluestem
	<i>Aristida lanosa</i>	woolysheath threeawn
	<i>Aristida purpurescens</i>	arrowfeather threeawn
	<i>Aristida stricta</i>	wiregrass, pineland threeawn
	<i>Bulbostylis warei</i>	hairsedge
	<i>Cyperus recurvata</i>	yellow nutsedge
	<i>Digitaria villosa</i>	shaggy crabgrass
	<i>Hypoxis</i> spp.	star grass
	<i>Panicum</i> spp.	panic grass
	<i>Rhynchospora</i> spp.	beakrush
	<i>Scleria</i> spp.	nutgrass
	<i>Sorghastrum secundum</i>	lopsided indiagrass
	<i>Sporobolus curtissii</i>	Curtiss dropseed
	<i>Sporobolus junceus</i>	pinedrop threeawn
	<i>Triplasis</i> spp.	sandgrass
	Forbs	<i>Agalinus fasciculata</i>
<i>Balduina angustifolia</i>		yellow buttons
<i>Baptisia lecontei</i>		false indigo
<i>Bonamia grandiflora</i>		bonamia
<i>Cassia chamaecrista</i>		partridge-pea
<i>Cladonia</i> spp.		lichen, reindeer moss
<i>Clitoria mariana</i>		butterfly pea
<i>Cnidoscopus stimulosus</i>		treadsoftly

Table 2 (continued)

Scientific name	Common name
<i>Conyza canadensis</i>	Horseweed
<i>Coreopsis</i> spp.	tickseed
<i>Crotalaria rotundifolia</i>	rattlebox
<i>Crotan argyranthemus</i>	doveweed
<i>Crotan punctatus</i>	beach tea
<i>Desmodium</i> spp.	tick trefoil
<i>Eriogonum tomentosum</i>	buckwheat
<i>Eupatorium album</i>	white thoroughwort
<i>Eupatorium compositaefolium</i>	dogfennel
<i>Euthamia minor</i>	false goldenrod
<i>Galactia elliotii</i>	milkpea
<i>Galactia regularis</i>	milkpea
<i>Galactia volubilis</i>	milkpea
<i>Hieracium gronovii</i>	hawkweed
<i>Hypericum</i> spp.	St. Johnswort
<i>Indigofera caroliniana</i>	wild indigo
<i>Lactuca</i> spp.	wild lettuce
<i>Lechea</i> spp.	pineweed
<i>Lespediza hirta</i>	bush clover
<i>Liatris</i> spp.	blazing star
<i>Linaria</i> spp.	toadflax
<i>Lycopodium</i> spp.	clubmoss
<i>Lygodesmia aphylla</i>	roserrush
<i>Palafoxia feayi</i>	palafoxia
<i>Palafoxia integrifolia</i>	palafoxia
<i>Pityopsis graminifolia</i>	silverthread goldaster
<i>Polygala lewtonii</i>	batchelor's button
<i>Polygonella gracilis</i>	wireweed
<i>Pterocaulon virgatum</i>	blackroot
<i>Rhynchosia difformis</i>	dollarweed
<i>Rhynchosia reniformis</i>	dollarweed
<i>Silphium asteriscus</i>	rosin-weed
<i>Sisyrinchium solstitiale</i>	blue-eyed grass
<i>Solidago</i> spp.	goldenrod
<i>Stillingia sylvatica</i>	queens delight
<i>Tragia urens</i>	tragia
<i>Trichostema dichotomum</i>	blue curls

Total plant species = 87.

appeared to be abundant. Yellow nutsedge, panic grass and sandgrass were well represented on some portions of the site. Forbs seemed to be present in great variety, but they typically persisted at low levels, approximating 5% cover, prior to hexazinone treatment.

During the first growing season following application, species richness (N_0) was generally unaffected by hexazinone, with nonsignificant increases in the number of plant species observed on control plots

Table 3
Plant species richness, diversity and evenness responses to hexazinone application

Hexazinone (kg/ha)	0.0	1.1 Broadcast	1.1 Spot	2.2 Spot
<i>Number of species</i>				
Spring 1991	15.0	18.2	16.0	17.0
Fall 1991	17.4	13.2 ^a	19.6	17.6
Fall 1992	18.4	17.6	20.8	21.6
Fall 1993	17.8	18.2	20.4	21.2
<i>Shannon's index</i>				
Spring 1991	1.11	1.50	1.51	1.51
Fall 1991	1.03	0.99 ^b	1.29	1.20
Fall 1992	1.23	1.37	1.54	1.44
Fall 1993	1.33	1.39	1.47	1.43
<i>Hill's index</i>				
Spring 1991	0.60	0.59	0.64	0.69
Fall 1991	0.61	0.69	0.59 ^b	0.58 ^b
Fall 1992	0.56	0.63	0.56 ^b	0.55 ^b
Fall 1993	0.61	0.62	0.57 ^b	0.54 ^b

^aSignificantly different from untreated control plots, $p \leq 0.05$.

^bSignificant change through time following treatment, $p \leq 0.05$.

and those receiving the liquid spot treatments (Table 3). However, the 1.1 kg/ha broadcast treatment resulted in a significant 28% decline in richness, from 18 species to 13 species in this period. During the 1992 and 1993 growing seasons, plant species richness had fully recovered on the broadcast treated plots and continued to increase on the liquid spot treated plots, exceeding 20 species present. Plots receiving the 2.2 kg/ha treatment contained as many as 22 species, while control plots typically supported no more than 18 species. Computations for the Margalef richness (R_1) and Menhinick richness (R_2) indices closely corresponded to these trends, as do the indices for abundant species (N_1) and very abundant species (N_2).

All hexazinone treatments caused a decline in plant species diversity during the first growing season following application (Table 3). The largest and only significant decrease in the Shannon diversity index (H'), from 1.50 to 0.99, was observed on the broadcast treated plots. Alpha diversity declines for the liquid spot applications were typically from 1.51 to 1.25. Broadcast values were comparable to those on control plots and liquid spot values exceeded those on controls. During the 1992 and 1993 growing seasons, species diversity recovered on all hex-

azinone treated plots, approaching values between 1.37 and 1.54. While diversity on the controls continued to rise over time from an initially low value of 1.11, Shannon index values approaching 1.33 remained less than those on hexazinone treated plots. The Simpson diversity index (λ), a reciprocal computation, showed an overall similar trend.

Hexazinone application also appeared to affect plant species evenness during the first growing season following application (Table 3). The broadcast treatment caused a nonsignificant increase in the Evenness Index of Hill (E_4), from 0.59 to 0.69. The liquid spot treatments resulted in a significant decline in evenness, from 0.64 to 0.59 for the 1.1 kg/ha application and from 0.69 to 0.58 for the 2.2 kg/ha application. During the 1992 and 1993 growing seasons, evenness declined on the broadcast treated plots to levels comparable to those on controls. The liquid spot treatments, however, produced significant declines in plant species evenness that continued throughout the study period. Computations for the other evenness indices (Pielou, E_5 ; Sheldon, E_6 ; Heip, E_3 ; Modified Hill, E_5) indicated similar trends.

3.3. Wiregrass biomass

Standing biomass values for wiregrass were highly variable over the period of study and thus, the trends reported are largely nonsignificant (Fig. 2). Pretreat-

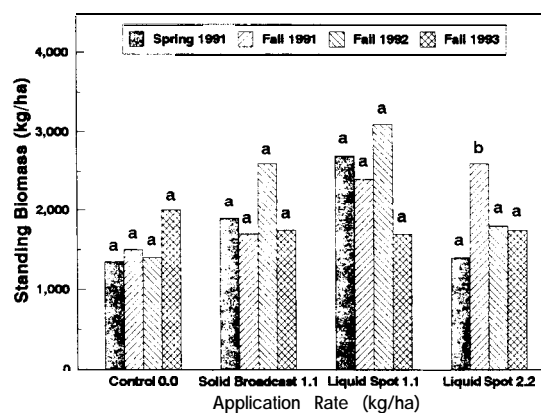


Fig. 2. Standing biomass of wiregrass following hexazinone application (means within the same treatment associated with a different letter are significantly different at the 0.05 level).

ment biomass typically ranged from 1400 to 1900 kg/ha; however, 2700 kg/ha was present on the liquid spot 1.1 kg/ha treatment plots. During the first growing season following application, only the liquid spot 2.2 kg/ha treatment produced a significant increase in wiregrass biomass. This increase, from 1400 to 2600 kg/ha, represented an 86% rise in wiregrass biomass during 1991. In the 1992 growing season, wiregrass biomass increased to 2600 kg/ha on the broadcast treatment and to 3100 kg/ha on the liquid spot 1.1 kg/ha treatment. However, these trends were not significant. During this season, biomass on the liquid spot 2.2 kg/ha treatment declined to approximate pretreatment levels. By the end of the 1993 growing season, biomass on all hexazinone treatments approximated that on controls, about 2000 kg/ha or less. The proportion of living green tissue (as contrasted with dead brown tissue) declined overall from a pretreatment value of 46% to a post-treatment level of 35%. There were, however, no significant differences among treatments.

4. Discussion

4.1. Foliar cover changes

Low-rate hexazinone application on these xeric sandhills nearly eliminated the turkey oak and related oaks that had begun to dominate this longleaf pine wiregrass ecosystem. This result is similar to that reported for higher-rate hexazinone applications of 1.7, 3.4 and 6.8 kg/ha in sandhill environments (Wilkins et al., 1993a) and low-rate applications of 0.3, 0.6 and 0.9 kg/ha on well-drained uplands (Long and Flinchum, 1992). Turkey oak mortality rates ranging from 83 to 93% indicate that low-rate hexazinone application may be a useful treatment in selectively shifting the balance of competition for water and other site resources to favor desirable plant species in the understory and developing overstory (Wilkins et al., 1993b; Brockway and Outcalt, 1994). While shrub cover was unaffected by all but the highest treatment rate, the overall 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 subsequent to successful dispersal and germination.

The method of hexazinone application (broadcast vs. spot-grid) may have had some degree of differential effect on understory plant species. While not impairing the growth response of wiregrass or other graminoids, the broadcast application method appears to have adversely affected forb cover during the first growing season, causing a 56% decrease. 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. However, in subsequent years forb cover recovered to the highest observed levels, reaching nearly 15%. Thus, low-rates of hexazinone applied by the broadcast method may initially depress and subsequently stimulate the growth of some understory plants.

In contrast, the spot grid application method deposits a 2 ml dose of liquid on the soil surface in a 2 m X 2 m grid pattern, thus creating numerous large interstitial zones that are free of hexazinone. As their crowns and root systems are typically not widely spreading, the probability of any individual plant being directly 'hit' by the spot is quite low, thus most understory plants escaped the effects of this type of herbicide treatment. Individual clusters of wiregrass contacted by spot treatment, were noted to decrease their proportion of green to brown tissue. However, rarely was an entire cluster observed to completely succumb to the herbicide. The overall danger to understory plants when using the spot-grid 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.

Spot treatments resulted in progressive linear increases in wiregrass, all graminoids and forb cover throughout the first, second and third growing seasons following application. The highest mortality rate for turkey oak and the largest proportional and only significant increase in wiregrass cover were observed on plots receiving the 2.2 kg/ha treatment. This relationship is indicative of wiregrass having been released from competition with the declining turkey oak. Progressive increases in grass and forb cover on plots receiving 1.1 and 2.2 kg/ha identify

both liquid spot application rates as useful treatments for ecosystem restoration.

4.2. Plant diversity dynamics

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 87 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). 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). The action of hexazinone, causing selective mortality among different plant groups, altered the competitive relationships among species and thus, plant diversity dynamics.

The significant decline in plant species diversity during the first growing season following broadcast treatment was no doubt a result of the application method, which brought hexazinone into close physical contact with nearly all plants on the treated plot. This initial year decrease in diversity was closely related to the decline in plant species richness and can be largely attributed to decreases in turkey oak and several forbs. The corresponding increase in species evenness indicated that the fewer species remaining, and available site resources, were more equitably distributed across the site. Thus, the effect of broadcast applied hexazinone on the plant community appeared generalized over the entire plot during the first growing season following treatment. The subsequent recovery of species richness and diversity was largely related to the resurgence of forb species during later growing seasons. Species evenness was seen to decline as wiregrass increased during the 1992 and 1993 growing seasons. This overall response pattern is similar to that reported for single applications of herbicide used in site preparation, where initial depression of diversity is followed

by recovery along a trajectory similar to that of an untreated site (Neary, 1991).

Nonsignificant declines in plant species diversity were observed for both liquid spot hexazinone treatments during the initial growing season following application. Species richness was unaffected by treatment, due to the non-uniform manner in which spot application distributes hexazinone, thus, impacting fewer understory plants than broadcast application. The diversity decline was largely attributed to significant decreases in evenness among plant species. Declining plant species evenness resulted from the increasing dominance of wiregrass following reduction of turkey oak. Increases in plant species diversity in subsequent growing seasons was largely a product of increasing species richness. Over time, increasing forbs and grasses accounted for this trend on the 1.1 and 2.2 kg/ha treatments, where forbs persisted at about 4% cover prior to application. This progressive response by forbs is unlike that reported in other xeric sandhills ecosystems where higher application rates (1.7, 3.7 and 6.8 kg/ha) resulted in declining herbaceous plant diversity (Wilkins et al., 1993b). Plant species evenness for the liquid spot treatments continued to significantly decline, as wiregrass and other grasses gained increasing dominance over the course of study. 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).

4.3. Wiregrass biomass

The highly variable response of wiregrass to hexazinone application appears characteristic of a plant species with xerophytic adaptations that allow it to persist in the droughty sandhills environment (Stalter, 1984). A slow growth rate and limited investment in propagules constitute a conservative strategy that contributes to long-term survival (Grime, 1979). The 1.1 kg/ha applications, whether by broadcast or spot method, appeared insufficient to stimulate significant increases in wiregrass biomass. Neither the decline in turkey oak cover (83%) or forb cover (56%) during the first growing season affected biomass production. This finding is not surprising, considering the naturally slow growth rate of wiregrass. The

nonsignificant increases during the 1992 growing season may be attributed to lag-time effects, with wiregrass requiring at least two seasons to respond to reduced competition. However, declining biomass during the 1993 growing season indicates the absence of a genuine growth response by wiregrass to hexazinone applications at this low-rate.

By contrast, the 2.2 kg/ha treatment stimulated a significant increase (86%) in wiregrass growth during the initial growing season following application. The significant reduction (93%) in turkey oak cover very likely contributed to this increase in wiregrass standing biomass. Considering the typically slow growth rate of wiregrass, it is surprising that such a response was observed during the first post-treatment growing season. However, wiregrass is known to respond relatively quickly to the increased availability of site resources (Parrott, 1967).

4.4. Restoring the ecosystem with hexazinone

Decades of logging, reduction of regeneration by hogs, interruption of natural fire regimes and introduction of frequent low intensity winter burning which eliminated pine seedlings but failed to kill oaks has resulted in the creation of an extensive area of turkey oak dominated sandhills that once supported longleaf pine forests (Myers, 1985; Myers and White, 1987; Rebertus et al., 1989a; Myers, 1990). The close association of longleaf pine wiregrass communities with periodic fire has been long recognized (Cary, 1932; Garren, 1943; Bruce, 1947; Veno, 1976; Christensen, 1981; Wright and Bailey, 1982; Abrahamson, 1984) and need for frequent growing season burning to restore and sustain this ecosystem has become more recently understood (Noss, 1989; Rebertus et al., 1989b; Landers et al., 1990; Wade and Lundsford, 1990; Streng et al., 1993; Landers et al., 1995). The pattern of diversity in this ecosystem is largely a product of such natural periodic disturbance. However, under circumstances where fire cannot be effectively utilized, other techniques may prove useful in restoring such underrepresented or declining ecosystems.

A wide variety of methods are potentially available for restoring ecosystems. Physical techniques such as irrigation, tillage and mechanical manipulation of vegetation can be useful, but sometimes cause

excessive site disturbance or may not be economical. Biological techniques such as species introduction, though often effective, are costly and can produce uncertain results. Chemical techniques such as application of fertilizer or herbicide and use of prescribed fire also have advantages and disadvantages related to cost, safety and potential impacts upon non-target species. Prescribed fire is perhaps the most frequently suggested restoration method, because periodic fire is an essential ecological process for maintenance of 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 realized by use of fire alone. Restoration efforts currently underway in the sandhills of northwestern Florida use a combination of treatments to achieve multiple management objectives (McWhite et al., 1993).

Among the many beneficial roles herbicides may play in ecosystem management are (a) Restoration of damaged landscapes, (b) Control of alien and other undesirable plants and (c) Creation and maintenance of desired habitats (McMahon et al., 1993). When properly applied to longleaf pine sites which have been degraded through oak invasion, hexazinone has potential to provide these benefits, while causing minimal adverse impact to native plant diversity. When fuels present on a degraded site are insufficient to sustain a prescribed fire or too heavy to burn without risking destruction of desirable plant species or social constraints preclude the use of fire, hexazinone application may be considered.

Hexazinone application also provides the added benefit of time efficiency to longleaf pine wiregrass restoration efforts. 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 of 83 to 93% and corresponding increase in desirable understory plants. A single low-rate hexazinone application achieves this condition in a very brief period, thus, greatly shortening the timeframe required for restoration (phase I). The restored site can then be more quickly scheduled for fire maintenance (phase II). The second phase of this continuing

study will examine the differential recovery effects resulting in longleaf pine wiregrass ecosystems treated with hexazinone followed by prescribed burning as contrasted with those resulting from treatment with prescribed fire alone.

5. Conclusion

Within the first three growing seasons following treatment, single low-rate applications of hexazinone caused substantial changes in a former longleaf pine forest that had become dominated by turkey oak after a wildfire. All hexazinone treatments resulted in significant reductions in the foliar cover of turkey oak and other oaks during the first year. The resulting decline in competition from oaks produced progressive increases in foliar cover of wiregrass, other graminoids and forb species over time. Plant species richness generally increased, while species evenness declined over time, with the continued expansion of wiregrass on treated plots. Standing biomass of wiregrass initially increased then declined to pretreatment levels.

The broadcast 1.1 kg/ha treatment produced non-significant declines in forb cover and significant decreases in species richness and diversity during the first post-treatment growing season. Although these variables recovered in subsequent years, broadcast application may be a less desirable restoration method because pellets are widely distributed on the site, bringing the rooting zone of nearly all understory plants into close contact with herbicide. The possible overlap of edges during strip application may also create local areas where hexazinone dosages exceed prescribed rates. The risk to non-target plant species may therefore be unacceptably high.

The liquid spot 1.1 and 2.2 kg/ha applications caused declines in species diversity, which can be largely attributed to significant decreases in evenness resulting from the progressive expansion of wiregrass during the initial post-treatment growing season. Our overall findings suggest that these treatments resulted in increases in the cover of all graminoids and forbs and in the highest species richness. In addition, these treatments were highly effective in decreasing the dominance of turkey oak

and other oaks. However, the 2.2 kg/ha treatment proved most effective in controlling all woody plants and producing significant increases in wiregrass. Therefore, while both application rates are useful, we recommend the liquid spot 2.2 kg hexazinone/ha application be used for restoration of xeric sandhills and similar longleaf pine wiregrass ecosystems.

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