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Initial plant community responses to hardwood control treatments in restoration of remnant longleaf pine (*Pinus palustris*) woodlands

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ABSTRACT

Changes in land use over the past century have contributed to substantial losses of longleaf pine (*Pinus palustris*) woodlands in the southeastern USA and replacement with higher density, mixed pine and hardwood stands that suppress understory development and limit application of prescribed fire. To increase understanding of limiting factors and identify potential approaches for restoring longleaf pine woodlands, we studied initial availability of light and soil water and 2-year (2018–2019) plant community responses after controlling overstory hardwoods in five remnant longleaf pine woodlands having no evidence of previous agriculture at the Savannah River Site near Aiken, SC, USA. Seven hardwood control treatments and a non-treated check were compared in a randomized compete block experiment: cutting, cutting + shredding of logging residues, stem injection with imazapyr herbicide, cutting + basal spray with imazapyr herbicide, cutting + basal spray with triclopyr herbicide, cutting + directed foliar spray with a mixture of glyphosate and imazapyr herbicides, and cutting + broadcast foliar spray with the same herbicide mixture. In the year prior to hardwood cutting (2016), understory light availability averaged 23% of full sun. Throughout the year of treatment installation (2017), average soil water content (SWC) was below permanent wilting point (5.5% SWC) where overstory hardwoods were retained; whereas, it was above wilting point (7.5%) where they had been cut. Thus, combined effects of shade and root competition from overstory hardwoods probably limited cover of herbaceous species in the non-treated check. In the 2 years following treatment, hardwood survival averaged > 99%, 62%, 42% and < 1% for the non-treated check, cutting, shredding, and herbicide treatments, respectively. Relative to the non-treated check, herbaceous species richness was increased by shredding, stem injection, basal spray, or directed foliar treatments; herbaceous cover was increased by basal spray or directed foliar treatments; and woody cover was decreased by directed or broadcast foliar treatments. The directed foliar spray was the most effective treatment for achieving many of the desired understory characteristics of a longleaf pine woodland, including a diverse understory dominated by herbaceous vegetation capable of supporting periodic prescribed fires. Although the imazapyr basal spray treatment increased cover of remnant woodland indicator species, none of the treatments increased richness of this species group, suggesting that restoration of native species composition will be expedited by enrichment seedings or plantings.

1. Introduction

On a worldwide basis, savannas and woodlands, characterized by an open canopy of overstory trees, a relatively sparse midstory, and a diverse grass and forb understory, are increasingly recognized as important conservation habitat for both plant and animal species (Buisson et al., 2019). However, many of these ecosystems have suffered degradation because of land use history and are in critical need of restoration (Hanberry et al., 2017; Buisson et al., 2019). In longleaf pine (*Pinus palustris* Mill.) woodlands of the southeastern USA, periodic fires ignited by lightning or fire-setting by indigenous people fostered a plant community structure characterized by widely-spaced, uneven-aged

Abbreviations: PAR, photosynthetically active radiation; SWC, soil water content.

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pines and an open understory dominated by grasses and forbs with few shrubs or hardwoods (Harper, 1914; Bartram, 1928; Platt et al., 1988). Although the natural range of longleaf pine prior to European settlement encompassed much of the southeastern USA (Stout and Marion, 1993), remnant stands are estimated to occupy only 3% of this range, because agriculture, other land uses, and other forest types have displaced the species (Frost, 1993; Gilliam and Platt, 2006). Fire-maintained longleaf pine woodlands are among the most species-rich terrestrial plant communities outside of the tropics (Peet and Allard, 1993). Under low density pines with limited needle cast, fire-tolerant native grasses such as wiregrasses (*Aristida* spp.) and bluestems (*Andropogon* spp. and *Schizachyrium* spp.) contribute fine fuels that support the ignition and spread of low-intensity surface fires (Landers, 1991). However, decades of tillage agriculture, turpentine extraction, and wildfire suppression have degraded understory plant communities in longleaf pine woodlands. Although understory species richness of old-field longleaf pine communities can be like that of remnant woodlands (Brudvig and Damschen, 2011; Brudvig et al., 2013), species composition is sufficiently distinct to represent a substantial loss of phylogenetic diversity due to previous agriculture (Turley and Brudvig, 2016). Therefore, a common goal for restoration of remnant longleaf pine woodlands is to re-establish the relevant native herbaceous species (i.e., grasses and forbs, hereafter referred to as "herbs") that support frequent, low-intensity surface fires capable of reducing or limiting encroachment by woody species (i.e., vines, shrubs, and arborescent hardwoods).

Frequent application of prescribed fire (i.e., every 3 to 5 years) is essential for controlling understory hardwoods and promoting native herbs in longleaf pine woodlands. The absence of frequent fires in pine stands leads to successional change toward higher density, mixed pine-hardwood communities, which takes place both in remnant woodlands (Brockway and Lewis, 1997) and old-field stands. Oaks (*Quercus* L.) and hickories (*Carya* Nutt.) often dominate remnant woodlands that have not been tilled for agriculture; whereas, sweetgum (*Liquidambar styraciflua* L.), black gum (*Nyssa sylvatica* Marshall), and other early successional woody species often colonize old-field stands after pine thinning (Brudvig et al., 2013). As arborescent hardwoods grow to occupy the mid-story and overstory canopy, the understory experiences a higher intensity of shading, greater litter accumulation, and less herb cover to support surface fires (Harrington and Edwards, 1999; Harrington et al., 2003; Brudvig et al., 2013). High hardwood densities impede restoration efforts by preventing recovery of remnant herbs and by limiting the effectiveness of prescribed fire. However, once the native understory community is restored, presence of low-density hardwoods may not significantly impact cover or species richness of herbs (Veldman et al., 2013; Hiers et al., 2014).

Reintroduction of prescribed burning alone is often incapable of quickly killing or adequately controlling hardwoods and large shrubs; numerous cycles of surface fire through multiple decades may be required. Furthermore, the intensity and frequency of prescribed fire required for hardwood reduction is seldom practiced on most land ownerships because of concerns regarding smoke management, safety, and cost. Typically, only small diameter hardwoods (<5 cm stem diameter at breast height (dbh), 1.37 m above ground) are top killed by prescribed fires (Van Lear and Waldrop, 1991). For larger diameter stems, mechanical and/or herbicide treatments are required, and they may be better alternatives where prescribed fire is not feasible. However, unless cutting of overstory hardwoods is applied as part of a commercial forest products sale, it can be cost prohibitive for large scale use and must be reapplied when hardwood sprout development exceeds the effective fire control limit. On the other hand, modern forestry herbicides are very effective at controlling hardwoods and other woody species, and they provide sustained control at reasonable cost when applied properly.

Stem injections, cut-stem applications, basal stem sprays in oil, and directed foliar sprays have proven to be very effective as selective herbicide treatments for controlling hardwoods and other woody species (Zedaker et al., 1987; Miller et al., 2010). Control typically exceeds 90% for treated stems. The duration of hardwood control provided by herbicides is generally longer than observed for prescribed burning (Harrington et al., 1995), but the combined use of these approaches has been shown to accelerate the rate of ecosystem restoration over that achievable with either treatment alone (Brockway and Outcalt, 2000). For example, cover of woody species was substantially less where herbicides were applied 13 years previously in combination with prescribed burning (15%) compared to areas that only had received prescribed burning (35%) (Harrington, 2011).

Herbicides have been used to promote restoration of longleaf pine woodlands by killing or suppressing hardwoods, controlling their subsequent sprouting, and thereby reducing their competition with native understory species. Broadcast applications are normally used where hardwood densities are high, but the treatment may conflict with restoration objectives because of collateral damage to non-target species (Brockway et al., 1998). However, broadcast applications of hexazinone, imazapyr, and metsulfuron herbicides have been shown to increase cover of wiregrasses and bluestems, despite initial decreases in cover and species richness in some cases (Brockway et al., 1998; Hay-Smith and Tanner, 1999; Washburn and Barnes, 2000). Imazapyr is also known to promote legume and *Rubus* species which are physiologically tolerant of the herbicide (Minogue and Quick, 1999). Because the goal is to minimize damage to existing native herbs, broadcast herbicide applications are generally limited to highly degraded communities or old fields in which seedings or plantings of native species are planned.

Although some native herb species show tolerance to specific herbicides and are promoted by the selective removal of hardwoods, potential damage to susceptible species can be minimized or avoided by directed herbicide placement (i.e., the application is targeted for a very specific area or individual plant). Directed herbicide placement techniques in plant community restoration involve manual applications to individual hardwoods or shrubs via stem injection, cut-stem, or basal and foliar spray applications (Ballard and Nowak, 2006; Nelson et al., 2006; Minogue et al., 2007; Kochenderfer et al., 2012; Rainer et al., 2012). Directed herbicide placement methods offer the greatest opportunity to conserve herb species, especially rare plants, by focusing the treatment on target plant species.

Controlling overstory hardwoods in remnant longleaf pine woodlands is an initial step for restoring these native understory communities. In 2015, we initiated research in five remnant longleaf pine woodlands at the Savannah River Site, near Aiken, SC, USA, to test the hypothesis that directed herbicide placement treatments are effective at restoring the native understory community with minimal collateral damage relative to hardwood cutting alone, cutting plus mechanical shredding of logging residues, or cutting plus broadcast herbicide application. We compared seven herbicide or non-herbicide treatments and a non-treated check for their ability to control overstory hardwoods, reduce woody cover, and increase cover and species richness of herbs. Measurements of light and soil water availability were taken early in the experiment to elucidate some of the mechanisms underlying the overstory-understory interactions. This report focuses on initial plant community responses for 2 years after treatment (i.e., 2018–2019) and prior to the re-introduction of prescribed fire. Specifically, we compared treatment effects on: (1) microclimate (i.e., photosynthetically active radiation and soil water content), (2) survival of the five most abundant hardwood genera or species, (3) herb and woody species cover, (4) herb species richness, and (5) cover and richness of native species indicative of remnant woodlands versus post-agricultural communities. With these findings we identified the treatments having the greatest potential to restore native understory communities in remnant longleaf pine woodlands.

2. Methods

2.1. Study sites

The study was conducted at the Savannah River Site (SRS), a National Environmental Research Park near Aiken, SC, USA, that was established by the U.S. Department of Energy (DOE) in 1951. Under agreement with the DOE, the USDA Forest Service manages all forest lands on the SRS. In September 2015, five study sites (blocks) were selected that contained remnant longleaf pine woodlands having no known agricultural legacies of tillage and cropping based on aerial photographs and field evaluations (J. Ledvina, Arkansas Department of Transportation, personal communication). Remnants were generally small (0.1–10 ha), non-tilled woodlands between areas that historically were extensive agricultural fields established during European settlement (Kilgo and Blake, 2005; Turley and Brudvig, 2016). Often these remnant woodlands developed dense hardwood canopies because they were isolated from fire by the agricultural fields. Many of the remaining pines were used for turpentine extraction and subsequently removed by selective cutting, leaving a predominant hardwood canopy with an understory that included suppressed, fire-dependent woodland species. Common hardwood species include blackgum, blackjack oak (*Quercus marilandica* Münchh.), black oak (*Quercus velutina* Lam.), post oak (*Quercus stellata* Wangenh.), sand hickory (*Carya pallida* (Ashe) Engl. & Graebn.), sand post oak (*Quercus margaretta* [Ashe] Small), and southern red oak (*Quercus falcata* Michx.). In this study, stand basal area averaged 4.8 m^2 ha^{-1} for pines and 17.3 m^2 ha^{-1} for hardwoods, and stem density averaged 75 pines ha^{-1} and 728 hardwoods ha^{-1} (Table 1). A previous pine thinning had occurred at site 22, strips of disturbed soil were visually apparent from fire-plow site preparation for longleaf pine natural regeneration at site 24, and evidence of previous turpentine extraction was present at sites 57 and 85. Since 1979, each of the five study sites received prescribed fire every 3 to 5 years in conjunction with the surrounding forest.

The study sites had well-drained to excessively well-drained sandy soils, with five soil series accounting for 99% of survey points: Blanton (loamy, siliceous, semiactive, thermic Grossarenic Paleudults; 26% of survey points), Fuquay (loamy, kaolinitic, thermic Arenic Plinthic Kandiudults; 26%), Lakeland (Thermic, coated Typic Quartzipsamments; 6%), Troup (loamy, kaolinitic, thermic Grossarenic Kandiudults; 22%), and Vaucluse-Ailey complex (fine-loamy, kaolinitic, thermic Fragic and Arenic Kanhapludults; 19%) (Soil Survey Staff, USDA-NRCS, 2020) (Table 1). Notable and contrasting features of these soils include the very deep and excessively well-drained sands of the Lakeland series (i.e., extremely droughty) versus the presence of an argillic horizon in the Fuquay and Vaucluse series likely associated with a perched water table and increased soil water availability. Field capacity and permanent wilting points of the surface soils occur at approximately 12% and 6% volumetric water contents, respectively, for soils of similar texture (Baver et al., 1972).

Annual precipitation near the study sites averaged 1415 mm during the 4-year study period (i.e., 2016–2019), with 754 mm occurring during the growing season (i.e., May-October). Growing season precipitation was 805, 697, 911, and 602 mm in 2016, 2017, 2018, and 2019, respectively. The average growing season precipitation at SRS during 1952–2019 was 639 mm (s.e. = 18 mm) (Atmospheric Technologies Group, 2019).

2.2. Experimental design and treatments

In areas at each study site having a relatively uniform distribution of overstory hardwoods we located eight 0.5-ha treatment plots having dimensions of 70.7 m × 70.7 m. Seven hardwood control treatments and a non-treated check were compared within a randomized complete-block experimental design having five replications (i.e., sites). Table 2 lists activities and dates associated with the research.

The study included a non-treated check, two non-herbicide treatments (i.e., cutting and cutting + shredding), four directed herbicide placement treatments (i.e., stem injection, basal sprays with two different herbicides, and a directed foliar spray), and a broadcast foliar herbicide treatment having the following specifications:

Table 2
Activities and associated dates for research on initial plant community responses to hardwood control treatments in remnant longleaf pine woodlands at the Savannah River Site near Aiken, SC, USA.

Activity	Date
Study site selection	September 2015
Plot layout	June-July 2016
Understory vegetation measurements	September-October 2016
PAR[a] measurements	October 2016
Hardwood dbh[b] measurements	February 2017
Soil water measurements	April-November 2017
Cutting treatment	May 2017
Shredding treatment	May-June 2017
Understory vegetation measurements	August-October 2017
Herbicide treatments	October 2017
Understory vegetation measurements	September-October 2018
Understory vegetation measurements	September-October 2019

[a] Photosynthetically active radiation.
[b] Stem diameter at breast height (1.37 m above ground).

Table 1
Identification numbers, locations, pre-harvest stand conditions, and soil series of the five remnant longleaf pine woodlands used in the research on initial plant community responses to hardwood control treatments at the Savannah River Site near Aiken, SC, USA.

SRS i.d. nos.[a]		Locations		Pre-harvest stand conditions[b]				Soil series[c]					
Compt.	Stand	Latitude	Longitude	Pine BA	HW BA	HW age	PAR	B	D	F	L	T	V-A
				m^2 ha^{-1}		years	% of full sun	% of sample points per site					
22	20	33.3758°	−81.6015°	7.3 (1.3)	17.1 (1.8)	86.2 (2.6)	16.6 (3.7)	14	0	0	37	49	0
24	02	33.3793°	−81.5737°	2.3 (0.6)	20.2 (1.5)	80.3 (0.9)	18.7 (4.6)	0	0	22	0	78	0
57	23	33.2840°	−81.5219°	2.2 (0.8)	19.6 (1.9)	93.6 (1.7)	23.5 (2.7)	100	0	0	0	0	0
82	26	33.1672°	−81.5491°	9.6 (1.9)	11.1 (2.1)	91.8 (2.9)	30.0 (5.7)	0	0	100	0	0	0
85	41	33.1555°	−81.5469°	2.8 (1.1)	18.7 (2.0)	90.3 (4.9)	28.2 (4.7)	0	5	0	0	0	95
				Mean (standard error)				% of total sample points					
				4.8 (1.5)	17.3 (1.7)	88.4 (2.4)	23.4 (2.6)	26	1	26	6	22	19

[a] Savannah River Site (SRS) identification numbers: Compt. = timber stand compartment; Stand = stand number within compartment.
[b] Average stand basal areas (BA) of pines and hardwoods (HW), ages of hardwood trees, and photosynthetically active radiation (PAR) prior to initiation of the research (standard error in parentheses). Hardwood ages are based on counts of growth rings from the stumps of 8, 11, 7, 12, and 6 *Quercus falcata* trees from sites (i.e., compartments) 22, 24, 57, 82, and 85, respectively.
[c] Soil series (B = Blanton, D = Dothan, F = Fuquay, L = Lakeland, T = Troup, and V-A = Vaucluse-Ailey; Soil Survey Staff, USDA-NRCS, 2020) at each study site based on a survey of 35 to 48 points per site.

1. *Non-treated check*. Overstory hardwoods were left standing with no treatment.
2. *Cutting*. Overstory hardwoods were cut and stems and branches were removed with a Tigercat 726E feller-buncher (Tigercat Industries Inc., 54 Morton Ave E, Brantford, Ontario, Canada, N3R 7 J7) during May 2017.
3. *Cutting + shredding*. Overstory hardwoods were cut as described in Treatment 2 but stems and branches were shredded with a Fecon FGT 9025 mulching attachment (Fecon Inc., 3460 Grant Dr., Lebanon, OH, USA, 45036) during May-June 2017.
4. *Stem injection*. Overstory hardwoods were left standing, and in October 2017, a downward angled cut 2 to 3 cm in depth was made at about 45-cm height of each hardwood for each 7.6 cm of dbh. One ml of a 50% solution of Arsenal® Applicators Concentrate (AC) herbicide (i.e., imazapyr; BASF Corporation, 26 Davis Dr., Research Triangle Park, NC, USA, 27709) in water was immediately applied to each cut.
5. *Cutting + basal spray (triclopyr)*. Overstory hardwoods were cut and removed as described in Treatment 2. In October 2017, a 25% solution of Garlon® 4 Ultra herbicide (i.e., triclopyr ester; Corteva, 9330 Zionsville Rd., Indianapolis, IN, USA, 46268) in Loveland Bark Oil (Loveland Products, Inc., PO Box 1286, Greeley, CO, USA, 80632) was applied to wet the sides of the stump and associated sprouts of each hardwood.
6. *Cutting + basal spray (imazapyr)*. Overstory hardwoods were cut and removed as described in Treatment 2. In October 2017, a 10% solution of Polaris® SP herbicide (i.e., imazapyr; Nufarm Americas, Inc., 11901 S. Austin Avenue, Alsip, IL, USA, 60803) in Loveland Bark Oil was applied to wet the sides of the stump and associated sprouts of each hardwood.
7. *Cutting + directed foliar spray*. Overstory hardwoods were cut and removed as described in Treatment 2. In October 2017, an aqueous solution of imazapyr (0.6% Arsenal® AC herbicide), glyphosate (2% Accord® XRT II, Corteva, 9330 Zionsville Rd., Indianapolis, IN, USA, 46268), and non-ionic surfactant (0.5% Cide-Kick II®, Brewer International, PO Box 690037, Vero Beach, FL, USA, 32969) was applied to wet the foliage of sprouts from each hardwood stump.
8. *Cutting + broadcast foliar spray*. Overstory hardwoods were cut and removed as described in Treatment 2. In October 2017, the same herbicide solution listed above for Treatment 7 was applied as a broadcast treatment with a spray volume of 281 L ha^{-1}. The equivalent herbicide rates are 0.8 and 2.6 kg a.e. (i.e., acid equivalent) ha^{-1} for imazapyr and glyphosate, respectively.

The non-treated check provided an overall experimental control for all treatments, while the cutting treatment provided a control for the other cutting treatments that included shredding or herbicides. Compared to the other treatments, the shredding treatment is relatively expensive (two to four times the cost) because of slow production rates and high machine operating costs, and residual debris is likely to temporarily smother understory vegetation and increase fuel loads, but the treatment avoids herbicide collateral damage and soil disturbances associated with transportation of logs. The stem injection treatment is relatively low cost, uses less herbicide than other methods, and, as with shredding, can be applied when commercial harvest is not feasible. The basal spray treatments minimize the area treated with herbicides. The directed foliar spray impacts a larger area than the stem injection and basal spray treatments, but it is likely to provide more complete control of sprouting hardwoods. The broadcast foliar spray is a common site preparation treatment in southern USA forestry. Although collateral damage to herb species is likely from the broadcast foliar treatment, the effects have not been evaluated for remnant longleaf pine woodlands.

2.3. Microclimate measurements

To provide a basis for interpreting how the hardwood control treatments influenced growth-limiting resources and subsequent vegetation responses, we took measurements of photosynthetically active radiation (PAR) and soil water content (SWC). The Delta-T Devices SunScan canopy analysis system (Dynamax Inc., 10808 Fallstone, Suite #350, Houston, TX 77099, USA) was used to measure PAR. In October 2016, prior to cutting overstory hardwoods, above-canopy readings of PAR were taken on cloudless days within 1 h of solar noon. The above-canopy readings were automatically recorded at 1-minute intervals with a type BF3 Sunshine Sensor located on the forest floor within a nearby forest opening at each study site. Below-canopy readings of PAR were taken simultaneously at a given site with a leveled SunScan wand located on the forest floor at each of five systematically located points within each treatment plot. Above- and below-canopy readings were merged according to the nearest minute, and PAR was expressed as a percentage of full sun.

The Trime FM-3 soil moisture measuring system was used to measure volumetric SWC (IMKO Micromodultechnik GmbH, Im Stoeck 2, D-76275 Ettlingen, Germany). We took readings of SWC on the following dates in 2017 during the different phases of treatment application (Table 2): April 17 and 27; May 11 and 17; July 13 and 31; August 11, 18, and 29; September 15; October 5; and November 7. Readings of SWC at 0–16 cm soil depth were taken with a P3 probe at each of four systematically located points within each treatment plot. The probe was calibrated in saturated sand prior to each set of periodic measurements.

2.4. Vegetation measurements

During February 2017, species, dbh (nearest 0.1 cm), and distance (nearest 0.1 m) and azimuth (nearest 0.1°) from the nearest plot corner were recorded for each tree of dbh > 2.5 cm rooted within a centrally located 30- × 30-m measurement plot within each of the 40 0.5-ha treatment plots. Trees in the genus, *Carya* Nutt. (i.e., hickory), were not identified to species because hybridization among species influenced critical taxonomic features. Likewise, the species sand post oak, also was assigned to occasional post oaks and to hybrids of the two species. From these data we found that the five most abundant hardwood genera or species were hickory, blackgum, southern red oak, blackjack oak, and sand post oak, having average stand basal areas of 5.6, 0.4, 5.8, 0.8, and 3.6 m^2 ha^{-1}, respectively. These species had adequate sample sizes across the 40 treatment plots to enable statistical analyses of their survival after treatment. We estimated age of the most common hardwood species, southern red oak, based on counts of growth rings from the stumps of 6–12 trees per site.

To quantify treatment effects on hardwood survival, ten candidate trees per genus or species present were randomly selected for each treatment plot from the hardwood inventory data. In September 2017, four months after cutting the hardwoods (June-September) but prior to the herbicide treatments, we located trees or stumps from the candidate list for each treatment plot based on their location and dbh. Up to five living trees or sprout clumps per genus or species were flagged and tagged on a given treatment plot to evaluate post-treatment survival. In treatments that included cutting, hardwood stumps with no evidence of sprouting were noted and presumed to be dead. The sample included a total of 823 hardwoods (i.e., 266 non-sprouting stumps plus 557 tagged living trees or sprout clumps) distributed among the genera or species as follows: hickory, $n = 262$; blackgum, $n = 51$; southern red oak, $n = 198$; blackjack oak, $n = 61$; and sand post oak, $n = 251$. In September 2018 and 2019, each tagged hardwood was revisited to record its survival status.

During September and October of 2016–2019, understory vegetation (i.e., all herb species and those woody species having a dbh ≤ 2.5 cm) was surveyed to quantify cover and species richness. Species nomenclature and life form are as given in Plants Database (USDA-NRCS, 2020). Plants from two monocot genera, *Andropogon* and *Dichanthelium*, often could not be identified to species because of the absence of floral structures; therefore, their cover responses were combined at the genus level. Three 10- x 10-m subplots were located along a common diagonal of each treatment plot. Within the centrally located subplot, beginning and end points were permanently marked for ten parallel line transects, each 10 m long and spaced 1 m apart. The line-intercept method was used to estimate cover of each herb and woody species along a given transect (Mueller-Dombois and Ellenberg, 1974). Beginning and ending distances were recorded where a given line transect intersected the crown of an understory species when viewed from above. Cover (%) of a given species was calculated as the sum of its crown intersections divided by total transect length of the measurement plot (i.e., 100 m) and multiplied by 100.

To quantify treatment effects on the relationship of the number of herb species versus area sampled, an array of nested quadrats of area, 0.1, 1, and 10 m^2, aligned along a common diagonal was located at each of the four corners of the remaining two subplots within each treatment plot. Each herb or woody species was recorded as it occurred within a given nested quadrat and the 100-m^2 subplot in which the nested quadrat arrays were located. This sampling approach provided a total of 26 estimates of the number of species per area sampled for each treatment plot. Richness of herb, woody, and all species combined were estimated as the average number of species per understory group from the two 100-m^2 subplots per treatment plot.

2.5. Data analysis

All statistical analyses were conducted in SAS (SAS Institute Inc., 2013) with a significance level of $\alpha = 0.05$, except for the ordination analysis (described below). Prior to analysis of variance (ANOVA), an arc-sine, square-root transformation was applied to each variable that was expressed as a proportion (i.e., PAR, SWC, hardwood survival, and individual species cover) to normalize its residual variance (Sokal and Rohlf, 1981). Repeated measures ANOVA was conducted to partition variation appropriately among treatments and measurement years after adjusting for a pre-treatment covariate (included in the ANOVA when statistically significant); however, measurement-year means were not reported because of expected and often opposing differences due to variation in growing season rainfall and increasing community recovery with time since disturbance. If a significant F statistic was observed in the ANOVA for treatment main effects, Tukey's HSD test was used to conduct multiple comparisons of covariate-adjusted means (Sokal and Rohlf, 1981). If a significant treatment-by-year interaction was detected, multiple comparisons of treatment means were conducted with Bonferroni-adjusted probabilities to identify how treatment differences varied between measurement years (Quinn and Keough, 2002). Reported values for the coefficient of determination were adjusted for degrees of freedom (i.e., adjusted R^2).

Measurements of PAR were averaged by treatment plot, and the mean values were subjected to ANOVA in SAS PROC Mixed to determine if the variable differed significantly among treatments after adjusting for random effects of blocks. Measurements of SWC were averaged by treatment plot and measurement date. The first reading of SWC, taken before any treatment activities, was used as a covariate in the ANOVA to adjust treatment responses for variation attributable to microsite. Mean values of SWC were subjected to repeated measures ANOVA in SAS PROC Mixed to test the fixed effects of treatments, measurement dates, and their interaction after adjusting for the covariate and random effects of blocks.

We used observations of sprouting four months after cutting (June-September) but prior to the herbicide treatments to estimate the probability of sprouting for the five most abundant hardwood genera or species. Data selected were from all treatments except the non-treated check, shredding, and stem injection treatments. Logistic regression models were fitted for each genera or species in SAS PROC Logistic to predict the probability of sprouting from parent-tree dbh. The proportion of hardwood stumps that sprouted was calculated for each treatment plot and genus or species, and then the proportions were averaged by site and genus or species. ANOVA was conducted in SAS PROC Mixed to determine if average sprouting proportions differed significantly among the five hardwood genera or species after adjusting for covariate effects of parent-tree dbh (i.e., prior to cutting) and random effects of blocks. The same analytical approach was used to compare average dbh among genera or species.

Using the sample of non-sprouting hardwood stumps and tagged living hardwood trees and sprout clumps ($n = 823$), we averaged survival by genus or species, treatment plot, and measurement year (i.e., 2018 and 2019). For each hardwood genus or species, mean survival was subjected to repeated-measures ANOVA in SAS PROC Mixed to test for fixed effects of treatment, measurement year, and their interaction after adjusting for the random effects of blocks. The potential covariate, parent-tree dbh, was not significant in the hardwood genus' or species' ANOVAs for survival ($P > 0.05$).

Cover values for each herb and woody genus or species were averaged by treatment plot and measurement year (i.e., 2018 and 2019). The means for the most abundant genera or species (i.e., average cover $\geq$ 1%) were subjected to repeated measures ANOVA in SAS PROC Mixed to test for fixed effects of treatment, measurement year, and their interaction after adjusting for the covariate, pre-treatment (2016) cover, and random effects of blocks. Repeated measures ANOVA also was conducted for total cover of the following understory species groups: dicot herb species (i.e., forbs), monocot herb species (i.e., grasses, sedges, rushes, and other graminoids), all herb species, all woody species (i.e., species having cambial growth), and all species. Reported treatment means of the component covers for a given species group do not sum to equal the total values because of ANOVA adjustments associated with the covariate, pre-treatment cover. Cover responses to treatment are reported as changes in absolute percentage values.

The relationship of the number of herb species versus area sampled (i.e., species-area curves) was studied because it provided a quantitative measure of understory diversity expressed as species density. Treatment effects on species-area curves were tested using the extra sums-of-squares approach in linear regression (Neter et al., 1989) via SAS PROC Reg. Each of the relationships for 2018 and 2019 was linearized by transforming both the number of herb species and area sampled to natural logarithms according to the following model:

$$\log_e(S+1) = b_0 + b_1(\log_e(A)) + b_2(\log_e(S_0)) \quad [1]$$

where S is the number of herb species per area sampled, b_0-b_2 are regression coefficients to be estimated, A is the area sampled (m^2), and S_0 is the covariate, pre-treatment (2016) number of herb species per area sampled. The constant, 1, was added to S in equation [1] to enable logarithmic transformation when $S = 0$. The full regression model for each year included indicator variables for blocks, separate intercept (b_0) and slope (b_1) variables for each of the eight treatments, and a separate slope (b_2) variable for the covariate. F-tests were applied to compare the full model to reduced models having a common intercept, a common slope, or both. In reporting the final models, the regression intercept was calculated as the mean of coefficients for the five blocks, and covariate effects were adjusted for the overall mean number of herb species observed prior to treatment.

Values of species richness from 2018 and 2019 for each of the herb, woody, and all-species understory groups were subjected to repeated measures ANOVA in SAS PROC Mixed to test the fixed effects of treatment, measurement year, and their interaction after adjusting for the covariate, pre-treatment (2016) species richness, and random effects of blocks. To provide a measure of restoration efficacy for remnant longleaf pine woodlands on the SRS, we used the lists developed by Brudvig et al. (2013) and revised by Turley et al. (2017) to determine the number of indicator species present on each of the two 100-m^2 subplots for each treatment plot in 2018 and 2019 that were typical of plant communities having a history of previous agriculture versus those from remnant woodlands. The lists included 68 and 59 native herb and woody species found to be significant indicators for post-agricultural and remnant woodland communities, respectively, based on indicator species analysis. For each indicator species group, treatment plot average values of indicator species richness were subjected to repeated-measures ANOVA in SAS PROC Mixed to test the fixed effects of treatment, measurement year, and their interaction after adjusting for the covariate, pre-treatment (2016) number of indicator species, and random effects of blocks. A similar approach was used to analyze treatment effects on total cover for each indicator species group.

We used PC-Ord v5.31 (McCune and Mefford, 2006) to conduct a nonmetric multidimensional scaling ordination of plots in species space. Because we wanted to adjust the analysis of treatment effects on the plant community for pre-treatment conditions, we combined the data for the cover estimations that were done in 2016 (pre-treatment) and 2019 (2 years after treatment). Thus, we input individual species' covers for 80 plots (40 pre-treatment and 40 post-treatment) for a combined list of 233 species representing the seven hardwood control treatments and the non-treated check from the five study sites. We used the default settings for PC-Ord (Sorenson distance measure, six axes, 500 iterations, random starting coordinates, reduction in dimensionality of one at each cycle, and a step length of 0.20). Autopilot and thoroughness were specified. This resulted in a 3-dimensional solution with a final stress of 16.1 in 129 iterations. The coefficients of determination for the correlations between ordination distances and distances in the original n-dimensional space were 0.254 for axis 1, 0.266 for axis 2, and 0.249 for axis 3 for a cumulative ordination r^2 of 0.769. We presented the ordination results as values of the plot coordinates for 2016 and 2019 averaged either by study site or by hardwood control treatment. Because the greatest changes in plant community composition from 2016 to 2019 were shown for axes 2 and 3, we focused our presentation on these relationships. We also used PC-Ord to correlate potential explanatory variables in a secondary matrix with the ordination axes to explore their meanings. We used the joint plot routine to display the correlations of two soil series, Lakeland and Fuquay, and the correlations of pre-treatment stand basal areas of pines and hardwoods with the ordination axes. We conducted permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) and pairwise comparisons within PC-Ord to test the null hypothesis that the treatment centroids and their associated dispersion within ordination space do not differ significantly from the non-treated check.

To understand how differences in plant community composition among sites and treatments may have affected results from the ordination analysis, we conducted ANOVA on mean cover per species (i.e., cover divided by species richness for a given understory group) in 2019 for herb, woody, and all-species understory groups. The analysis tested the fixed effects of treatment after adjusting for the covariate, pre-treatment (2016) mean cover per species, and random effects of blocks. Because site differences could not be tested statistically, we assumed that site responses in mean cover per species like those observed for the treatments indicated presence of similar growth-limiting factors, such as competition and soil disturbance.

3. Results

3.1. Microclimate

Prior to application of the hardwood control treatments (October 2016), photosynthetically active radiation on the forest floor averaged 23% of full sun (s.e. = 2.6; Table 1). During the year of treatment application (2017), when growing season precipitation was close to the long-term average, soil water content averaged lower in the non-treated check and stem injection treatment (5.0–5.9%, s.e. = 0.2) than in treatments where overstory hardwoods had been cut in May (7.1–7.9%, s.e. = 0.3) (Fig. 1).

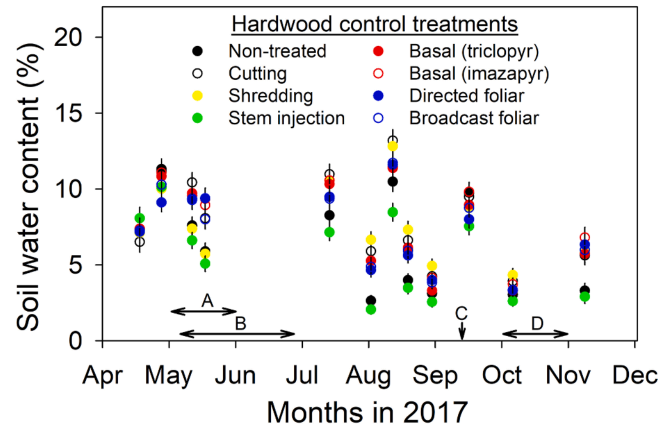

Fig. 1. Mean values of volumetric soil water content within 0–16 cm soil depth in the year of application (2017) of seven hardwood control treatments and a non-treated check to remnant longleaf pine woodlands at the Savannah River Site near Aiken, SC, USA. Arrows indicate approximate timings of: (A) cutting (i.e., all treatments except the non-treated check and stem injection), (B) shredding, (C) Hurricane Irma which provided approximately 127 mm of precipitation, and (D) herbicide applications. See text for a discussion of treatment effects.

3.2. Hardwood sprouting and survival

Across the five study sites, age of southern red oaks averaged 88.4 years (s.e. = 2.4), ranging from 75 to 104 years (Table 1). Similar average ages were observed for blackjack oak (90.0 years, s.e. = 3.0, n = 2) and sand post oak (102.5 years, s.e. = 4.0, n = 4) at site 85. Parent-tree dbh varied among species with mean values ranging from 8 cm for blackgum to 23 cm for southern red oak (Table 3). Average dbh was greater for southern red oak than for either blackgum or sand post oak. The average percentage of trees sprouting four months after cutting (June-September) was lower for sand post oak (43%) than for hickory (84%) or blackgum (93%). Logistic regression models for predicting the probability of sprouting four months after cutting from parent-tree dbh were significant for all species ($P \leq 0.012$) except blackgum ($P = 0.411$), with concordance values of 64–84% (Table S1). None of the species' logistic regression models had significant lack of fit ($P \geq 0.089$). The model for sand post oak predicted a 28% probability of sprouting after cutting parent trees with a dbh of 20 cm; whereas, predicted probabilities for hickory, southern red oak, and blackjack oak trees of the same size were 75%, 68%, and 69%, respectively (Fig. 2).

In the 2 years since treatment, survival of the five hardwood genera or species averaged > 99%, 62%, 42% and < 1% for the non-treated check, cutting, shredding, and herbicide treatments, respectively (Table 4). Relative to the non-treated check, cutting alone reduced survival of southern red oak and sand post oak by 30% and 63%, respectively, and the combination of cutting and shredding reduced survival of hickory and blackjack oak by 77% and 49%, respectively.

Table 3
Mean values for parent-tree diameter at breast height (dbh; 1.37 m above ground), the percentage of trees sprouting four months (June-September) after cutting (standard error in parentheses) and sample sizes for the five most abundant hardwood genera or species in remnant longleaf pine woodlands at the Savannah River Site near Aiken, SC, USA. Means for a given variable followed by the same letter do not differ significantly among genera or species ($P > 0.05$).

Hardwood genus or species	Dbh (cm)	Percentage sprouting (%)	n
Carya spp.	18.0 (1.4) ab	84.2 (5.0) a	168
Nyssa sylvatica	8.1 (1.6) c	92.8 (5.6) a	36
Quercus falcata	23.2 (1.4) a	74.2 (8.3) ab	145
Quercus marilandica	17.8 (1.6) ab	70.8 (6.9) ab	49
Quercus margaretta	12.9 (1.4) bc	43.1 (7.3) b	175

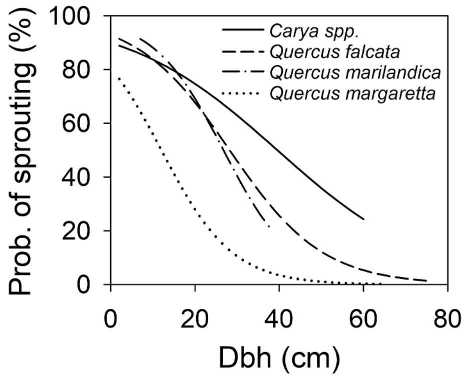

Fig. 2. Logistic regression models for predicting the probability of sprouting four months after cutting (June-September) from parent-tree stem diameter at breast height (dbh; 1.37 m above ground) of the most abundant hardwood genera or species in remnant longleaf pine woodlands at the Savannah River Site near Aiken, SC, USA. The model for *Nyssa sylvatica* (not shown) was not statistically significant ($P > 0.05$). See Table S1 for model statistics.

There were no differences in hardwood survival among herbicide treatments, and mean values were <2% with one exception: hickory survival after the broadcast foliar treatment was 6%. Although treatment responses for blackgum

mirrored those of the other species, the treatment F statistic was not significant ($P = 0.078$) for this species likely because of a limited sample size ($n = 51$). The treatment-by-year interaction for survival was not significant for any of the hardwood genera or species ($P \geq 0.142$).

3.3. Understory vegetation responses

Twelve plant genera or species had an average cover ≥ 1%, including three grasses (*Andropogon* spp L., *Dichanthelium* spp. (Hitchc. & Chase) Gould, and *Piptochaetium avenaceum* (L.)), one fern (*Pteridium aquilinum* (L.) Kuhn), one forb (*Conyza canadensis* (L.) Cronquist and), two vines (*Gelsemium sempervirens* (L.) W.T. Aiton and *Vitis rotundifolia* Michx.), two shrubs (*Vaccinium arboreum* Marshall and *Vaccinium stamineum* L.), and three arborescent hardwoods (hickory, sand post oak, and *Sassafras albidum* (Nutt.) Nees). The highest covers for the grass species were in the basal spray and directed foliar treatments, whereas, the highest covers for the fern and forb species were in the directed foliar treatment (Table S2). The lowest covers for the vine, shrub, and hardwood species were in the directed and broadcast foliar treatments.

The treatment-by-year interaction was significant for both herb cover ($P = 0.016$) and woody cover ($P = 0.041$). Increases in herb cover from 2018 to 2019 for the directed and broadcast foliar treatments (i.e., 40–53%) greatly exceeded those observed for the remaining treatments (Table S3). Likewise, increases in woody cover from 2018 to 2019 for the cutting, shredding, and stem injection treatments (i.e., 17–30%) exceeded those observed for the remaining treatments (Table S3). These differences in vegetation recovery increased the separation among treatment means.

Regarding treatment main effects, herb cover in the basal spray and directed foliar treatments (66–72%) was greater than in the non-treated check (17%) (Table 5). Herb cover in the broadcast foliar treatment (28%) was lower than in the directed foliar treatment (72%), but it did not differ significantly from that in the non-treated check (17%). Woody covers in the directed and broadcast foliar treatments (13% and 4%, respectively) were lower than in all other treatments (46–72%) and the non-treated check (50%). The highest cover of all species combined was in the imazapyr basal spray treatment (125%), which was greater than those in the non-treated check (71%) and broadcast foliar treatment (36%). Cover of post-agricultural woodland indicator species in the directed foliar treatment (23%) exceeded that in the non-treated check (2%). Cover of remnant woodland indicator species in the imazapyr basal spray treatment (69%) was greater than that in the non-treated check (32%). Covers of remnant species in the cutting, shredding, stem injection, and basal spray treatments were numerically higher than in the non-treated check, yet these differences were not statistically significant. Note that treatment responses of *Vitis rotundifolia*, a common vine species classified as a remnant woodland indicator (Brudvig et al. 2013), strongly influenced total cover for this indicator species group (Table S2).

In both the first (2018) and second (2019) years after treatment, the relationships of the number of herb species versus area sampled for most treatments differed from that of the non-treated check because they had larger values for their regression model intercepts (Fig. 3 and Table S4). Only the broadcast foliar treatment had a relationship in 2018 that did not differ significantly from the non-treated check. In 2019, the species-area curves spanned a broader range of herb species richness than observed in 2018, and the treatment rankings changed. For example, in the 2018 relationships, the shredding and basal spray treatments had the highest number of herb species per area sampled; whereas, in the 2019 relationships, the directed and broadcast foliar treatments had the highest number of herb species. The regression coefficient for the co-variate, pre-treatment number of herb species, decreased 26% from 2018 (0.519) to 2019 (0.385) indicating diminishing effects of the pre-treatment plant community on post-treatment species richness (Table S4).

Herb species richness in the non-treated check (21 species) was exceeded by most of the treatments (28–30 species) except the cutting (27 species) and broadcast foliar treatments (25 species) (Table 6). Richness of post-agricultural woodland indicator species in the shredding, basal spray, and directed foliar treatments (7–8 species) exceeded that in the non-treated check (4 species). The broadcast foliar treatment had lower richness of remnant woodland indicator species (9 species) than the non-treated check (13 species), and none of the treatments had significantly greater richness of remnant woodland indicator species

Table 4
Mean survival (%) (standard error in parentheses) of the five most abundant hardwood genera or species for 2 years (2018 and 2019) after application of seven hardwood control treatments and a non-treated check in remnant longleaf pine woodlands at the Savannah River Site near Aiken, SC, USA. For a given genus or species, means followed by the same letter do not differ significantly ($P > 0.05$).

Hardwood genus or species	Hardwood control treatments Non-treated	Cutting	Shredding	Stem injection	Basal spray (triclopyr)	Basal spray (imazapyr)	Directed foliar	Broadcast foliar
Carya spp.	100.0 (0.2) a	89.8 (5.2) a	22.7 (7.1) b	0.0 (0.0) c	0.9 (1.6) c	0.2 (0.7) c	0.7 (1.4) c	5.7 (3.9) bc
Nyssa sylvatica	100.0 (0.0) a	25.0 (6.3) a	50.0 (7.2) a	0.0 (0.0) a	0.0 (0.0) a	0.0 (0.0) a	0.8 (0.9) a	0.0 (0.0) a
Quercus falcata	98.9 (2.1) a	68.3 (9.5) b	37.3 (11.4) b	0.3 (1.2) c	0.0 (0.0) c	0.0 (0.0) c	0.0 (0.0) c	0.0 (0.0) c
Quercus marilandica	99.5 (1.6) a	88.3 (4.5) a	50.1 (8.5) b	0.1 (0.6) c	0.0 (0.0) c	0.5 (1.6) c	0.0 (0.1) c	1.5 (2.1) c
Quercus margaretta	99.3 (1.3) a	36.1 (8.6) b	50.1 (8.0) b	0.2 (0.7) c	0.0 (0.0) c	0.0 (0.0) c	0.0 (0.0) c	0.6 (1.3) c

Table 5
Mean cover (%) of understory species groups (standard error in parentheses) for 2 years (2018 and 2019) after application of seven hardwood control treatments and a non-treated check in remnant longleaf pine woodlands at the Savannah River Site near Aiken, SC, USA. For a given species group, means followed by the same letter do not differ significantly ($P > 0.05$).

Species group	Non-treated	Cutting	Shredding	Stem injection	Basal spray (triclopyr)	Basal spray (imazapyr)	Directed foliar	Broadcast foliar
Dicot herb species	3.2 (3.7) c	8.6 (3.4) bc	16.7 (3.4) abc	8.0 (3.4) bc	10.3 (3.4) bc	16.4 (3.4) abc	30.6 (3.4) a	20.6 (3.4) ab
Monocot herb species	17.9 (7.2) bc	36.1 (7.2) abc	42.8 (7.3) ab	28.9 (7.2) abc	53.9 (7.3) a	53.6 (7.2) a	42.5 (7.3) ab	5.9 (7.3) c
Herb species	17.2 (9.4) c	44.5 (9.2) abc	58.5 (9.3) abc	38.2 (9.2) abc	66.4 (9.3) ab	70.6 (9.3) ab	72.3 (9.3) a	28.4 (9.3) bc
Woody species	49.6 (7.0) a	71.7 (6.9) a	65.6 (7.0) a	49.7 (7.0) a	45.6 (7.2) a	57.1 (6.9) a	13.0 (7.1) b	4.3 (6.9) b
All species	70.6 (11.2) bc	116.4 (10.8) ab	121.3 (11.1) ab	87.0 (10.8) ab	115.4 (10.9) ab	124.7 (10.9) a	81.5 (10.8) abc	35.9 (10.8) c
Post-agricultural woodland indicator species	2.5 (4.5) b	8.4 (4.5) ab	16.2 (4.5) ab	4.4 (4.5) ab	18.5 (4.5) ab	16.6 (4.5) ab	23.3 (4.5) a	19.8 (4.5) ab
Remnant woodland indicator species	31.6 (6.7) bc	50.8 (6.3) ab	56.1 (6.4) ab	48.0 (6.3) ab	54.6 (6.2) ab	68.6 (6.3) a	32.1 (6.3) bc	7.9 (6.2) c

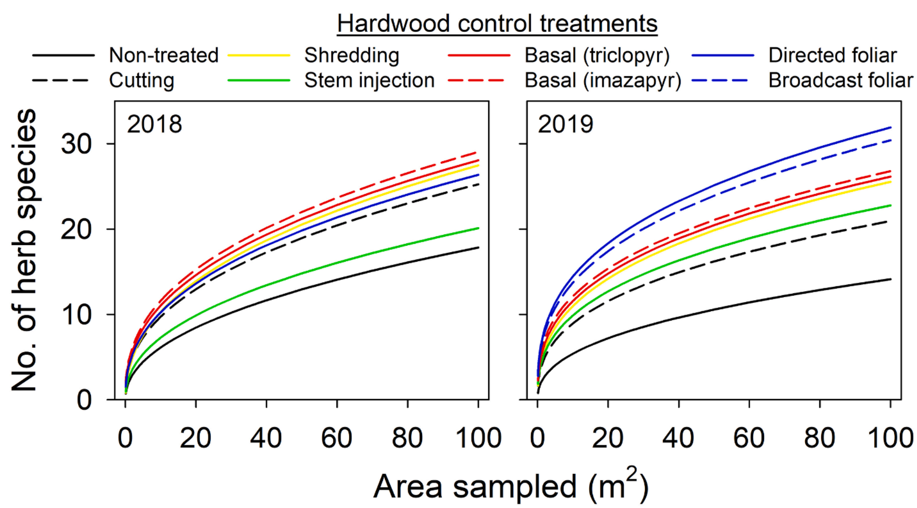

Fig. 3. Regression relationships for the number of herb species versus area sampled for 2 years (2018 and 2019) after application of seven hardwood control treatments and a non-treated check in remnant longleaf pine woodlands at the Savannah River Site near Aiken, SC, USA. For each year, a regression relationship is shown for treatments that differed significantly from the non-treated check ($P \leq 0.05$). See Table S4 for regression model statistics.

Table 6
Mean species richness (number of species per 100 m^2; standard error in parentheses) of understory species groups for 2 years (2018 and 2019) after application of seven hardwood control treatments and a non-treated check in remnant longleaf pine woodlands at the Savannah River Site near Aiken, SC, USA. For a given species group, means followed by the same letter do not differ significantly ($P > 0.05$).

Species group[a]	Hardwood control treatments Non-treated	Cutting	Shredding	Stem injection	Basal spray (triclopyr)	Basal spray (imazapyr)	Directed foliar	Broadcast foliar
Herb species	20.9 (2.4) b	26.8 (2.4) ab	30.1 (2.4) a	27.8 (2.4) a	29.1 (2.4) a	31.5 (2.4) a	30.4 (2.4) a	25.5 (2.4) ab
Woody species	22.3 (0.9) a	21.0 (1.0) ab	20.3 (0.9) ab	21.1 (1.0) ab	20.4 (0.9) ab	22.4 (0.9) a	17.8 (0.9) b	13.4 (1.0) c
All species	43.0 (3.1) bc	47.9 (3.1) ab	50.5 (3.1) ab	49.3 (3.1) ab	49.5 (3.1) ab	53.9 (3.1) a	48.1 (3.1) ab	38.7 (3.1) c
Post-agricultural woodland indicator species	4.5 (0.8) b	6.4 (0.8) ab	8.2 (0.8) a	6.5 (0.8) ab	7.1 (0.8) a	8.5 (0.8) a	7.4 (0.8) a	7.0 (0.8) ab
Remnant woodland indicator species	13.1 (0.9) a	13.3 (0.9) a	11.7 (0.9) ab	13.6 (0.9) a	13.5 (0.9) a	12.9 (0.9) a	12.2 (0.9) a	9.3 (0.9) b

[a] Species richness values for the post-agricultural and remnant woodland indicator species groups include both herb and woody species (Brudvig et al., 2013).

than the non-treated check.

3.4. Ordination analysis

Results of the ordination analysis indicated that changes in plant community composition from 2016 (i.e., prior to treatment) to 2019 (i.e., 2 years after treatment) varied both among study sites and among hardwood control treatments. The ordination axes were correlated with soil properties and stand basal area (Fig. 4A). Opposing correlations with axis 2 for the Lakeland (r = -0.454) and Fuquay soil series (r = 0.453) suggested a soil moisture gradient from dry to moist conditions. The opposing correlations with axis 3 for pre-treatment stand basal areas of hardwoods ($r = 0.488$) and pines ($r = -0.460$) suggested a gradient of increasing fire disturbance history with increasing pine density. Each of the sites showed similar intensities of change, as indicated by the length of vectors connecting the two vegetation measurements. Vector lengths varied 0.61–0.74 ordination axis units among sites. However, the direction of change for site 24 was more closely aligned with ordination axis 2, while those for the other four sites were aligned almost equally with axes 2 and 3.

Results of the PERMANOVA test indicated that the treatment centroids differed significantly ($F_{7,28} = 1.89$; $P < 0.001$); however, only the cutting and broadcast foliar treatments demonstrated marginally significant pairwise comparisons with the non-treated check ($P \leq 0.067$). In contrast to the relatively uniform changes in plant community composition observed among the study sites (i.e., similar vector lengths and directions with the exception of site 24), changes associated with the hardwood control treatments varied both in terms of intensity (i.e., vector length) and direction (Fig. 4B). Intensity of change in plant community composition was ranked among treatments as follows: non-treated check (0.05 ordination axis units) < stem injection (0.37) < cutting (0.57) < imazapyr basal spray (0.65) < shredding (0.76) < basal spray (triclopyr) (0.83) < directed foliar (0.99) < broadcast foliar (1.05). Direction of change in plant community composition was aligned almost equally with ordination axes 2 and 3 for the shredding, stem injection, and basal spray treatments, but it was aligned more closely with ordination axis 3 (i.e., correlated with pine and hardwood basal areas) for the cutting and directed foliar treatments and with ordination axis 2 (i.e., correlated with soil properties) for the non-treated check and broadcast foliar treatment.

Mean covers per herb (1.3%) and woody species (1.7%) were numerically lower for site 24 than for the other four study sites (1.8–3.5% and 2.2–3.4%, respectively) (Table 7). Treatment effects on mean cover per species were significant for herb ($P = 0.038$), woody ($P < 0.001$), and all-species ($P = 0.008$) understory groups. The lowest values of mean cover per herb species were in the non-treated check and in the cutting and stem injection treatments (1.3–1.7%), although multiple comparisons failed to detect differences among treatment means (Table 7). Mean covers per woody species in the directed (0.9%) and broadcast foliar (0.3%) treatments were lower than in the cutting, shredding, stem injection, and imazapyr basal spray treatments (2.7–4.3%).

4. Discussion

4.1. Microclimate

With a mean PAR value of 23% of full sun on the forest floor prior to cutting overstory hardwoods, understory light availability was limiting to reproduction and growth of heliophytic species native to longleaf pine woodlands. The same light environment existed within the non-treated check for the duration of the study. This level of canopy transmittance is lower than the minimum value observed at 1 m above ground for longleaf pine woodlands in Georgia, USA (38% of full sun) (Battaglia et al., 2003), likely because the overstory of our remnant woodland study sites had a higher level of crown closure; it was dominated by mature, deciduous hardwoods having a higher leaf area than that of southern pines; and the understory was well developed with a variety of herb and woody species.

Given the timing of the SWC readings in 2017 with respect to the cutting of overstory hardwoods (May), shredding of logging residues (May-June), and herbicide treatments (October) (Fig. 1), results of the multiple comparisons were indicative of overstory hardwood presence (i.e., non-treated check and stem injection treatment) versus absence (i.e., the other six treatments). Corresponding mean SWC values during 2017 for the presence versus absence of overstory hardwoods were 5.5% and 7.5%, respectively. This indicates that presence of overstory hardwoods resulted in a mean SWC value that was below the permanent wilting point throughout the 2017 growing season (Baver et al., 1972), growing conditions which undoubtedly imposed severe limitations on establishment and growth of herb species. Therefore, as found by Harrington et al. (2003), it was probably the combined effects of shade and root competition from overstory trees that limited understory vegetation development in the non-treated check compared to the other treatments.

4.2. Hardwood sprouting and survival

The lower percentage of trees sprouting four months after cutting for sand post oak (43%) than for the other hardwood species (70–92%) was not expected (Table 3), because generally trees of most angiosperm species < 15 cm dbh produce numerous sprouts from the root collar after cutting (Burns et al., 1990). However, the percentage of trees that sprout after cutting generally declines with increasing tree dbh and age because genetic, physiological, and anatomical factors limit the life span of root collar buds (Del Tredici, 2001). Of the five hardwood genera or species studied, blackgum had both the smallest average dbh (i.e., 8 cm; Table 3) and the highest percentage of trees sprouting (i.e., 93%), supporting an expectation of vigorous sprouting for this species. The average dbh of sand post oak was 13 cm, yet previous research in the Missouri Ozarks, USA with a closely related species, post oak, predicted first-year sprouting for 74% of trees of this size (Johnson, 1977). Cutting of hardwoods after full leaf development has been shown to reduce sprout development of several western USA hardwoods compared to dormant season cutting, with the best control occurring on drier sites

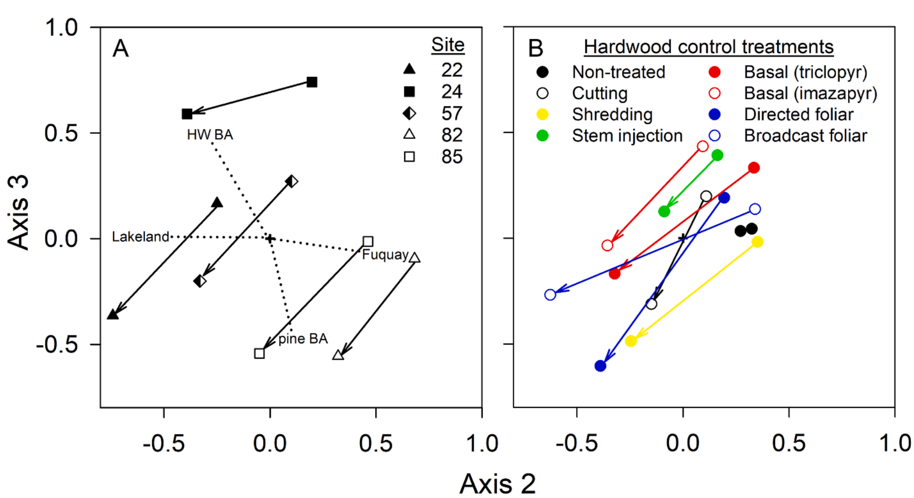

Fig. 4. Vegetation-based ordination group centroids by (A) study sites and (B) hardwood control treatments in remnant longleaf pine woodlands at the Savannah River Site near Aiken, SC, USA. The overall ordination centroid is indicated with a "+" symbol. For each plotted point, $n = 8$ and 5 for site and treatment responses, respectively. Arrows indicate the intensity (i.e., vector length) and direction of change in plant community composition from prior to treatment (2016) to 2 years after treatment (2019). Length and direction of dotted lines indicate correlations of the Lakeland and Fuquay soil series and pine and hardwood (HW) stand basal areas (BA) with the ordination axes.

Table 7
Mean cover (%) per species (standard error in parentheses) of understory species groups in 2019 by: (A) study sites and (B) hardwood control treatments in remnant longleaf pine woodlands at the Savannah River Site near Aiken, SC, USA. For a given species group, means for the hardwood control treatments followed by the same letter do not differ significantly ($P > 0.05$).

	(A) Study sites				
Species group	22	24	57	82	85
Herb species	2.0 (0.6)	1.3 (0.2)	3.5 (0.5)	2.7 (0.5)	1.8 (0.2)
Woody species	3.4 (0.6)	1.7 (0.3)	2.5 (0.7)	2.5 (0.6)	2.2 (0.3)
All species	2.9 (0.2)	1.4 (0.2)	3.1 (0.4)	2.5 (0.2)	2.0 (0.2)

	(B) Hardwood control treatments							
Species group	Non-treated	Cutting	Shredding	Stem injection	Basal spray (triclopyr)	Basal spray (imazapyr)	Directed foliar	Broadcast foliar
Herb species	1.7 (0.5) a	1.7 (0.5) a	2.4 (0.5) a	1.3 (0.5) a	2.9 (0.5) a	2.8 (0.5) a	3.1 (0.5) a	2.1 (0.5) a
Woody species	2.3 (0.4) bc	3.9 (0.4) ab	4.3 (0.4) a	2.7 (0.4) ab	2.4 (0.4) bc	2.9 (0.4) ab	0.9 (0.4) cd	0.3 (0.4) d
All species	2.3 (0.4) ab	2.7 (0.4) ab	3.0 (0.4) a	2.0 (0.4) ab	2.6 (0.4) ab	2.7 (0.4) a	2.2 (0.4) ab	1.6 (0.4) b

(Hart and Comeau, 1992). Findings from our research suggest that cutting alone may be adequate for controlling up to 64% and 32% of sand post oak and southern red oak trees, respectively, at least for xeric sites like those on the SRS (Table 4). Furthermore, cutting plus shredding of logging residues resulted in the cumulative mortality of 49–77% of trees of the five hardwood genera or species. We speculate that the additional effect of shredding on sprouting is likely a result of smothering hardwood sprouts by masticated logging residues. However, even the reduced sprouting may lead to the eventual recovery and long-term dominance by these hardwoods without the use of prescribed fire of sufficient intensity.

It can be argued that once the trees are cut the hardwoods can be readily controlled by frequent prescribed fires and that herbicides are unnecessary. However, the experience associated with equivalent operations at the SRS suggests success with applying prescribed fire is far more complex. A critical feature for prescribed fire in remnant longleaf pine woodlands is the presence of occasional mature pines, which provide additional flashy fuels to promote frequent, low-intensity surface fires needed to reduce woody encroachment (Knapp et al., 2014; Dell et al., 2017) and stimulate germination of native species from the seedbank (Cohen et al., 2004). On our study sites, many of the large pines that provided fine fuels were historically removed, and the often-sparse understory vegetation may require many years to develop a continuous and adequate fuel load to support periodic prescribed fire. Furthermore, smoke management and hazardous fire weather conditions can restrict the window for burning in a manner that limits the frequency and intensity of fire required for hardwood control. Herbicide treatments provide an effective approach for eliminating factors that prevent reintroduction of fire (i.e., dense overstory hardwoods and limited ground fuels) while encouraging factors that promote fire (i.e., a daylighted understory composed of herbaceous vegetation and longleaf pine regeneration), thereby re-establishing an alternative community state maintained by frequent disturbance (Freeman and Jose, 2009; Martin and Kirkman, 2009).

Each of the herbicide treatments effectively controlled the five hardwood genera or species (0–6% survival) compared to the non-treated check (99–100% survival) and cutting treatment (25–90% survival), as expected based on previous research (Quicke et al., 1996; Minogue and Quicke, 1999) (Table 4). This result means that long-term reductions in hardwood canopy cover can be achieved to prevent re-emergence of their competitive effects on understory vegetation and natural regeneration of longleaf pine.

Visual indicators of potential collateral damage to vegetation from the herbicide treatments were evident in 2018. We observed gaps devoid of all vegetation up to 2 m wide at the base of hardwood stems injected with a 50% solution of imazapyr herbicide. Similar gaps up to 0.5 m wide at the base of cut hardwoods were observed in the directed foliar treatment. As expected, the broadcast foliar treatment visually approached bare-ground conditions during the first year after treatment because the treatment is known as an effective method of forestry site preparation (Shepard et al., 2004; Dickens et al., 2018). These are known types of collateral damage based on previous research that can occur to understory vegetation with operational application of certain herbicide treatments, especially for soil active chemicals like imazapyr. Tu et al. (2001) advised caution when applying imazapyr because the herbicide is known to damage nearby untreated vegetation via spillage of excess chemical, soil movement, root leakage, root grafting, and transfer of treated soil.

4.3. Understory vegetation responses

Increases in herb cover from the treatments were the result of increased availability of light and soil water from the hardwood control treatments. Root competition in these xeric ecosystems can strongly impact understory plant development and flowering (Harrington et al., 2003; Harrington, 2006). The combined effects of cutting with either the basal spray or directed foliar treatments increased herb cover by 49–55% over that observed in the non-treated check (Table 5). Each of the basal spray and directed foliar treatments performed as hypothesized: they effectively controlled the hardwoods and increased herb cover compared to the non-treated check. In contrast, the cutting, shredding, and stem injection treatments did not increase herb cover relative to the non-treated check. As described previously, the stem injection treatment suffered from collateral damage due to the vegetation gaps it caused around individual trees. In the shredding treatment, collateral damage to herb cover from smothering of vegetation by masticated logging debris was not observed in 2018 or 2019. Although the broadcast foliar treatment was effective at reducing woody cover by 45%, it also did not facilitate an increase in herb cover relative to the non-treated check because of collateral damage from the herbicides.

The shredding, stem injection, basal spray, and directed foliar treatments increased herb species richness by 7 to 11 species over that observed in the non-treated check (Table 6). The species-area curve analysis demonstrated how treatment ranking shifted from 2018 to 2019 as the stem injection and directed and broadcast foliar treatments added additional species as they recovered from collateral damage from the herbicides. Treatment differences in the species-area curves were the result of variation in regression model intercepts (Table S4), indicating that treatment effects on herb species diversity occurred at the 1-m^2 sampling scale because $\log_e(1) = 0$ in equation [1] (Catano et al., 2020).

Although the hardwood control treatments increased richness of post-agricultural woodland indicator species, they did not increase richness of remnant woodland indicator species. These findings suggest that the pool of remnant species on these sites is currently limited and that a century or more of isolation from fire and overstory competition may have depleted the seed and bud banks (Turley and Brudvig, 2016; Buisson et al., 2019). Therefore, restoration of the native plant community in remnant longleaf pine woodlands is not complete; dispersal limitations are likely preventing additional remnant indicator species from becoming established (Turley et al., 2017). Enrichment seedings or plantings are likely to aid restoration of native species composition to remnant longleaf pine woodlands (Aschenbach et al., 2010; Turley and Brudvig, 2016). Given the large pool of remnant species across sites at the landscape level, providing better environmental conditions by hardwood removal coupled with subsequent prescribed fire should facilitate establishment of new species once their propagules arrive, at least during the first 3 to 5 years after treatment.

4.4. Ordination analysis

The ordination analysis revealed that changes in plant community composition after treatment were similar for four of the five study sites: from 2016 to 2019, the communities became more xeric like those found on the Lakeland soil series (i.e., site 22) and those typical of pine-dominated woodlands (Fig. 4A). Site 24, which had visual evidence of soil disturbance from fire-plow site preparation for longleaf pine natural regeneration, demonstrated changes that were more closely aligned with plant communities typical of the Lakeland soil series. Average covers per herb and woody species at site 24 were the lowest of all study sites (Table 7), suggesting that growth limiting factors associated with disturbance of the forest floor and surface soil layer, constrained the site occupancy of each species group.

For the shredding, stem injection, and basal spray treatments, changes in plant community composition followed a similar direction of change as observed for four of the study sites (i.e., equal alignment with ordination axes 2 and 3) (Fig. 4B). The direction of change for the broadcast foliar treatment was like that observed for site 24 probably because the treatment had a similar limiting effect on mean cover per woody species (Table 7). Using this same reasoning, we deduced that competition from overstory hardwoods in the non-treated check and from the greater site occupancy of woody species in the cutting and shredding treatments limited site occupancy of herb species; whereas, collateral damage from the herbicide treatments limited site occupancy of herb species in the stem injection and broadcast foliar treatments.

The PERMANOVA test indicated that plant community composition in treated areas differed from that in the non-treated check, particularly for the cutting and broadcast foliar treatments. This test result appears to be driven by the wide range of average covers per woody species observed among the non-treated check (2.3%), cutting (3.9%), and broadcast foliar treatments (0.3%). The intensity of change in plant community composition (i.e., vector length) was directly associated with the amount of plot area impacted by each treatment, with the following ranking of vector lengths: non-treated check $\ll$ stem injection $\ll$ basal sprays and shedding $<$ directed and broadcast foliar sprays.

In this early phase of long-term research on restoration of longleaf pine woodlands, initial plant community responses were found to be attributable to variation among treatments in control of overstory hardwoods, collateral damage of herb species, and relative site occupancies (i.e., average cover per species) of understory species groups. With the introduction of prescribed fire in the next phase of this research, it is unknown how subsequent plant community development will differ among treatments. Prescribed fire effects on the plant community could differ substantially among treatments, resulting in unique developmental trajectories, or they could homogenize the current differences among sites and hardwood control treatments that we have observed. Based on previous longleaf pine research that combined herbicide treatments for woody plant control with periodic prescribed fire (Harrington, 2011, 2020), we expect with the addition of fire a continuation of large differences in woody cover between herbicide- and mechanically treated areas. As a result of their low abundance of woody vegetation, the herbicide-treated areas are expected to experience hot, uniform burns likely to promote establishment of remnant woodland species. Long-term research like ours is essential for a complete understanding of the influences of site and treatment characteristics on patterns of plant community development in remnant woodlands.

5. Conclusions

The research has identified a wide range of treatment options for controlling hardwoods in remnant longleaf pine woodlands prior to the establishment of an effective prescribed fire regime. In terms of community structure, the directed foliar treatment shows the greatest potential for restoring the native ground-layer community of longleaf pine woodlands because it resulted in the highest cover of herb species (72%), the second lowest cover of woody species (13%), and the second highest richness of herb species (30 species per 100 m^2). Note that the two basal spray treatments also increased cover and richness of herb species, but they failed to reduce woody cover relative to the non-treated check and may require retreatment depending upon the effectiveness of the fire regime. The cutting and shredding treatments increased site occupancy (i.e., average cover) of woody species, and their longer-term performance in terms of restoring the native woodland community will depend on how their plant communities respond to prescribed fire. The community structure of the directed foliar treatment is likely to support periodic prescribed fires of adequate intensity to suppress woody encroachment, sustain an herb-dominated community, and promote regeneration of longleaf pine.

Observed collateral damage to the herb community from several of the herbicide treatments (e.g., vegetation gaps around trees in the stem injection and directed foliar treatments, bare-ground conditions in the first year after the broadcast foliar treatment) appeared to be short term, and recovery of herb species richness in these treatments was evident by year 2 (2019) (Fig. 3). Treatment-associated increases in species richness were observed for post-agricultural woodland indicator species but not for remnant woodland indicator species. This suggests that enrichment seedings or plantings will be useful for expediting restoration of the native species composition in remnant longleaf pine woodlands. Plant community responses to potential treatment interactions with periodic prescribed fire (e.g., Glitzenstein et al., 2003) will be the future focus of this long-term study.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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