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Influence of selection systems and shelterwood methods on understory plant communities of longleaf pine forests in flatwoods and uplands

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ABSTRACT

Although longleaf pine (*Pinus palustris* Mill.) forests have mostly been managed with even-aged methods, interest has been rising in uneven-aged systems, as a means of achieving a broader range of stewardship objectives. Selection silviculture has been practiced on a limited scale in longleaf pine, but difficulty of using traditional approaches and absence of an evaluation across a range of site types has left managers in doubt about its suitability. This study was conducted to quantify the effects on understory plant communities of applying single-tree selection, group selection, irregular shelterwood and uniform shelterwood in longleaf pine forests on flatwoods and uplands of the southeastern United States. Wiregrass (*Aristida beyrichiana* Trin. & Rupr.) and numerous other graminoids are highly desirable understory species, because they facilitate the essential ecological process of recurrent surface fire that sustains longleaf pine ecosystems. Forbs such as partridge pea (*Chamaecrista fasciculata* (Michx.) Greene) and low shrubs such as gopherapple (*Licania michauxii* Prance), blueberries (*Vaccinium* spp. L.) and huckleberries (*Gaylussacia* spp. Kunth) are also desirable as components of good wildlife habitat. Selection treatments reduced stand basal area to $\sim$11.5 m^2 ha^{-1} and shelterwood treatments left a basal area of $\sim$5.8 m^2 ha^{-1}. While higher levels of logging traffic from shelterwood treatment caused a significant decline in saw-palmetto (*Serenoa repens* W. Bartram) cover and increases in wiregrass at the flatwoods site, on the upland site it resulted in a sharp decline in wiregrass and silverthread goldaster (*Pityopsis graminifolia* (Michx.) Nutt.). Absence of prescribed fire during the post-treatment years led to progressive increases for shrub cover broadly across the flatwoods. Group selection caused modest understory change in flatwoods (temporary decrease in shrubs and increase in wiregrass), but resulted in a doubling of understory plant cover on uplands, with significant increases for hardwood tree seedlings, shrubs, vines, wiregrass, forbs and ferns. Single-tree selection caused no lasting impact on saw-palmetto, a decline in gallberry (*Ilex glabra* (L.) A. Gray) and increase in wiregrass in flatwoods and was related on uplands to increases in oak (*Quercus* spp. L.), dangleberry (*Gaylusaccia frondosa* (L.) Torr. & A. Gray ex. Torr.), broomsedge bluestem (*Andropogon virginicus* L.) and several forbs. Single-tree selection produced less change in the forest than group selection, which caused less alteration than shelterwood treatment. Selection silviculture appears to be a lower risk option for guiding longleaf pine forests along a trajectory of gradual improvement, with adjustments provided by frequent surface fires and periodic tree harvest. Long-term observation is needed to verify that selection can sustain diverse plant communities on sites characterized by differing environments.

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1. Introduction

Longleaf pine (*Pinus palustris* Mill.) forests were once among the most extensive ecosystems in North America, spanning 37 million ha from Texas to Florida to Virginia along the southeastern Coastal Plain, Piedmont and mountains. As a result of logging, land use conversion and interruption of natural fire regimes, longleaf pine occupancy within its natural range was reduced by 97% to about 1 million ha (Frost, 2006). Longleaf pine forests are reported to be among the most endangered terrestrial ecosystems in the Southeastern United States (Noss et al., 1995). In recent times, the remaining longleaf pine ecosystems have become valued for a variety of resources of substantial ecological, economic and cultural importance. Interest among resource professionals and the public has therefore increased, concerning appropriate manage-

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ment methods for sustaining (and where possible restoring) longleaf pine ecosystems (Brockway et al., 2005b; Van Lear et al., 2005).

Scientific research, in recent decades, has fostered improved technological applications to assist forest managers with the establishment, recovery and maintenance of longleaf pine ecosystems (Jose et al., 2006). Interest in the private sector and management direction in the public sector has recently emphasized improved management of existing longleaf pine forests and, on suitable sites, eventual expansion of the area occupied by longleaf pine ecosystems. To these ends, the principal goal of sustainable forest management should be application of silvicultural methods that ensure the maintenance of longleaf pine ecosystems in perpetuity. Such methods will incorporate natural regeneration and, to the degree possible, simulate disturbance events and other ecological processes that contributed to maintaining longleaf pine ecosystems prior to European settlement. However rather than relying upon random chance, management will deliberately manipulate ecosystems in a systematic manner to achieve specific stewardship objectives (Brockway et al., 2006).

Longleaf pine forests can grow on a wide variety of site types (e.g., wet flatwoods, mesic uplands, xeric sandhills, mountains), each characterized by a distinctly different environment. Across its range, longleaf pine is often found in association with slash pine (*Pinus elliottii* Englem.) on flatwoods sites, loblolly pine (*Pinus taeda* L.) and shortleaf pine (*Pinus echinata* Mill.) on upland sites, and various hardwood species on many site types (Boyer, 1990a). Therefore, no single management prescription is appropriate for sustaining longleaf pine forests everywhere. Prudent managers will typically select a combination of methods that is appropriate for their specific environment and that allows for the trajectory of forest development to proceed from current status to future conditions, which will be suitable for meeting their differing management goals.

It is desirable to restore and maintain the plant community through appropriate application of prescribed burning and cutting treatments, since an understory with a suitable composition of native groundcover plants will not only support higher levels of biological diversity, but will also minimize regeneration difficulty (Brockway et al., 2009; Outcalt and Brockway, 2010). In the absence of an understory dominated mostly by herbaceous plants, management activities may increase competition from woody species, thereby jeopardizing longleaf pine sustainability. Regardless of the stand reproduction method chosen, managers should keep in mind the crucial importance of frequent prescribed burning. Periodic surface fire is essential for restoring and maintaining composition, structure and function, primarily by curtailing development of competing woody plants (i.e., other pines, hardwoods, shrubs). The resulting understory conditions are suitable for herbaceous groundcover species and create seedbed conditions favorable for regeneration and development of longleaf pine seedlings (Brockway and Lewis, 1997; Waldrop et al., 1989; Brockway and Outcalt, 2000; Wade et al., 2000; Outcalt, 2000, 2006; Haywood et al., 2001; Outcalt and Wade, 2004).

Longleaf pine ecosystems are classified into 132 plant associations (Peet, 2006). With understories capable of supporting as many as 40 vascular plant species per m^2 (Walker and Peet, 1984), these are among the most species-rich habitats outside the tropics (Walker and Silletti, 2006). Of the hundreds of species that occur in these ecosystems, certain plants serve important functions and are therefore desirable. Wiregrass (*Aristida beyrichiana* Trin. & Rupr.) and bluestem grasses (*Schizachyrium scoparium* (Michx.) Nash and *Andropogon* spp. L.) are keystone ecosystem components, in that their flammable tissue and structural contiguity promotes the recurrent surface fire needed to sustain longleaf pine. Frequent fire favors an understory community where graminoids are prominent, such as Indiangrass (*Sorghastrum* spp. Nash), dropseed (*Sporobolus* spp. R. Br.), crowngrass (*Paspalum* spp. L.) and numerous other grasses (Brockway et al., 2005b). Although oak (*Quercus* spp. L.) seedlings and shrubs such as gallberry (*Ilex glabra* (L.) A. Gray), yaupon (*Ilex vomitoria* Aiton), staggerbush (*Lyonia* spp. Nutt.), wax myrtle (*Myrica cerifera* L.) and rosemary (*Ceratiola ericoides* Michx.) may also occur, their cover is limited by periodic fire. This limitation creates conditions favorable for the flourishing of forbs and other herbaceous plants, hence the great species diversity found here. Forbs commonly observed include asters (*Aster* spp. L.), wild indigo (*Baptisia lanceolata* (Walter) Elliott), vanillaleaf (*Carphephorus odoratissimus* (J.F. Gmel.) H. Hebert), partridge pea (*Chamaecrista fasciculata* (Michx.) Greene), elephant's foot (*Elephantopus tomentosum* L.), milkpea (*Galactia* spp. P. Browne), silverthread goldaster (*Pityopsis graminifolia* (Michx.) Nutt.), noseburn (*Tragia urens* L.) and many others.

On frequently-burned uplands, herbaceous plants should dominate the understory community, with woody plants occurring infrequently across the site. On frequently-burned flatwoods, grasses and forbs may also dominate, with woody plants such as saw-palmetto (*Serenoa repens* W. Bartram) relegated to small "islands" that may comprise 25% or less of the site. Such understory conditions are desirable goals for these sites (Brockway et al., 2005b). However, logging traffic is likely to be greater for shelterwood methods (more trees removed ha^{-1}) than for selection systems and this contrast may differentially influence the rate and direction of understory change. Skidding greater numbers of trees from a site could have beneficial effects for herbaceous plants, by reducing woody plants where they are already abundant, as in the flatwoods. But, such high traffic could be disruptive to understory communities that are already in desirable condition, such as those in frequently-burned uplands. Also worth noting, when timber harvest disturbance is limited and frequent fire is absent, saw-palmetto can gain dominance and occupy 75% or more of a flatwoods site, forming a dense shrub canopy that excludes many other species (Brockway et al., 2005b).

Although even-aged methods have been most often chosen for longleaf pine management, uneven-aged systems, which create and maintain multi-cohort stands with continuous regeneration and higher levels of canopy cover, have recently received increasing interest, as a better way to achieve a broad range of forest stewardship objectives. While an extensive body of research exists about even-aged methods for longleaf pine, uneven-aged silviculture has received less attention (Brockway et al., 2005a; Guldin, 2006). Uneven-aged approaches have been practiced on a limited scale in longleaf pine forests, often with encouraging results (Farrar, 1996; Jack et al., 2006). But, the difficulty of learning and applying traditional approaches and lack of a thorough scientific evaluation across the range of site types comprising these ecosystems has left managers with doubt concerning the appropriateness of uneven-aged silviculture. Yet, the public has expressed a desire that forests be managed (1) over longer rotations, (2) with methods that mimic natural processes, (3) by approaches that are sustainable in the long term and (4) in a manner that conserves the unique biological diversity of these ecosystems. Although uneven-aged silviculture can mimic natural stand replacement dynamics that occur in longleaf pine forests, scientists and managers have had little experience applying uneven-aged approaches in longleaf pine and it was unclear whether selection systems could ensure that sustainability and biodiversity goals would be met.

Therefore, a comparative analysis was needed to evaluate the benefits and risks associated with the principal stand reproduction methods for longleaf pine when implemented on sites with different environmental conditions. In this operational-scale study, our principal objective was to quantify the influence of two selection systems and two shelterwood methods on (1) foliar cover by species and life-form and (2) alpha diversity of understory plants present in flatwoods and uplands. Our secondary objective was to assess the merits of applying each silvicultural approach, relative to sustaining the understory plant community and related resource values.

2. Methods

2.1. Study sites and management history

2.1.1. Goethe State Forest flatwoods

The Goethe State Forest is located 24 km east of the Gulf of Mexico (29°13′N, 82°33′W), on the Lower Coastal Plain of the Florida peninsula. Temperatures in the humid subtropical climate range from a maximum of 33 °C in summer to a minimum of 5 °C in winter. Annual precipitation averages 1448 mm, arriving mostly from April to September. At 15 m above sea level, topography is nearly level and dominated by Smyrna fine sand (Aeric Alaquod), which is very deep, poorly-drained, low in organic matter and nutrients and low in water holding capacity (Slabaugh et al., 1996).

The overstory was dominated by longleaf pine, with lesser amounts of slash pine and very few hardwoods. Tree seedlings were few and mostly comprised of slash pine, longleaf pine, sweetgum (*Liquidambar styraciflua* L.) and oaks. Understory plants were dominated by shrubs, primarily saw-palmetto and gallberry, with lesser amounts of wax myrtle, dwarf live oak (*Quercus minima* (Sarg.) Small), shiny blueberry (*Vaccinium myrsinites* Lam.) and fetterbush (*Lyonia lucida* (Lam.) K. Koch). Because of shrub dominance, the herbaceous layer was poorly developed, with wiregrass, broomsedge bluestem (*Andropogon virginicus* L.), witchgrass (*Dichanthelium* spp. Willemet) and nodding fescue (*Festuca obtusa* (Pers.) E.B. Alexeev) the most prominent grasses.

These flatwoods were cutover about 100 years ago and then subjected to a 50-year period of fire exclusion, during which trees recovered and saw-palmetto expanded to now dominate the understory. Since 1992, active programs of prescribed burning on a 3-year cycle and timber harvest have been implemented to foster multiple-use management and restore the ecosystem. The most recent prescribed fire was applied to the study area during April 2005 (pretreatment). Stands received improvement cuts between 1997 and 2004. Overstory pines were 48–74 years in age and site index ranges from 21 to 24 m at 50 years.

2.1.2. Blackwater River State Forest uplands

The Blackwater River State Forest is located 48 km north of the Gulf of Mexico (30°47′N, 86°44′W), on the Middle Coastal Plain of the Florida panhandle. Average temperatures range from 27 °C in summer to 12 °C in winter. Annual precipitation averages 1651 mm, with about half arriving from June to September. At 61 m above sea level, topography is nearly level to gently inclined. Soils include the Troup (Grossarenic Paleudult), Orangeburg (Typic Paleudult), Lucy (Arenic Paleudult) and Dothan (Plinthic Paleudult) series, which are deep, well-drained and sandy soils, low in organic matter and nutrients and low to moderate in water holding capacity (Weeks et al., 1980).

The overstory was dominated by longleaf pine, with a smaller component of hardwoods and slash pine. Tree seedlings were abundant in the understory, with southern red oak (*Quercus falcata* Michx.), bluejack oak (*Quercus incana* W. Bartram), post oak (*Quercus stellata* Wangenh.), persimmon (*Diospyros virginiana* L.) and longleaf pine most common. Dangleberry (*Gaylussacia frondosa* (L.) Torr. & A. Gray ex. Torr.), blueberries (*Vaccinium* spp. L.), blackberries (*Rubus* spp. L.), wax myrtle, gallberry, winged sumac (*Rhus copallinum* L.) and gopherapple (*Licania michauxii* Prance) were the most prominent shrubs. The herbaceous layer was well developed and species-rich, with wiregrass and broomsedge bluestem dominating the grasses, with lesser amounts of witchgrass, crowngrass, lopsided Indiangrass (*Soghastrum secundum* (Elliott) Nash) and purpletop (*Tridens flavus* L.). The most common forbs were silverthread goldaster, morning-glory (*Ipomea* spp. L.), milkpea (*Galactia volubilis* (L.) Britton) and noseburn.

These uplands were occupied by second-growth longleaf pine that naturally regenerated following cutover of the original forest during the 1920s. Most of the overstory pines were about 66 years old, with the oldest being 80 years in age. Site index is 24 m at 50 years. This site has been managed with numerous prescribed fires since 1970, on a 3-year burning cycle. The most recent prescribed fires were applied to the study area during December 2004 (pretreatment) and February 2010 and September 2011 (post-treatment). Improvement cutting during 1981 and 1991 and hurricane–salvage in late 2004 were followed by waves of natural regeneration that resulted in an uneven-aged structure.

2.2. Study design

In June and July 2004, a randomized complete block study design was installed as three replications of the four silvicultural treatments (single-tree selection, group selection, irregular shelterwood and uniform shelterwood), plus three control stands (no timber harvest), at each site. During May 2005, treatments were randomly assigned within the three replications that were aggregated as blocks to topographically account for moisture gradient or spatial differences. The 15 plots (stands) are each 9 ha (300 × 300 m) and total 135 ha at each forest. Within each treatment plot, five 0.1-ha measurement subplots were randomly located, each 20 × 50 m with the long axis oriented in a north–south direction. Midway along the southern boundary of each subplot is a 15-m line-transect, oriented in a north–south direction.

2.3. Experimental treatments

In all selection-treated stands, the forest matrix was tended by reducing basal area to 11.5 $m^2\,ha^{-1}$ using the Pro-B method (Brockway et al., 2014) and, in group selection stands, three 0.1–0.2-ha gaps were then created in each 9-ha plot. Canopy gap width ranged from 1.4 to 2 times the height of adjacent dominant trees. Proportional Basal Area or Pro-B is an accurate and easy-to-use method for implementing selection silviculture that aggregates many diameter classes into three diameter-class groups, thereby improving efficiency by requiring tree markers to remember only three fractions, while making a single pass through the stand. In meeting both ecosystem stewardship goals and timber production objectives, trees of large size, specific species and with good form, broad crowns and cavities can be retained, while adjusting spacing to release residuals. In shelterwood-treated stands, the forest was reduced to a basal area of 5.8 $m^2\,ha^{-1}$, leaving substantial distance between crowns of the residual overstory trees. Overall basal area at both sites, prior to cutting treatment (and hurricane disturbance on uplands), was ~16 $m^2\,ha^{-1}$. In November and December 2006, marked trees were harvested by private logging contractors.

During September 2004, Hurricane Ivan passed close enough to cause substantial windthrow damage to the eastern portion of the Blackwater River State Forest uplands. Following tree-salvage in winter 2005, three plots were too badly damaged to retain in the study. Since the uniform shelterwood method in longleaf pine forests had earlier received more scientific study and was more extensively documented in the literature than the other treatments in this study, it was deleted at that site. The analysis was modified to evaluate only the control and single-tree selection, group selection and irregular shelterwood treatments at that location.

2.4. Measurements

In September 2005, foliar cover (vertical projection of canopy) for each understory plant species was measured by the line-intercept method along each of the five 15-m line-transects in each treatment plot, to establish pretreatment conditions (Bonham, 1989). Foliar cover for individual species was then summed to determine cover for each functional group and the total foliar cover, which at times exceeded 100% from multiple canopy layers present in the understory. Repeated post-treatment measurements were completed during the early fall of 2007, 2008, 2010 and 2012 to ascertain the response of the understory plant community to treatments. Identification and nomenclature for plant species were consistent with taxonomic authorities (Clewell, 1985; Godfrey, 1988; Wunderlin, 1998; Duncan and Duncan, 1999; Miller and Miller, 1999).

2.5. Analysis

Foliar cover data for understory plant species were summarized as estimates of the mean for each 9-ha plot and analyzed by treatment and change through time. These data were used as importance values for computing several diversity indices (Ludwig and Reynolds, 1988). Species richness (N_0) was characterized on each plot by counting the number of species present, evenness was calculated using the modified Hill ratio (E_5) (Alatalo, 1981) and diversity was estimated using the Shannon diversity index (H') (Shannon and Weaver, 1949).

Means of the dependent variables for each plot were used to estimate the means and variances for the treatment units. A repeated measures ANOVA, using initial conditions as covariates, was used to evaluate time and treatment effects and interactions (Hintze, 2007). Responses of treatments were compared using pairwise contrasts. The trend through time after treatment was analyzed using orthogonal polynomials. Statistical analysis of the time and treatment interaction for computed diversity indices was completed using the bootstrap technique PROC MULTTEST in SAS (Efron and Tibshirani, 1993; Westfall and Young, 1993; SAS Institute, 1996). Adjusted *p*-values, which maintain a constant Type I error across the full range of comparisons, were used to determine significant differences among means (10,000 bootstrap iterations were used). Unless otherwise indicated, significant differences were discerned at the 0.05 level.

3. Results

3.1. Goethe State Forest flatwoods

The mechanical action of logging machines resulted in significant overall declines in the foliar cover of understory plants (from 146% to 133% cover) during the first year after treatment (2007) in single-tree selection, group selection and irregular shelterwood stands (Table 1). Understory plant cover recovered in the group selection and irregular shelterwood stands by the second year after treatment (2008) and in the single-tree selection stands by the fourth year after treatment (2010). By the sixth year after treatment (2012), plant cover in group selection, irregular shelterwood and uniform shelterwood stands (~163% cover) exceeded pretreatment levels and that in single-tree selection stands recovered to pretreatment levels. With no effect on the very few trees present in the understory, these fluctuations resulted from changes in the cover of shrub and herbaceous species.

Shrub cover declined significantly during the first year after treatment in all stands (from 110% to 96% cover), but failed to recover during the second year only in stands treated with shelterwood methods. A decline in saw-palmetto, the most prominent shrub, is largely responsible for this trend. The cover of saw-palmetto decreased significantly in single-tree selection (from 65% to 58% cover), group selection (from 54% to 45% cover), irregular shelterwood (from 53% to 30% cover) and uniform shelterwood (from 65% to 46% cover) stands immediately after treatment and did not recover by the second post-treatment growing season, except in the single-tree selection stands. Greater disturbance from higher levels of machine traffic related to more overstory tree removal in group selection stands and shelterwood stands very likely accounted for saw-palmetto cover being significantly lower there than in the single-tree selection and control stands. By the sixth year after treatment, shrub cover in all treated stands (~128% cover) exceeded pretreatment levels and the cover of saw-palmetto recovered in all treated stands except those treated by irregular shelterwood. A similar decline and recovery trend was noted for gallberry in shelterwood stands; however, gallberry failed to fully recover in selection stands, even six years after logging. Conversely, fetterbush cover progressively increased through time in all stands, wax myrtle increased in shelterwood and group selection stands and blueberry increased in irregular shelterwood stands. Vine cover was unaffected by treatment.

While remaining largely unchanged in single-tree selection, group selection and control stands, herbaceous plant cover increased significantly following irregular shelterwood (from 36% to 52% cover) and uniform shelterwood (from 20% to 33% cover) treatments. These increases were mostly driven by a significant rise in graminoids (from 33% to 49% cover and from 15% to 27% cover), following the decline of saw-palmetto. Increases in wiregrass (from 6% to 15% cover) and nodding fescue (from 4% to 11% cover) contributed to this rise. However, herbaceous plant cover declined by the sixth year after treatment, as saw-palmetto, fetterbush and wax myrtle expanded. No significant changes were observed among forbs and ferns, which were present at low levels (~1–8% cover).

By the second year after treatment, plant species richness increased (from 17 to 21) across all stands (Table 2). Although this trend is somewhat weak ($p = 0.09$), it is indicative of progress toward restoring biological diversity in these stands. Only group selection stands contained species numbers (25) that were significantly greater than those in control stands (18). However, as saw-palmetto and other shrubs expanded, species richness fell once again to pretreatment levels, by the sixth year after treatment. Although initially declining in single-tree selection (from 0.61 to 0.54) and control (from 0.62 to 0.56) stands, species evenness significantly increased in the irregular shelterwood (from 0.64 to 0.70) and uniform shelterwood (from 0.55 to 0.63) stands, two years after treatment. By the sixth year after treatment, evenness in single-tree selection and control stands returned to pretreatment levels and continued to increase in group selection and shelterwood treatments. Increased evenness indicates an improved equitability in the distribution of resources among many species, thus a decreased likelihood that a few species disproportionally dominate a site. Despite the rise in evenness for group selection and shelterwood stands, increases in plant species diversity were transitory for these treatments and returned to pretreatment levels by the sixth year after logging. These cyclic trends in species richness and diversity and progressively rising trend for species evenness point to potential for future improvement in the understory plant community following repeated cycles of prescribed fire and tree harvest.

Table 1
Understory plant response (% foliar cover) to stand reproduction methods at the Goethe State Forest flatwoods for pretreatment (2005) and post-treatment (2007–2012) years.

	Control	Single-tree selection	Group selection	Irregular shelterwood	Uniform shelterwood
All plants					
2005	132.1	146.8	149.1	141.9	140.5
2007	131.9	132.1[t]	137.8[t]	129.4[t]	137.1
2008	136.6	138.5[t]	146.8	149.0	138.9
2010	134.4	144.7	159.5[at]	159.3[at]	165.6[at]
2012	141.7	145.7	161.7[at]	162.9[at]	163.1[at]
Trees					
2005	0.0	0.1	0.3	0.1	0.3
2007	2.2	0.1	1.1	0.2	0.0
2008	2.2	0.2	2.7	0.5	0.3
2010	2.5	0.7	2.3	0.8	1.3
2012	2.2	0.6	2.5	1.5	1.5
Shrubs					
2005	101.0	112.0	113.0	104.9	117.5
2007	90.8	99.3[t]	103.5[t]	81.2[t]	102.7[t]
2008	100.4	106.8	109.7	96.9[t]	104.4[t]
2010	103.6	117.8	124.3[at]	108.9	133.5[at]
2012	119.0	120.2	129.0[t]	127.1[t]	135.6[at]
Saw-palmetto					
2005	59.5	65.3	54.2	53.2	64.9
2007	52.2	57.7	44.7[t]	29.9[at]	46.3[t]
2008	61.3	64.2	46.5[a]	35.2[at]	46.9[at]
2010	52.9	62.6	46.6	37.7[at]	60.4
2012	56.9	66.9	51.6	40.2[at]	60.4
Gallberry					
2005	26.3	31.7	37.1[a]	32.0	26.9
2007	16.8[t]	22.9[t]	29.1[at]	20.6[t]	24.7
2008	16.9[t]	21.2[t]	30.5[at]	25.3	21.3
2010	21.6	31.1	32.9[a]	28.8	33.7[a]
2012	15.9[t]	21.4[t]	28.6[at]	37.8[a]	34.2[a]
Fetterbush					
2005	0.5	0.7	1.7	2.2	2.4
2007	5.4[t]	4.4	6.5[t]	7.5[t]	6.8[t]
2008	8.2[t]	5.2[t]	8.5[t]	3.8	8.7[t]
2010	9.5[t]	3.3	11.5[t]	8.8[t]	9.7[t]
2012	11.0[t]	8.5[t]	14.5[t]	11.6[t]	10.6[t]
Wax myrtle					
2005	2.5	2.1	3.7	7.7[a]	3.6
2007	2.4	1.5	2.9	9.1[a]	4.1
2008	1.7	2.3	4.7	12.7[at]	5.4
2010	4.0	5.1	6.7	13.6[at]	8.8[t]
2012	4.2	5.1	8.9[t]	19.5[at]	9.3[t]
Dwarf live oak					
2005	5.1	3.5	5.5	3.1	6.8
2007	6.3	3.9	7.3	5.4	8.1
2008	5.2	3.8	4.9	5.0	7.9
2010	6.5	4.7	8.1	6.0	8.7
2012	6.6	3.3	4.7	2.9	4.6
Shiny blueberry					
2005	2.9	4.9	6.6	2.4	4.2
2007	3.5	4.7	7.7	4.8[t]	6.5[t]
2008	3.6	2.7[t]	6.1	4.8[t]	3.5
2010	3.5	3.1[t]	5.3	5.9[t]	3.1
2012	3.1	4.1	7.3	5.5[t]	4.1
Vines					
2005	2.3	0.7	0.4	0.5	2.3
2007	0.7	0.4	0.3	0.0	1.3
2008	1.1	0.6	0.4	0.1	0.9
2010	0.9	0.3	1.3	0.1	0.9
2012	2.5	0.5	2.1	0.6	3.8
Woody plants					
2005	103.3	112.8	113.7	105.5	120.1
2007	93.7	99.8[t]	104.9[t]	81.4[t]	104.0[t]
2008	103.7	107.6	112.8	97.5	105.6[t]
2010	106.9	118.8	127.8[at]	109.9	135.7[at]
2012	123.7[t]	121.3	133.7[t]	129.3[t]	140.9[at]
Herbaceous plants					
2005	28.7	34.0	35.4	36.4	20.4
2007	38.2	32.3	32.9	48.0[at]	33.1[t]

Table 1 (*continued*)

	Control	Single-tree selection	Group selection	Irregular shelterwood	Uniform shelterwood
2008	32.9	30.9	34.0	51.5[at]	33.3[t]
2010	27.5	25.9	31.7	49.4[at]	29.9[t]
2012	18.0	24.4	28.1	33.6[a]	22.3
Graminoids					
2005	24.8	31.1	26.7	33.1	15.3
2007	34.3	29.8	27.1	43.6[t]	23.3[t]
2008	29.1	27.0	26.9	49.3[at]	27.3[t]
2010	22.9	23.1	26.1	43.8[at]	24.3[t]
2012	17.6	22.5	25.1	31.3	16.6
Wiregrass					
2005	13.9	13.5	11.9	6.3	7.1
2007	24.2[t]	19.9[t]	16.1	9.6	11.4
2008	22.1[t]	17.9	15.5	12.0[t]	13.5[t]
2010	8.9	18.5	19.2[t]	14.9[t]	15.2[t]
2012	15.3	20.1[t]	20.7[t]	15.9[t]	13.5[t]
Broomsedge bluestem					
2005	2.3	3.3	1.1	8.7	0.1
2007	4.3	1.9	1.3	7.3	1.7
2008	1.4	0.6[t]	2.4	9.5[a]	2.2
2010	8.0	0.7[at]	2.0	11.9	2.6
2012	1.2	0.2[t]	0.6	5.7	1.0
Witchgrass					
2005	2.2	7.6	8.7	9.7[a]	3.9
2007	1.8	4.4	3.3	11.3[a]	5.9
2008	0.7	2.5[t]	2.9[t]	4.5	3.8
2010	0.2[t]	1.0[t]	1.7[t]	3.8	2.9
2012	0.9	0.3[t]	2.2[t]	2.7[t]	1.3[t]
Nodding fescue					
2005	0.6	3.7	0.0	4.4	0.3
2007	2.6	2.5	3.1	9.7[at]	2.9
2008	2.1	0.3	1.6	11.4[at]	3.5
2010	2.9	2.5	3.1	11.0[at]	3.4
2012	0.1	0.0	1.5	5.3	0.7
Forbs					
2005	3.9	1.6	4.9	2.7	1.7
2007	3.9	1.0	4.1	2.7	2.0
2008	3.4	2.5	5.5	1.9	1.9
2010	4.1	1.1	2.9	3.1	2.3
2012	0.3[t]	0.7	0.5[t]	0.7	1.2
Ferns					
2005	0.0	1.3	3.8	0.6	3.4
2007	0.0	1.5	1.7	1.7	7.8[a]
2008	0.4	1.4	1.6	0.3	4.1
2010	0.5	1.7	2.7	2.5	3.3
2012	0.1	1.2	2.5	1.6	4.5

[a] Significantly different from control, $p < 0.05$.
[t] Significant change through time from pretreatment condition, $p < 0.05$.

3.2. Blackwater River State Forest uplands

Substantial overall variation (85–168% cover) was present prior to treatment, with single-tree selection and irregular shelterwood stands having significantly greater understory plant cover than group selection and control stands (Table 3). This initial differential in foliar cover was the result of many plant species, with blueberries, wiregrass and silverthread goldaster being most prominent. Significant post-treatment increases in overall plant cover were observed only in group selection and control stands (i.e., those having the lowest initial values). Thus, the net effect after six years was to nearly equalize overall understory plant cover (157–181% cover).

A similar differential and pattern of change was noted for woody plants (39–60% initially becoming 65–78% cover after six years), although trends vary for different components of this group. By six years after treatment, woody plants had expanded in all stands, with the greatest gains noted in group selection (from 39% to 78% cover) and control stands (from 40% to 78%). Gains were more modest in single-tree selection (from 60% to 72% cover) and irregular shelterwood stands (from 57% to 66% cover).

Understory tree cover progressively increased in shelterwood and control stands (from 14% to 22% cover), but rose within two years (to ∼23% cover) and then declined after six years (to 16–21% cover) in selection stands. Such trends were largely driven by southern red oak, bluejack oak and, to a lesser degree, persimmon. However, near its peak, southern red oak cover was significantly lower in group selection and irregular shelterwood stands (<8% cover) than in single-tree selection and control stands (10–16% cover).

The initial differential and pattern of change was also observed for shrubs (19–40% cover). But, while some species like dangleberry and gopherapple increased threefold or more, others like blackberries and blueberries responded with increases and decreases. Six years after treatment, the greatest shrub gains were observed in group selection (from 19% to 54% cover) and control stands (from 24% to 53% cover). These resulted mostly from increases in dangleberry, blueberry and gopherapple in group

Table 2
Understory plant species richness, diversity and evenness response to stand reproduction methods at the Goethe State Forest flatwoods for pretreatment (2005) and post-treatment (2007–2012) years.

	Control	Single-tree Selection	Group Selection	Irregular Shelterwood	Uniform Shelterwood
Number of species (richness)					
2005	15.0	15.0	19.0	18.7	17.3
2007	17.3	17.3	18.7	21.3	18.3
2008	18.3[u]	19.0[u]	25.0[at]	22.3[u]	19.3
2010	16.7	16.7	19.7	20.7	19.0
2012	15.3	16.0	16.3	19.0	18.0
Shannon index (diversity)					
2005	1.65	1.71	1.93	1.90	1.78
2007	1.84	1.78	2.08	2.25[at]	2.04[t]
2008	1.75	1.79	2.23[at]	2.29[at]	2.13[at]
2010	1.91	1.73	2.16[t]	2.23[at]	1.95
2012	1.94	1.77	2.08	2.12	1.94
Modified Hill ratio (evenness)					
2005	0.62	0.61	0.61	0.64	0.55
2007	0.60	0.60	0.64	0.74[at]	0.66[t]
2008	0.56[t]	0.54[t]	0.59	0.70[at]	0.63[t]
2010	0.63	0.60	0.67[t]	0.72[at]	0.63[t]
2012	0.64	0.58	0.67[t]	0.74[at]	0.63[t]

[a] Significantly different from control, $p < 0.05$.
[t] Significant change through time from pretreatment condition, $p < 0.05$.
[u] Significant change through time from pretreatment condition, $p < 0.10$.

selection stands and dangleberry, blueberry, blackberry and gallberry in control stands. Vines increased significantly only in group selection stands (from 5% to 11% cover).

Herbaceous plant cover was significant lower than controls only in group selection stands (46%) and significantly higher only in irregular shelterwood stands (111%), prior to treatment. However, one year after treatment, there was no significant difference in herbs across all treatments (92–110% cover) and the expansive pattern in group selection (from 46% to 103% cover) and control stands (from 78% to 113% cover) continued through all years. This trend was driven by increases in graminoids (from 31% to 65% cover) and forbs (from 15% to 32% cover) for group selection and forbs (from 23% to 47% cover) for control stands. While broomsedge bluestem steadily increased following treatment, wiregrass increased only in group selection (from 20% to 44% cover) and control stands (from 35% to 44% cover) and decreased in single-tree selection (from 55% to 31% cover) and irregular shelterwood stands (from 52% to 35% cover), by six years after logging.

Forb cover, that was initially highest in irregular shelterwood stands (37%) and lowest in group selection stands (15%), oscillated during the seven years of observation, reaching a peak four years after treatment (2010) that ranged from 39% to 57% cover. Six years after treatment, forbs more than doubled in group selection (from 15% to 32% cover) and control stands (from 23% to 47% cover). Although morning-glory, milkpea and noseburn were contributors, much of this trend can be traced to fluctuations in silver-thread goldaster, which also peaked four years after treatment (12–30% cover). Silver-thread goldaster also exhibited a significant early decline only in the irregular shelterwood stands (from 23% to 8% cover), an indication (along with the decline of wiregrass) that the greater disturbance resulting from higher levels of machine traffic to extract more overstory trees may have been detrimental to these species during the early post-harvest time period. Fern cover increased significantly only in group selection (from 1% to 7% cover) and irregular shelterwood stands (from 1% to 14% cover), where higher levels of sunlight were likely present.

Prior to treatment, species richness in the single-tree selection (37) and irregular shelterwood (31) stands were significantly lower than in control (47) stands (Table 4). One year after treatment, species numbers declined in group selection and control stands and increased in irregular shelterwood stands ($p = 0.08$). By end of the second post-treatment growing season, there were no significant differences in richness across all treatments (34–37) and this continued throughout the remaining years of observation. While group selection and control stands remained largely unchanged, species evenness significantly increased in single-tree selection (from 0.50 to 0.70) and irregular shelterwood stands (from 0.55 to 0.72 before declining to 0.64). The rise in species evenness and relatively stable richness values resulted in progressively increasing species diversity for single-tree selection stands (from 2.61 to 2.89), during the six years following tree harvest. Improving species evenness and elevated species richness produced higher species diversity in irregular shelterwood stands, during the first two years following logging (from 2.58 to 3.02 and 2.91). Species diversity declined in group selection stands (from 2.99 to 2.73) following treatment, a result reflected in the decline of species richness after disturbance.

4. Discussion

4.1. Goethe State Forest flatwoods

When our study began, these stands were in a condition typical of many longleaf pine forests that had been burned little. Shrubs, principally saw-palmetto, came to dominate the understory during the period of fire exclusion, prior to public acquisition of the forest. Saw-palmetto and similar shrubs created groundcover conditions that are adverse to those required for herbaceous plants and for regeneration of longleaf pine (Brockway et al., 2006). Saw-palmetto was visibly widespread and often tall as 1.5 m or more. The forest floor below saw-palmetto plants was typically covered by a thick mat of fallen saw-palmetto fronds and surface soil was occupied by numerous large saw-palmetto rhizomes. There were very few openings in the shrub canopy where herbaceous species could thrive or longleaf pine seedlings could become established. Pretreatment surface fires (most recently in April 2005) somewhat moderated these conditions; however, the shrub canopy progressively expanded during subsequent years, when these stands could not be safely burned. Plant community dynamics, following treatment, reflected differing degrees of stand density reduction from implementing two selection systems and two shelterwood methods and the consequences of postponing prescribed fire during post-treatment years.

Shrub cover was diminished, during the first year after treatment, by the mechanical disturbance of logging and then rose at differential rates among the treatments, in the absence of periodic surface fire. This trend was most pronounced for saw-palmetto, recovering more rapidly in selection stands than in shelterwood stands. This difference was not unexpected, since about two-thirds of the trees were removed from the shelterwood stands, necessitating more logging machinery traffic than to extract only about one-third of the trees from the selection stands (Brockway et al., 2006). Across substantial portions of the shelterwood stands, saw-palmetto no longer dominated the understory, but rather had retreated to “islands” that were surrounded by recently-emerged swards of grass. This increase in herbaceous plant cover, primarily graminoids, was led by the expansion of wiregrass, witchgrass and nodding fescue. In the ensuing years, the foliar cover of saw-palmetto and other shrubs increased, since no further mechanical disturbance occurred and prescribed fires, that had been planned, could not be implemented under the hazardous conditions of a multi-year drought. Surprisingly, the gains achieved by wiregrass, following logging, continued for at least six years after treatment, even as shrub cover expanded.

Table 3
Understory plant response (% foliar cover) to stand reproduction methods at the Blackwater River State Forest uplands for pretreatment (2005) and post-treatment (2007–2012) years.

	Control	Single-tree selection	Group selection	Irregular shelterwood
All plants				
2005	119.3	156.9[a]	85.4	167.9[a]
2007	175.6[t]	153.3	174.0[t]	160.4
2008	164.4[t]	155.3	181.6[t]	155.9
2010	205.8[t]	187.1	194.0[t]	200.0
2012	191.5[t]	157.7	181.4[t]	178.6
Trees				
2005	14.0	17.5	15.3	15.5
2007	23.6[t]	19.6	20.9	14.9
2008	29.4[t]	23.4[t]	23.7[t]	23.9[t]
2010	17.7	20.4	18.4	21.8[t]
2012	22.1[t]	20.8	15.7	21.9[t]
Longleaf pine				
2005	5.1	8.7	5.6	4.7
2007	6.1	2.3	3.1	1.9
2008	4.6	2.6	3.4	1.7
2010	3.1	1.8	2.0	3.8
2012	5.4	2.5	2.0	5.3
Southern red oak				
2005	4.5	6.3	3.8	7.3
2007	9.1[t]	10.0[t]	6.4	5.5
2008	15.5[t]	10.4[t]	7.7[at]	7.5[a]
2010	7.7	10.9[t]	8.1[t]	6.3
2012	7.4	9.4	6.6	7.3
Bluejack oak				
2005	2.4	0.0	3.1	1.7
2007	3.4	2.8	5.1	2.9
2008	4.9	5.5[t]	5.2	7.9[t]
2010	1.6	2.9	2.7	5.7
2012	2.1	2.3	2.7	3.5
Persimmon				
2005	1.1	1.8	0.7	0.8
2007	3.8	1.6	3.1	0.9
2008	3.5	1.6	2.9	1.3
2010	4.5[t]	2.9	3.3	1.7
2012	4.8[t]	6.1[t]	3.0	2.3
Shrubs				
2005	24.5	40.0[a]	19.0	37.7[a]
2007	37.7[t]	39.4	44.2[t]	40.5
2008	35.9[t]	35.9	45.9[t]	36.9
2010	56.3[t]	53.3	60.1[t]	44.1[a]
2012	53.1[t]	47.5	54.0[t]	40.8[a]
Dangleberry				
2005	1.9	2.3	5.2	4.5
2007	11.9[t]	13.3[t]	15.7[t]	12.1[t]
2008	9.6[t]	11.1[t]	15.9[t]	12.0[t]
2010	19.1[t]	14.8[t]	20.8[t]	14.5[t]
2012	16.5[t]	16.0[t]	20.6[t]	13.4[t]
Blueberries				
2005	5.4	14.2[a]	3.6	10.0[a]
2007	6.9	7.1[t]	8.7[t]	6.9
2008	7.1	10.1	7.8	8.5
2010	10.3[t]	13.0	11.6[t]	9.1
2012	12.3[t]	10.3	10.3[t]	7.2[a]
Gopherapple				
2005	0.3	3.6[a]	4.4[a]	0.8
2007	1.3	3.8	9.5[at]	1.5
2008	1.0	5.2[a]	11.5[at]	0.9
2010	0.9	6.2[a]	12.8[at]	2.3
2012	1.1	4.9	10.6[at]	1.9
Blackberries				
2005	7.9	8.7	1.7[a]	4.5
2007	5.4	3.0[t]	2.3	2.9
2008	5.1	4.6	2.3	4.1
2010	11.5[t]	6.9	5.1[at]	4.6[a]
2012	8.5	5.9	2.7[a]	3.8
Gallberry				
2005	2.3	2.3	2.3	7.9

(*continued on next page*)

Table 3 (*continued*)

	Control	Single-tree selection	Group selection	Irregular shelterwood
2007	3.7	1.8	2.2	6.6
2008	4.4	1.1	2.7	6.0
2010	6.7[t]	5.3	3.4	7.3
2012	7.7[t]	4.0	4.9	7.9
Winged sumac				
2005	3.7	2.5	0.9	2.9
2007	4.2	4.7	2.1	4.4
2008	4.7	4.1	1.8	3.1
2010	4.2	4.7	2.9	3.4
2012	5.1	4.7	2.2	3.3
Vines				
2005	2.4	2.9	4.7	3.4
2007	4.2	2.1	10.9[at]	2.9
2008	3.8	2.0	10.9[at]	2.9
2010	2.6	3.3	10.7[at]	3.2
2012	3.3	3.7	8.5[at]	3.1
Woody plants				
2005	40.9	60.4[a]	39.0	56.6[a]
2007	65.5[t]	61.1	76.0[t]	58.3
2008	69.1[t]	64.6	80.5[t]	63.7
2010	76.6[t]	77.0[t]	89.2[t]	69.1
2012	78.5[t]	72.0	78.2[t]	65.8
Herbaceous plants				
2005	78.4	96.5	46.4[a]	111.3[a]
2007	110.1[t]	92.2	98.0[t]	102.1
2008	95.7	90.7	101.1[t]	95.2
2010	129.2[t]	87.7[a]	104.8[t]	130.9
2012	113.0[t]	85.7[a]	103.2[t]	112.8
Graminoids				
2005	54.9	73.3	30.5[a]	72.7
2007	89.5[t]	64.2	69.7[t]	57.9
2008	76.9	65.3	71.9[t]	63.3
2010	77.4	59.7	61.2[t]	64.6
2012	64.1	52.2	64.7[t]	57.7
Wiregrass				
2005	35.5	54.9	19.8	51.5
2007	58.5[t]	38.2	48.9[t]	27.0[at]
2008	51.3	39.5	50.7[t]	27.9[at]
2010	53.5	33.3	40.8[t]	36.0
2012	44.3	30.7[t]	44.2[t]	35.1
Broomsedge bluestem				
2005	10.0	7.5	5.7	8.0
2007	11.3	12.5[t]	11.3[t]	14.5[t]
2008	12.2	12.9[t]	16.3[t]	12.9[t]
2010	9.8	11.6	8.7	11.9
2012	14.9	15.7[t]	15.8[t]	15.7[t]
Witchgrass				
2005	3.0	5.4	1.9	4.2
2007	3.9	3.1	2.3	6.8
2008	3.1	4.9	1.6	7.3
2010	2.7	1.6	0.5	4.3
2012	2.7	2.9	3.5	3.7
Forbs				
2005	23.2	23.2	14.9	37.3[a]
2007	20.0	26.5	24.6[t]	39.9[a]
2008	18.2	22.3	24.3[t]	24.7
2010	50.1[t]	48.9[t]	39.2[t]	56.9[t]
2012	47.0[t]	29.4[a]	31.8[at]	41.5
Silverthread goldaster				
2005	6.7	8.3	3.5	23.3[a]
2007	4.2	6.6	9.9	14.3[a]
2008	5.1	3.7	5.7	7.9[t]
2010	16.5[t]	14.1[t]	12.0[t]	30.1[a]
2012	12.0	5.9	6.1	15.9
Morning-glory				
2005	0.5	0.4	0.9	0.0
2007	5.0[t]	5.7[t]	2.9	4.3[t]
2008	3.5	2.8	2.5	0.7
2010	5.1[t]	5.4[t]	2.3	2.4
2012	5.1[t]	3.1	2.5	1.9

Table 3 (*continued*)

	Control	Single-tree selection	Group selection	Irregular shelterwood
Milkpea				
2005	1.3	3.9	0.3	1.9
2007	1.2	3.3	2.2	3.1
2008	1.1	4.2	3.1	3.4
2010	1.3	1.5	2.7	3.2
2012	5.9[t]	8.2[t]	7.9[t]	6.8[t]
Noseburn				
2005	0.7	0.4	1.3	0.0
2007	2.6	2.3	1.3	0.8
2008	2.9	2.0	2.5	0.7
2010	3.1	4.9[t]	2.3	2.1
2012	4.3[t]	3.5[t]	2.8	2.2
Elephant's foot				
2005	1.1	0.8	0.5	3.6
2007	1.7	1.1	0.8	3.2
2008	1.3	0.8	1.3	1.9
2010	3.4	0.5[a]	1.5	2.0
2012	2.9	0.9	1.9	2.7
Ferns				
2005	0.3	0.0	1.0	1.3
2007	0.6	1.5	3.7	4.3
2008	0.6	3.1	4.9	7.2[at]
2010	1.7	1.5	4.4	9.4[at]
2012	1.9	4.1	6.7[at]	13.6[at]

[a] Significantly different from control, $p < 0.05$.
[t] Significant change through time from pretreatment condition, $p < 0.05$.

Table 4
Understory plant species richness, diversity and evenness response to stand reproduction methods at the Blackwater River State Forest uplands for pretreatment (2005) and post-treatment (2007–2012) years.

	Control	Single-tree Selection	Group Selection	Irregular Shelterwood
Number of species (richness)				
2005	47.0	36.7[a]	48.0	31.3[a]
2007	36.0[u]	40.7	38.3[u]	42.7[u]
2008	34.7[u]	34.0	37.0[u]	35.7
2010	38.0[u]	38.3	37.7[u]	35.0
2012	36.0[u]	34.0	34.7[u]	37.0
Shannon index (diversity)				
2005	2.88	2.61	2.99	2.58
2007	2.61[u]	2.89[u]	2.76[u]	3.02[at]
2008	2.63[u]	2.77[u]	2.72[u]	2.91[u]
2010	2.81	2.98[u]	2.88	2.78
2012	2.88	2.89[u]	2.73[u]	2.81
Modified Hill ratio (evenness)				
2005	0.54	0.50	0.61	0.55
2007	0.49	0.59[t]	0.55	0.69[at]
2008	0.51	0.60[t]	0.56	0.72[at]
2010	0.56	0.68[t]	0.63	0.64
2012	0.61	0.70[t]	0.60	0.64

[a] Significantly different from control, $p < 0.05$.
[t] Significant change through time from pretreatment condition, $p < 0.05$.
[u] Significant change through time from pretreatment condition, $p < 0.10$.

There is a strong relationship between fire and the condition of understory vegetation in longleaf pine forests (Outcalt, 2000), with more frequently burned stands having fewer woody plants and a greater prominence of herbaceous plants (Glitzenstein et al., 2003). Although prescribed fire can reduce the cover of dominant shrubs like gallberry (Brockway and Lewis, 1997), many burning cycles may be required to reduce the cover of a robust shrub species like saw-palmetto, with its extensive system of below-ground rhizomes and capacity for rapid regrowth. Therefore, the application of mechanical disturbance may also be helpful in diminishing saw-palmetto dominance and creating opportunities for herbaceous plants, especially grasses, to establish and flourish.

These trends are also reflected in the modest rise and decline for plant species richness overall and increase for evenness in group selection and shelterwood stands, which point to improved species diversity for several years after treatment. Given that longleaf pine ecosystems are prone to and highly resilient to disturbances like surface fire and partial reduction of the forest canopy (Stanturf et al., 2007; Outcalt, 2008), they appear well suited to management regimes which incorporate periodic prescribed burning and regular cycles of thinning through application of selection systems and shelterwood methods.

4.2. Blackwater River State Forest uplands

At the beginning of our study, these stands were in excellent condition, having a well developed longleaf pine overstory with a lesser component of hardwoods and a grass-dominated understory with abundant longleaf pine regeneration. This forest was typical of well managed longleaf pine that is regularly thinned and burned with prescribed fire (Brockway et al., 2005a,b). Although the forest was impacted by high winds during September 2004, necessitating follow-up tree salvage operations and subsequent withdrawal of three badly damaged stands from the study, machine traffic in the remaining stands appeared to have little adverse effect on understory conditions, where herbaceous plants flourished and shrubs and hardwoods were inhibited by periodic fire (most recently in December 2004) and mechanical disturbance. While localized expansion in the cover of oak seedlings and saplings created smaller spots where competition for resources may be higher, large herbaceous-dominated areas still existed in the understory, where longleaf pine seedlings could readily establish and develop. Plant community dynamics, following treatment, reflected differing levels of stand density reduction from implementation of two selection systems and the irregular shelterwood method and the influence of prescribed fires during February 2010 and September 2011.

Pretreatment variation for herbaceous and woody plant cover in 2005 may have partly resulted from a differential response of the understory to variable rates of overstory tree removal by hurricane winds in 2004. With significant increases in control stands and group selection stands by 2007, only one year after implementing the selection systems and shelterwood method, the net major influence of treatment appeared to be a near equalization of overall foliar cover for understory plants. However, along with the positive trend for desirable plants such as wiregrass and low shrubs like dangleberry, blueberry and gopherapple were increases in the cover of oak seedlings and saplings, specifically southern red oak and bluejack oak. This rise in hardwoods is worthy of note, since they are vigorous competitors and may impair longleaf pine regeneration (Boyer and White, 1990). Frequent cycles of prescribed fire and mechanical disturbance from periodic thinning should curtail their development and discourage young hardwoods from ascending to the canopy and gaining dominance in the forest (Boyer, 1990b; Glitzenstein et al., 1995, 2003; Kush et al., 1999, 2004; Outcalt, 2000; Provencher et al., 2001; Outcalt and Brockway, 2010). By the sixth year after treatment, two additional cycles of fire began to diminish oak cover. While also increasing in control stands and group selection stands through time, the major shrubs occurred in a relatively stable assemblage of species, many of which (e.g., dangleberry, gopherapple, blackberry, blueberry) are valued for their importance to wildlife (Miller and Miller, 1999). Not only did shrub cover not decline with the application of two additional prescribed fires, species such as dangleberry, steadily expanded during the post-treatment period.

Although broomsedge bluestem increased in all treated stands and wiregrass cover rose in group selection and control stands, both wiregrass and silverthread goldaster declined in irregular shelterwood stands, soon after logging. These two herbaceous species are known to decrease on disturbed areas (Outcalt, 1995; Brewer et al., 1996) and the higher level of machine traffic required to remove greater numbers of trees in the irregular shelterwood stands was perhaps detrimental to them during the short-term. However, both species can recover from relatively modest densities (Brewer et al., 1996; Outcalt et al., 1999; Mulligan et al., 2002), so this decline may be only temporary in nature. By the sixth year after treatment, these species somewhat recovered, contributing to stability in the overall cover of herbaceous plants. The progressive increase of fern cover paralleled that of certain forbs, such as milkpea and noseburn, indicating their positive relationship with frequent fire and periodic tree harvest. Given the strong relationship between frequent fire and understory conditions in longleaf pine forests, continued cycles of prescribed burning should result in diminished foliar cover for woody species and increased cover for herbaceous plants in the future.

The above trends are reflected in species richness, with declines in group selection and control stands, a rise in irregular shelterwood stands and little change in single-tree selection stands, one year after treatment. Species loss likely resulted from environmental stress brought on by widespread drought that favored fewer species, better adapted to such conditions. Species gain was perhaps an outcome of so greatly reducing competition from overstory trees in the shelterwood stands that more resources were available to support a wider variety of understory species. With little change in species evenness and declines in species richness, the fluctuation in species diversity for control stands was small and the decline in group selection stands was modest. Although richness changed little in single-tree selection stands, evenness progressively increased, resulting in elevated diversity following treatment. Perhaps the lower degree of disturbance accompanying the single-tree selection system created conditions that improved the equitability in distribution of resources among species, thus a lower probability that few species can disproportionally dominate the understory. The rise in richness and evenness in irregular shelterwood stands translated into an early increase in diversity, on such areas with greatly reduced overstory canopies and more light and soil resources available to groundcover species. As highly-resilient disturbance-dependent ecosystems (Stanturf et al., 2007; Outcalt, 2008), longleaf pine forests are well adapted to management that includes frequent cycles of prescribed fire and periodic thinning through application of selection systems and the irregular shelterwood method.

4.3. Impacts on understory plant communities

Application of the two shelterwood methods in the shrub-dominated flatwoods at the Goethe State Forest was beneficial in significantly reducing the foliar cover of saw-palmetto and creating opportunities for the emergence and expansion of grasses. This change in relative dominance was clearly the result of mechanical damage to the saw-palmetto from the higher levels of machine traffic necessary to remove about two-thirds of the mature trees present in these stands. With the exception of continuing gains for wiregrass cover, this desirable increase among herbaceous species was short-lived. In the absence of prescribed fire during the six post-treatment growing seasons, the overall cover of grasses and other herbaceous plants declined, as saw-palmetto and other shrubs, such as gallberry, fetterbush and wax myrtle, expanded. The early rise and subsequent decline in plant species diversity levels also reflect these foliar cover dynamics. Although mechanical disturbance from logging may be helpful for improving the balance among lifeform groups of understory plants, these events underscore the essential role of frequent surface fire for restoring and maintaining desirable composition and structure in longleaf pine plant communities (Outcalt, 2006, 2008; Brockway et al., 2009).

By contrast, when the irregular shelterwood method was implemented in the herb-rich uplands at the Blackwater River State Forest, higher levels of machine traffic produced undesirable declines in the cover of wiregrass and silverthread goldaster. So before prescribing shelterwood methods, a practitioner may wish to consider the current status of the understory plant community relative to its desired future condition. This is especially true if the uniform shelterwood method is planned, since it requires a second stand entry to perform a complete overwood removal, thus further disturbing the understory with additional logging machine traffic. Fortunately, the two post-treatment prescribed fires (February 2010 and September 2011) appeared to facilitate a recovery of herbaceous cover, characterized by a later rise in wiregrass and silverthread goldaster and expansion of milkpea and ferns (Outcalt et al., 1999).

Applying the two selection systems at the Goethe State Forest had less impact on the shrub-dominated understory, with only the group selection treatment causing reductions in saw-palmetto cover that were significant, but of lower magnitude than those resulting from shelterwood methods. This was not unexpected, since the level of logging traffic in group selection stands was expected to be lower than that in shelterwood stands and higher than in single-tree selection stands. Without continuing prescribed fires, saw-palmetto fully recovered in group selection stands by the sixth post-treatment growing season. While gallberry declined in single-tree selection and group selection stands, these treatments did not sufficiently disturb stands to impede the longer-term overall rise of shrubs and expansion of wiregrass. However, the increasing shrub cover in group selection stands appeared to be related to the decreasing forb cover there. Therefore, with exception of the continuing expansion of wiregrass, plant community composition and structure did not substantially improve, in the absence of frequent surface fires (Brockway et al., 2005b; Outcalt and Brockway, 2010).

Implementing the two selection systems in the herb-rich uplands at the Blackwater River State Forest resulted in a doubling of understory plant cover in group selection stands, with significant increases in trees (southern red oak), shrubs (dangleberry, blueberries, gopherapple), vines (yellow jessamine [*Gelsemium sempervirens* (L.) Aiton]), grasses (wiregrass, broomsedge bluestem), forbs and ferns. Changes in single-tree selection stands were related to increases in southern red oak, bluejack oak, dangleberry, broomsedge bluestem, silverthread goldaster, morning-glory, milkpea, noseburn and ferns. When single-tree selection stands were examined by life form, each plant group remained relatively stable during the period of observation, except for graminoids (declining from 73% to 52% cover overall). Thus, the single-tree selection system produced less dramatic change in the forest than did group selection. This was not unexpected, since the deliberate cutting of gaps in the forest canopy substantially alters the spatial pattern of overstory retention, thus creating a somewhat different environment for the understory plant community, as well as for longleaf pine seedlings (Brockway et al., 2006).

5. Conclusion

Selection systems and shelterwood methods appeared to be beneficial treatments in these longleaf pine forests, by reducing overstory canopy cover and improving the availability of light, soil resources and growing space for understory plants. Although the higher levels of logging machine traffic necessary for implementing shelterwood methods can be beneficial by helping curtail growth of aggressively-competing woody plants, such as saw-palmetto, and stimulate the expansion of wiregrass in flatwoods, mechanical impact of this degree may also be detrimental to herbaceous plants, such as wiregrass and silverthread goldaster growing on upland sites. Selection systems (1) result in less precipitous changes in the forest, (2) better mimic a number of smaller-scale natural disturbance patterns and processes, (3) maintain an aesthetically desirable open stand structure, (4) produce a regular stream of forest products and (5) preserve a greater range of management options for the future. Thus, selection silviculture is a lower risk procedure for guiding longleaf pine ecosystems along a developmental trajectory of more gradual change through time, with regular adjustments provided by frequent prescribed fires and periodic tree harvest.

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